

The Biological Effects of Light Pollution on Terrestrial and Marine Organisms

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Abstract

Humans first began using artificial light at night (ALAN) during the industrial revolution and sources of light have diversified and intensified considerably over the last century. Light pollution has previously been defined under two separate branches, “ecological light pollution” where the natural light patterns are altered in marine and terrestrial environments, and “astronomical light pollution” where the view of the night sky is reduced. Natural light is vital for the regulation of animal behaviour and interactions. Surprisingly, this environmental stressor did not become a worldwide concern until 2009. Since then, research into this subject has substantially increased, with studies highlighting the detrimental effects of ALAN. These effects can be serious for many organisms and include the disruption of the essential circadian rhythms that most organisms use to time important behaviours such as foraging, reproduction, and sleep. Whether all organisms possess phenotypic plasticity to effectively adapt to increasing and changing artificial light pollution is not yet known. Here, we summarise the effects of light pollution among many different species, from marine to terrestrial, with a focus on the areas that require further research to enhance our knowledge of this subject. The aim of this review is to raise awareness and enhance understanding about this little-discussed environmental concern, including some novel ideas on camouflage and polarised light pollution, hopefully encouraging future research into the effects of light pollution on organism behaviour.

Keywords: ALAN, animal behaviour, camouflage, circadian rhythms, light pollution, polarised light pollution

1. Introduction

Humans have long been using artificial light at night (ALAN) to extend their diurnal behaviour [45, 46, 68, 100, 111, 140, 144, 172, 176, 203, 204, 219, 232, 235, 306]. In pre-industrial times this light came from burning a wide range of materials, from wood to oil [168]. The years of 1760-1830 marked the industrial revolution [10] where vast numbers of technological innovations occurred, most notably in the manufacturing industry. Among this rapid emergence of knowledge and modernisation, was the development of the electrical bulb [95, 168] which changed the way humans lit their homes and their surroundings, creating a world filled with anthropogenically generated artificial light at levels never seen before. As lighting technology advanced, the price of artificial lights fell which widened its accessibility to consumers [95] and increased the demand which increased its prevalence around the world, termed the “rebound” effect [95, 108, 148, 293]. Although scientists have been aware of many anthropogenic stressors affecting the environment, such as the release of carbon dioxide inducing global warming, and fertilisers causing wide-spread eutrophication in aquatic systems, light pollution itself was not recognised as a worldwide concern until 2009 during the UN’s International Year of Astronomy [120].

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The quantity of light pollution has been increasing globally over the last six decades by about 6% each year [67, 121, 159, 278], with an increase in brightness of 2.2% in areas that are constantly lit, between 2012-2016 [148]. Light pollution is widespread [49, 67] affecting 80% of the surface of the earth [89], with its prevalence highest in coastal areas [49, 84, 193]. In addition, the quality of the light has also been changing, for example, low pressure sodium lamps have been replaced with light-emitting diodes (LEDs), which are more effective light sources and conserve more energy compared to sodium lamps [266] and has broadened the emission spectra produced by streetlights. Therefore, more organisms are now able to detect this light, putting them at risk from this stressor [121, 159, 221]. Rich and Longcore (2006) divided the term “*light pollution*” into two separate branches; “*astronomical light pollution*” where the view of the night sky is reduced, and “*ecological light pollution*” where the natural light patterns are altered in aquatic and terrestrial environments [221].

One of the largest impacts of light pollution on organisms is the disruption to their biological rhythms. Most organisms have a circadian clock which controls the timings of behaviour, biological and metabolic reactions, body temperature, and activity [9]. This biological clock requires a predictable change of light during a 24-hour period to maintain its and so, light pollution has the potential to disrupt this important system [100]. For example, animals use their visual systems to sense the shift from bright light during the day to darkness at night [121] which is essential for their fitness and reproduction. This means that altering the natural light levels in the environment has the ability to affect numerous biological aspects of organismal functioning including sleep, hormone production, foraging, and reproduction in animals, as well as photosynthesis in plants, to name only a few.

The aim of this review is to discuss and predict (where research has not yet been done) the biological effects of both astronomical and ecological light pollution on terrestrial and marine organisms, including humans and plants, by understanding their anatomy, physiology and behaviour. This review also proposes future research avenues to further understand the effects of light pollution on organisms, the extent of their phenotypic plasticity to changing light environments, and possible mitigation strategies.

2. The biological effects of light pollution on organisms

Light can be defined as “*a series of waves of changing electric and magnetic field strength that have phase, amplitude, and wavelength*” [131, Fig.1]. There are three components of light that are of relevance to biological systems: wavelength, intensity, and polarisation [142]. The electromagnetic spectrum shows the different wavelengths of light which are measured in nanometres ranging from long wave radio waves to short wave gamma rays. Animals (humans and many primate species) that have colour vision, or trichromatic vision, are sensitive to wavelengths of around 350-700nm [54, Fig.2]. In the eye, light is focused onto the retina where the photoreceptor cells (rod cells for vision in low light conditions, or scotopic vision, and three different groups of cone cells that are sensitive to short, medium, and long wavelengths, facilitate vision in brighter conditions, or photopic vision, and enable colour perception) convert light to electrical energy which is then processed in the brain via the optic nerve, creating an image [155]. Most other mammals (rodents, felines, canines etc.) have dichromatic vision, where their eyes have only two types of cone cell, as opposed to three types, and are sensitive to only one or two colours, e.g., blue and green, but are often more efficient at distinguishing between colours in low light conditions [155]. Animals utilise the properties of light for a range of visual tasks, including predator detection, communication, and navigation. Therefore, light pollution can affect the visual systems of animals, disrupting the efficacy of many aspects of chemical and biological mechanisms in organisms. This includes the disruption of endocrinology and circadian rhythms which affects behaviour such as reproduction, sleep quality, communication, courtship, and foraging. In addition to this, signalling patterns and camouflage can also be affected, as well as photosynthesis in plants. In the following section we discuss these biological effects in more detail and propose future avenues of research.

2.1 Circadian rhythms

Circadian rhythms are daily cycles and oscillations in activity which are present in most organisms, from plants to humans, and are innate and endogenous [9]. In mammals, circadian rhythms are periods of about 24 hours [223] and are generated in the suprachiasmatic nuclei (SCN) of the hypothalamus [Fig.3, 227, 228] which contain a population of heterogenous neurones that entrain these rhythmic patterns [216]. Generation of this ‘biological clock’ stretches to the intracellular level where interactions between

en molecular processes and transcription rates of specific genes are important to maintain the rhythmicity [239]. Circadian rhythms are regulated by the solar cycle from a direct extension from the retina, called the retinohypothalamic tract [Fig.3, 113] thus, a predictable change in light and dark conditions throughout the day is essential in maintaining rhythmicity. Although these central circadian rhythms are created in the brain, peripheral circadian rhythms also exist in other organs and tissues, with control maintained by the SCN ('central controller') via chemical (not light) cues and oscillations from local cells via a molecular processes [190, 248]. These peripheral rhythms control many different mammalian processes including body weight, glucose homeostasis, and ovulation [209].

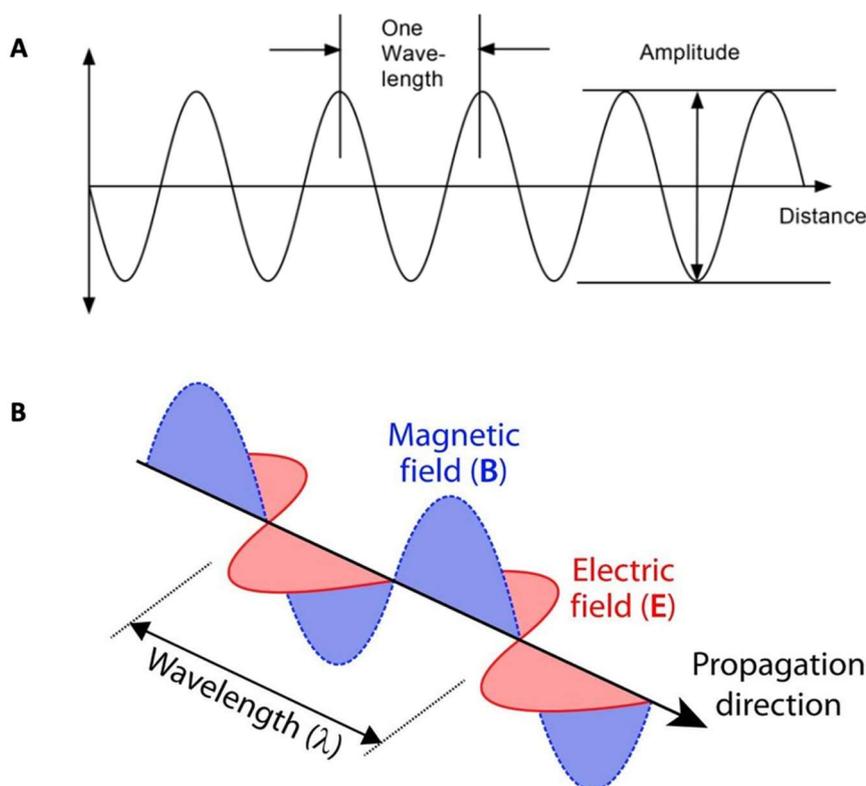


Fig 1. Transverse waves (e.g., light) with their associated properties; the relationship between wavelength and amplitude (A), and the magnetic and electric fields (B), where the blue dotted lines show the magnetic field, and the red area shows the electric field along the direction of propagation. The phase is the distance between two different light waves (measured between peaks or troughs). The horizontal arrows indicate the direction that the waves are travelling left to right. Adapted and obtained from De Mayo 2015 (A) [74] and Verhoeven 2017 (B) [282].

In contrast to the vertebrate circadian mechanism, it is thought that invertebrates generate the central oscillations in their optical lobes (as opposed to the SCN), controlling overall behaviours such as activity, mating, and foraging [Fig.3, 26, 275]. For example, the location of this oscillator in sea slugs (*Aplysia*) is thought to be in its photoreceptor cells with serotonin in the optic nerve playing an important role in its functioning [26, 53]. Insects control specific behaviours from the central circadian clocks in their optical lobes via peripherally generated circadian rhythms, located in organs around their body, including the timing of sperm release from the testes, the control digestive processes in the gut [Fig. 3, 275], and the formation of the cuticle from the epidermis [127]. The mating activity of *Drosophila melanogaster* is controlled by a collection of clock genes *timeless*, *period*, *cycle*, and *Clock* which transcribe the CRY photoreceptor cry (a cryptochrome gene), involved in photosensitivity and the setting of circadian rhythms, and is also involved in the setting of some of the peripheral circadian rhythms [85, 233, 275]. Additionally, it has been well documented that circadian rhythms are controlled not only by light, but also by the tides in intertidal organisms, circatidal control, [4, 15, 41, 42, 70, 72, 207, 274].

Many animals utilise their innate biological clock to carry out photoperiodism which is the ability to gauge day length (photoperiod) and use this as a cue to time seasonal processes [32, 160], such as timing of reproduction, foraging, and migration [33, 64, 160, 210].

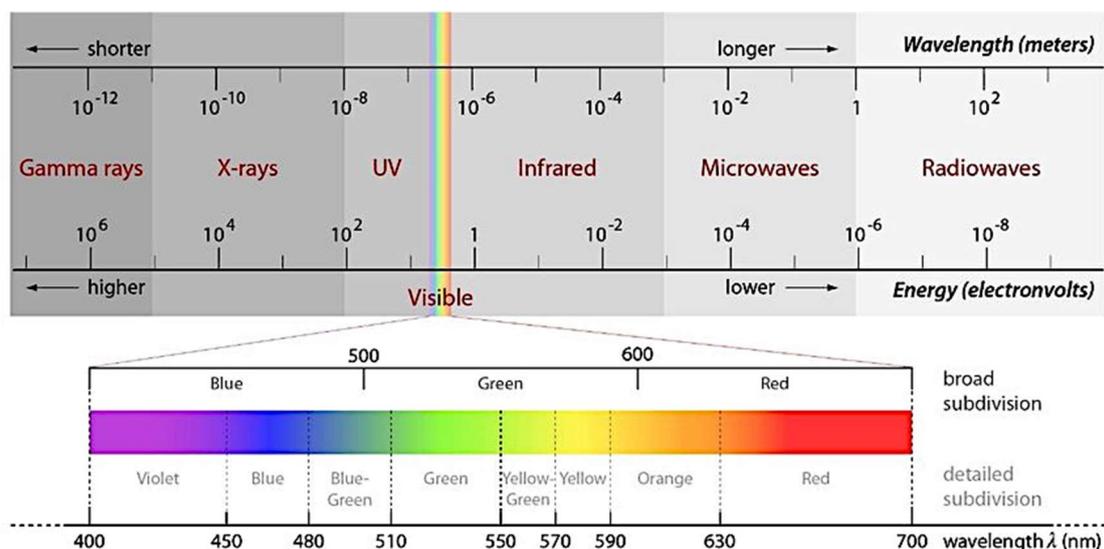


Fig 2. The electromagnetic spectrum with human- visible light shown in detail. Obtained from Verhoeven 2017 [282]. It should be noted that the International Commission on Illumination recognises visible light in humans as 380-780 nm, a slightly wider range than is illustrated on the diagram.

2.2 Communication; visual signalling, camouflage, reproduction, and mate choice

Communication falls into two categories: inter-specific and intra-specific. The former describes communication between different species, e.g., between predator and prey. The latter describes communication within the same species, e.g., competition for resources. Communication is essential for animal survival, reproduction, and overall organism fitness.

Intra-specific communication is important in animal mating and courtship behaviour. Fireflies (*Photinus pyralis*) use bioluminescent flashes to locate and attract mates via reactions using an enzyme-substrate mechanism; luciferase and luciferin [181, 244, 292]. A study found that artificial light decreases the number of flashes per minute produced by a species of dark-active firefly (*Photuris versicolor*) and reduces the activity of courtship behaviour thus, disrupting mating and reproductive success [93]. Studies have shown similar results in other terrestrial species; low levels of artificial light obstruct reproductive signalling and phototaxis in male glow-worms (*Lampyris nocticula* L.) which disrupts their ability to locate female mates, which has raised concerns that this may be reducing their numbers [28]. Some marine species also use bioluminescence in sexual communication such as ostracods and ponyfishes (*Leiognathidae*) [67, 110]. As with fireflies, light pollution has the potential to disrupt the communication and mating activity of these marine organisms by disrupting bioluminescent signals and future experiments could investigate these marine animals in more detail.

In addition to the rate of courtship communication, the rate of sexual signals can also be affected in the presence of light pollution. For example, green frogs (*Rana clamitans melanota*) generate fewer calls and move more frequently when exposed to artificial lights. Thus, recruitment rates may drop in the future with the potential to negatively affect the dynamics of the population and recruitment rates of individuals [14]. This is thought to be an anti-predator response to reduce their visibility to predators under lit conditions.

Light pollution also has the potential to affect inter-specific communication which has been shown in the predator-prey relationships between bats and moths. Minnaar *et al.* (2014) used mathematical and experimental methods to look at these relationships and found that Cape serotine bats (*Neoromicia capensis*) consumed six times more eared moths under lit conditions and the moth abundance decreased under these settings, with the models suggesting that this was due to decreased defensive behaviour of the moths [188]. Similar results were shown by Wakefield *et al.* (2015); moths (probable families: Geometridae, Noctuidae, or Notodontidae) flying

under lit conditions performed fewer anti-predatory behaviours in response to bat calls (*Nyctalus* spp.), such as in-flight ‘powerdives’ [286]. This is potentially a deliberate adaptation of the moths to turn off their ultrasound mechanism under lit conditions (whether natural or unnatural light) when it is not required as a defence strategy. These results are further demonstrated in a study by Cravens *et al.* (2017) where red, grey, little brown, and big brown bats all consumed more moths in artificially lit areas [55]. Therefore, moths may face increased predatory pressures from bats with increasing prevalence of light pollution, possibly contributing to the decline in their populations [188]. Further, there is evidence to suggest that ALAN can negatively affect moth reproduction, development of larvae, and diapause in pupae [31]. European moth abundance has been declining over the last few decades (decline recorded from 1982-2017 in Britain) [175] and increased light pollution due to urbanisation may be playing a role in this population fall [96, 188, 202]. Future research should investigate the impact of light pollution on insect populations relative to other environmental stressors, such as climate change, insecticides, and invasive species.

The behaviour of birds can be disrupted by light pollution, in particular the timing of their song. Light pollution can disturb photoperiodism, and some species such as American robins (*Turdus migratorius*) begin their singing earlier in the day when exposed to artificial light [187]. Conversely, other species such as the song thrush (*Turdus philomelos*) sang earlier in areas that were not lit [62-65] suggesting that light pollution has the potential to alter inter-specific communication between different bird species. However, many of these bird song studies are correlational and are unable to separate the effects of light pollution with other confounding factors [62]. For example, other research has suggested that anthropogenic noise pollution affects the phenology of bird song through enhanced stress and disruption of vocalisation signals which alters behaviour [8, 78, 137, 265].

Another behaviour that can be affected by artificial light, is roosting. Ayudyanti & Hidayati (2021) showed that there is a positive correlation between ALAN and the number of roosting sites of barn swallows (*Hirundo rustica*) in Indonesia, resulting in a greater number of birds building nests and breeding in urban areas between 2013-2018 [13]. Whether this has impacted the fitness or numbers of barn swallows is not known, and this could be an interesting area of research for the future (the number and success of fledglings may or may not be affected when birds move into urban areas).

Some studies have shown that a disruption of breeding phenology does have negative consequences for bird species. For example, Bewick’s swans (*Cygnus columbianus bewickii*) migrate earlier under artificially lit conditions and therefore, reach breeding areas out of synchrony with the phenologies of local species which could disturb the normal inter-specific behaviours [167, 220]. Future research should look at the effects of song phenology in more detail (including in different sexes) to see whether there are other factors playing a role in the negative effects mentioned in the previous studies, e.g., wind direction.

Artificial light may affect males and females of a species differently [100]. For example, male tree weta (*Hemideina thoracica*) move away from artificial light sources whereas females do not, which has an impact on intra-specific communication and possibly sex ratios of this species [90]. This difference between sexes has also been demonstrated in moths; male caterpillars of the moth *Mamestra brassicae* (Noctuidae) exposed to white and green artificial light grew to a lower mass compared to males that were exposed to red light, whereas this effect was not seen in female caterpillars [281]. However, both sexes of this moth species emerged earlier from their pupa under green (85% of moths) and white light (83% of moths) when compared to the dark treatment where only one moth had emerged. It is interesting to see how not only differences in the effects of ALAN between the sexes of species are there sometimes, but how these differences are absent in certain biological processes, such as pupation.

Light pollution has the potential to cause effects on camouflage but, there are almost no studies which have endeavoured to show this, and so this should be highlighted as an important area of research in the future. Some hypotheses and predictions can be made from the studies that have looked at effects of other anthropogenic factors on camouflage. For example, interrupted camouflage and signalling can result in an increased predation risk to some animals. This can have profound effects on the demographics and fitness of whole populations [73]. Furthermore, altered camouflage may result in disturbed inter/intra-specific communication and recognition which affects mate choice. Thus, light pollution has the potential to damage the fitness of whole communities by disturbing camouflage mechanisms.

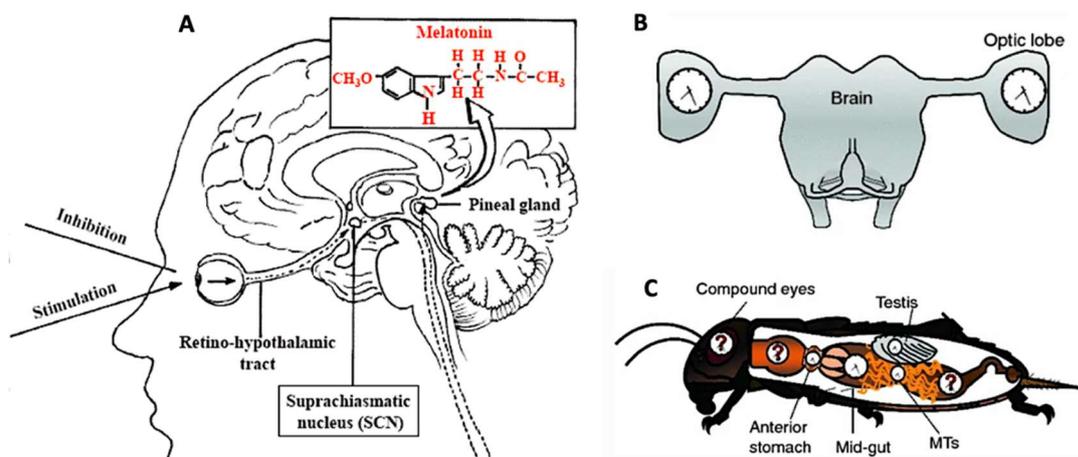


Fig 3. A) schematic of the neural pathway that generates the central circadian rhythm in the human brain with the location of the key anatomical features, in particular the suprachiasmatic nucleus which creates this biological clock. The production of melatonin (chemical structure shown) is stimulated by darkness, inhibited when it is light and is released from the pineal gland which stimulates sleep. This information passes from the eye to the retinohypothalamic tract to the SCN, and pineal gland. Adapted from Konturek et al. 2007 [143]. B) the optic lobes in the brain of crickets, where the central circadian rhythms are generated, indicated by clocks. These central rhythms control behaviour such as feeding, mating, and activity. C) parts of the cricket body where peripheral circadian rhythms are generated, controlling specific functions to that region. Compound eyes help to regulate timing and levels of activity during the day and night, the stomach and midgut are involved in digestion, the testes control sperm release for reproduction, and the Malpighian tubules (MTs) are involved in the excretory system. Adapted from Tomioka et al. 2012 [275].

Many animals use camouflage to disguise themselves from predators to minimise their chances of being eaten which enhances their longevity [263]. Within the umbrella term of ‘camouflage’ lies the term ‘crypsis’ which describes many mechanisms of camouflage with all of them functioning as an anti-predator mechanism by blending the animal in to the background environment [2, 87, 88, 261, 263]. In crypsis, animals conceal themselves from predators by matching their body shape, colouration, and contours to their environment thus, rendering it difficult for the predator to detect or recognise them [262, 263]. Many mechanisms of crypsis require natural light to function effectively. Such mechanisms include self-shadow concealment where animals use countershading to prevent shadows [Fig.4, 263]. In countershading, the animal has a dark dorsal surface, and a lighter ventral surface which creates a colour gradient that reduces the existence of shadows underneath the animal, making them appear 2D rather than 3D to predators and thus minimising their chances of detection [Fig.4, 135, 224, 272, 273]. This mechanism is utilised by many species, terrestrial and aquatic. For example, cephalopods such as the common cuttlefish (*Sepia officinalis*) [Fig.4] have colour pigments called chromatophores; ones which are located on the dorsal side of the body expand which creates darkening, but there are fewer of these on the ventral surface [Fig.4, 91], resulting in a paler area. The efficacy of countershading can be reduced when an animal is exposed to increased light intensities due to the prevalence of shadows [135, 198, 224, 272, 273] and therefore may enhance the likelihood of prey species escaping detection which would decrease the amount of food for predators. Altering the visual environment through light pollution can reduce the effectiveness of camouflage strategies which can enhance predation risk and may result in dysfunctional mate choices [73].

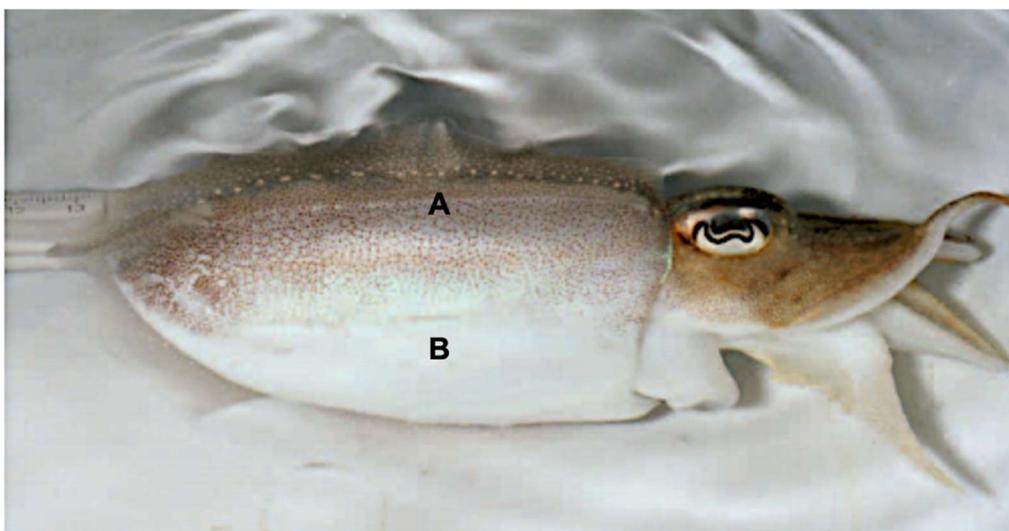


Fig 4. Countershading in the common cuttlefish *Sepia officinalis*. A= The darkened dorsal (upper) side of the body is created by the presence of expanding chromatophores in the surface of the skin. B= The paler ventral (lower) surface is created as a result of fewer chromatophores. Adapted from Ferguson et al. 1994 [92].

Light pollution affects the development of gametes in different species. For example, male Siberian hamsters (*Phodopus sungorus*) exposed to light during days consisting of short photoperiods (e.g., in winter months) had larger gonads and a higher sperm count than the control males [126, 160]. This is because exposure to dim light at night triggered shifts from a winter to summer phenotype due to decreased nocturnal melatonin release and affected the expression of the *Period1* gene which is part of the circadian clock thus, affects their biological rhythms and the molecular mechanisms involved in their response to photoperiod [126]. Cortisol concentrations are lowered in hamsters exposed to dim light during night hours and this may have effects on the expression on the biological clock proteins in the SCN [19]. Similar results have been found in European blackbirds (*Turdus merula*); light pollution progressed the growth of their gonads, increased testosterone production and sped-up the maturation of their reproductive system by one month compared to birds not exposed to artificial light [76].

A similar study was carried out in grey mouse lemurs (*Microcebus murinus*) and females of this species exhibited changes in their daily rhythm cycles during short and long-day photoperiods and altered the timing of their first seasonal oestrus due to a higher core body temperature in lit conditions [160]. Furthermore, their locomotor activity decreased during oestrus which could reduce their chances of meeting potential mates and could therefore reduce their reproductive success in the long-term [160]. Many studies have also been carried out in a range of fish species, including the European perch (*Perca fluviatilis*), haddock (*Melanogrammus aeglefinus*), and Atlantic salmon (*Salmo salar*), all of which support the hypothesis of light pollution decreasing nocturnal melatonin production and this reduction being directly linked to inhibited sexual maturation [36, 66, 128, 214].

Light pollution has also been found to have effects on reproduction in insects. For example, in the winter moth (*Operophtera brumata*, Lepidoptera: *Geometridae*), there was a reduction in the number of females attracted to oak trees, (*Quercus* spp.), that were illuminated and therefore, there were fewer opportunities for meeting mates which disrupted their reproductive behaviour and intra-specific communication [280]. ALAN also reduces and alters the composition of sex pheromones in some moth species, such as female *Mamestra brassicae*, showing that artificial light can affect moth reproduction [280]. It has been suggested that there may be a short-term and local increase in insect numbers when they are first attracted to artificial light [82, 133]. However, other studies have proposed that long-term exposure may result in decreases of abundance [133].

Plant reproductive success is also reduced by light pollution; when plant-pollinator communities are artificially lit, there is a 62% reduction of visits by nocturnal pollinators to the plants, resulting in a 13% decrease of fruit set which is predicted to decrease long-term fitness in the community and will have knock-on effects for diurnal pollinators [140]. Similar results were demonstrated in a study carried out by Macgregor *et al.* (2016) which described how pollination by moths (Lepidoptera) decreased in artificially lit areas, with a >25% reduction in species richness. It was also found that there was a 70% increase of moth activity near the lights, having potential impacts on the energy reserves and health of the population [174]. This is a real concern because of the worldwide

decline of pollinators [140, 215] and their associated importance in crops and food supply. However, Macgregor *et al.* (2016) notes that some moth families were more attracted to artificial lights than others, highlighting how the effects can vary depending on species [174]. This was further discussed in a more recent study carried out by Macgregor *et al.* (2019) where continuous ALAN increased pollination success. Their research did not focus on moths, but rather pollinators as a whole community which may account for the differences in findings, and again indicates the differences in pollinator species [175]. Although these studies have presented some interesting and important findings on the short-term effects of ALAN on pollination, and animal-pollinator interactions, other studies need to be established to consider the long-term effects of artificial light on these communities.

2.3 Foraging

Effective foraging behaviour is essential in animals to ensure they have a short-term supply of energy which is associated with long-term benefits such as reduced predation risk and overall fitness [27, 164]. Light pollution can affect this behaviour in terrestrial animals. For example, Santa Rosa beach mice (*Peromyscus polionotus leucocephalus*) utilize fewer areas of food when these patches were exposed to artificial lights compared to ones which were not lit [27]. This may be because they usually forage at night and therefore feed less in lit conditions. Inter-specific communication and foraging is affected by light pollution in two bat species; a non-desert species (*Pipistrellus kuhlii*) has a competitive advantage over a desert species (*Eptesicus bottae*) in artificially lit areas because the former forage in both dark and light conditions, whereas the latter species does not forage in lit conditions and flies away from the source of light [213]. Therefore, increased light in urban areas in the Negev desert may cause a decline in certain bat species. A study carried out by Schoeman (2015) found that four bat species; *Chaerephon pumilus*, *Tadarida aegyptiaca*, *Otomops martiensseni* and *Scotophilus dinganii*, were attracted to lit sports stadia and preferred to forage there, whereas one species, *Mops condylurus*, had higher activity in dark stadia [241]. This highlights that the effects of artificial light pollution are often species-specific, and also predicts that there may be increased competition between the four species preferring the lit areas due to clustering, resulting in altered interactions and foraging patterns. Competitive exclusion suggests that two or more (bat) species in this same environment would not be able to coexist if limited by the same resource [7, 283], supporting the idea of competition and reduction of resources between these species. A study using another species of bat, least horseshoe (*Rhinolophus pusillus*), found that the introduction of light pollution resulted in the bats leaving their roosts to forage 14 minutes later than without ALAN, therefore the timing between bat emergence and the highest density of nocturnal insects was disrupted and foraging decreased. Additionally, their flight period and echolocation signals also decreased, highlighting the negative impacts of ALAN on different bat species and the need for mitigation strategies.

Species differences are seen in other aerial species. For example, the common redshank (*Tringa tetanus*) utilises artificial light to its advantage because of enhanced visibility, and therefore has a longer period available for night-time foraging in these lit conditions [67, 80]. Similar results were found in five wader species; under lit conditions their intake rate of prey increased by an average of 83% [237]. However, this behaviour change may enhance the risk of predation and being injured when attracted to urban lights because they are more visible to predators [237]. Wild urban Blackbirds (*Turdus merula*) are another species that enhance their foraging behaviour under lit conditions. But surprisingly, their body condition did not benefit from the extended foraging orange-fin anemonefish, *Amphiprion chrysopterus*, decreased when exposed to long-term ALAN (four months) [240]. This may be due to an increase in predators and therefore, more time spent hiding rather than foraging, and less sleep due to the artificial light may also have played a role.

Many marine taxa carry out diel vertical migration (DVM) [152] which has an important function in predator-avoidance; organisms such as zooplankton migrate to the epipelagic zone at night to exploit the ample food resources and back to the deeper mesopelagic zone during the day to avoid predation [153, 169, 294]. Circadian rhythms are important in regulating DVM and light has exogenous and endogenous roles in maintaining this behaviour [52, 118]. Studies looking at the effects of light on the DVM of *Daphnia* found that DVM was affected by the presence of light pollution; the amplitude and magnitude of migration was reduced; *Daphnia* swam two metres lower than the usual peak height of migration and there was a reduction of 10-20% in the number of individuals migrating [171, 191]. This could reduce the mortality of marine algae but could also reduce the nutrient cycling therefore slowing algal growth [191, 260]. Additionally, the reduction of DVM may encourage

zooplankton to confine themselves to colder waters which could cause a decline their growth and reproduction [169, 191].

Nguyen *et al.* (2020) carried out a study on a different type of zooplankton, a copepod found in tropical waters, *Pseudodiaptomus incisus* [195]. When this species was exposed to continual artificial light, its sensitivity to warmer waters (34°C) compared to cooler waters (30°C, 26°C) increased, resulting in decreases of copepod body size, size of clutches, and successful hatchlings. Therefore, this suggests that zooplankton, as well as other coastal species, may be more susceptible to the effects of climate change (warming water) with exposure to ALAN. This could have serious consequences for many marine species and their ecosystems, and the presence of ALAN should be taken into consideration in future climate change studies.

The gut microbiome, the bacterial community located in the animal gastrointestinal tract, is important for many systems and processes in the body including disease resistance [115, 170, 236], metabolism and weight management [6, 21, 130], neurological functioning and regeneration [129, 194, 305], and nutrient absorption [147, 165, 257]. The presence of ALAN decreases the diversity, richness, and community structure of gut microorganisms in the Eurasian tree sparrow (*Passer montanus*), which could result in weight reduction, impaired digestion, and disturbance to foraging patterns [128]. This could have negative consequences for this species, as well as other bird species, and may have knock-on effects on seed dispersal and plant reproduction.

2.4 Migration

About 20% of bird species migrate twice each year from cold environments to warmer areas to exploit higher resources for optimal breeding success [253]. It is important for fledglings to be exposed to a normal celestial rotation to ensure that they orientate themselves correctly in migrations, and so astronomical light pollution is a potential driver for migratory disorientation in birds as it may disrupt vital celestial cues [13, 86]. However, other factors such as magnetic fields [295], atmospheric formation [136] and wind direction [101] also drive bird migration and it has been shown that these may be as important, if not more so, than the celestial pattern [295]. Thus, light pollution alone may not be the main driver of orientation disruption, although it has been suggested that the use of magnetic fields and celestial cues are tightly linked and that birds require both mechanisms to orientate themselves [51]. Such effects may also depend on whether the species migrates in the day or the night, which should be taken into consideration in future studies.

Cabrera-Cruz *et al.* (2018) suggested that some migrating birds are subjected to light pollution and its associated effects during the most important part of their migration [39]. Nocturnally migrating birds are attracted to ALAN [156] and therefore may alter their flight patterns towards urban environments which may have significant consequences for their behaviour, such as diminished flight speeds, increased vocalisations, and causing them to aggregate around light sources which can result in fatal collisions [184, 279]. It has been proposed that using flashing lights for communication towers rather than a continual glow may reduce the number of avian collisions [102]. In addition to this, it has been shown that changing the colours of lights ('spectral modified lighting') on offshore structures (such as oil and gas rigs) from red to green reduces the negative behaviours of migrating birds associated with increased mortality such as circling, collisions, and exhaustion around these man-made structures [102] which may be a useful mitigation strategy. However, further research is required to test whether there are any negative implications of altering the wavelength of artificial lights, e.g., for human health. Ecological light pollution may also affect the choice of stopover environments for migrators, thereby affecting the quality and mass of vital food resources along their journey which decreases the number of successful migrations and may have implications for their long-term fitness [184].

Diurnal insects use sunlight as a cue to begin migration [61], such as monarch butterflies (*Danaus plexippus*) [97]. Some insects such as African dung beetles (*Scarabaeus satyrus*) [57, 58] and the nocturnal bee (*Megalopta genalis*) [109] use celestial cues and polarisation signals for orientation and foraging. Astronomical light pollution may disrupt these signals and cues, which could alter behaviour of insects needed for their general fitness. However, many other factors are important in insect migration including weather and atmospheric structure [79], wind patterns [258], and temperature shifts, notably through anthropogenic climate change [256]. Insect migration is multi-factorial and therefore, light pollution itself may not be the main reason for disruption of insect migration. Future research should aim to investigate the relative importance of each factor, specifically light pollution, to further understand the possible effects of ALAN and to propose potential mitigation strategies.

2.4.1 Orientation

An area of significant research and interest has been the study of sea turtles (*Cheloniidae*) and effects of ALAN on their behaviour. Light pollution affects many aspects of their nocturnal behaviour such as their choice of nesting sites and migratory patterns, including the efficiency and success of the youngsters finding the sea once they have hatched [168, 234, 296]. Hatchlings become disorientated and often move inland towards artificial light sources along the beach. In addition to this, sea turtle hatchlings can still be attracted towards light at the top of the shore even if they managed to successfully reach the sea, and so light pollution has an impact on hatchling recruitment to the water [277]. Adult female turtles will preferentially choose nesting areas that are not illuminated by artificial lights [71]. This can result in less-than-optimal habitats being used for nesting sites, and may impact the number of hatchlings being produced, as well as possibly increasing the hatchling mortality rate [71]. Sea turtles have many other risks associated with their decline in numbers and nesting sites [112] such as fishing [208], marine plastic pollution [242], and climate change which can drive changes in their hatchling sex ratios [117]. Although light pollution may be affecting their behaviour and numbers, it is possible that other factors may be more associated with their decline, and modelling can hopefully be used in future studies to understand these risk factors in more detail.

2.5 Endocrinology and sleep

Sleep is important for many biological processes in birds, mammals, and invertebrates [3, 29, 186, 285] and can be defined as stages of decreased responsiveness and mobility [119]. For example, sleep can allow animals to overcome and recover from stresses inflicted during the day [218, 249, 291], whilst also aiding in memory [211, 285] and learning [300]. Sleep is also vital for the conservation of energy [23] and for strengthening the immune system to prevent infection by pathogens [37, 119]. The primary hormone for promoting sleep in mammals is melatonin [303] and does so by reducing core body temperature which decreases arousal and therefore increases the likelihood of a sleeping state [69]. Other hormones involved in sleep regulation, specifically in humans, include leptin, cortisol, and ghrelin [138]. Steroid hormones such as progesterone and oestrogen also influence the sleep process, with these hormones also being particularly important in the biological cycles of women [271].

Light synchronises and coordinates circadian rhythms in mammals which is important for many biological processes including hormone release and temperature homeostasis [45, 189, 204, 229]. Light activates the retinal ganglion cells in the eye [45, 105] and this triggers a response in the nuclei of the anterior hypothalamus and in the circadian pacemaker which reduces the amount of melatonin being released from the pineal gland [Fig.3, 34, 45]. This reduces the likelihood of a sleeping state and disrupts the neurophysiology of sleep including its regulation and pattern [172].

Research has been carried out to assess the relative effects of light pollution on sleep patterns, most notably in birds and humans. For example, great tits (*Parus major*), exposed to artificial light during the night are active for a longer period than usual and often start singing earlier in the morning [218] which may have effects on energy use and territorial behaviour. Similar effects have been studied in Zebra finches (*Taeniopygia guttata*), where continuous exposure to light led to reduced sleep and increased mortality [252]. Great tits have a weaker immune system when exposed to white light during their roosting, making them more prone to infections such as malaria [206], which may be due to an increased level of stress hormones [205, 206]. Artificial light caused reproductive inactivity and fluctuating patterns of moulting in European blackbirds (*Turdus merula*) due to stress and disruption of biological cycles which may affect their body condition [77]. Peahens (*Pavo cristatus*) increase their nocturnal vigilance when exposed to artificial light at night, spending less time sleeping and thereby reducing their overall fitness [301]. However, other species actually decrease their vigilance when exposed to low light levels, such as Allenby's gerbils (*Gerbilus andersoni allenbyi*) [145], and so the effects of light pollution on vigilance and resulting sleep patterns may vary between organisms and habitats. Very few positive effects from lack of sleep have been reported, but examples do exist. Male pectoral sandpipers (*Calidris melanotos*) sire larger numbers of offspring when they sleep less at night [157, 219] but the condition and mortality of the young has not been studied. The mechanisms behind this surprising result should be investigated further to understand whether this is a correlation or causation.

Cho *et al.* (2013) found that the patients in a hospital who slept with a bedside light displayed longer periods of shallow sleep and increased arousal compared to patients with their lights switched off [45]. In addition,

artificial light coming from computer screens has been shown to reduce melatonin secretion at night, disrupts biological rhythms, and disturbs the usual body temperature decline during the night, resulting in reduced performance during the day [106]. Other studies have made links between artificial light, reduced melatonin production, and the risk of developing breast cancer, explored in people who work night shifts and who have limited access to natural light [43, 139, 217, 231]. Similar risks have been found with prostate cancer [251], and the risk of obesity [144, 232, 306]. Reduced exposure to natural light can also increase the prevalence of psychiatric disorders in humans, such as depression, due to low levels of nocturnal melatonin and high levels of cortisol [114]. These results are further supported by analysing the sleep patterns and behaviours of patients suffering with seasonal affective disorder (SAD); the altered photoperiod during the winter months where there is a greater proportion of the day spent in darkness causes a change in sleep behaviour through circadian rhythm disruption, and results in depression [162]. However, being in complete darkness can be used for positive mental health, for example, dark therapy is used for bipolar disorder to stabilise mood [212], highlighting that altering light regimes can have large impacts on brain functioning and psychiatric disorders. This indicates that perhaps darkness itself is not causing depressive behaviours, rather the time spent in darkness relative to light. Further, there are many other factors, other than light, that may contribute to someone with SAD, including stress, motivation, and individual behaviour [276], and it is important to consider all these components when designing treatment plans.

Light pollution affects the sleep and endocrinology of birds and humans. However, more research needs to be done to look at how light pollution affects hormonal functioning and associated sleep patterns in a wider range of animals to obtain future predictions and mitigation strategies. It is also important to investigate how light pollution may have differing effects across seasons. For example, blue tits (*Cyanistes caeruleus*) sleep more during winter than spring [219, 259], and so artificial light pollution may affect the birds more in the winter period compared to the nesting season [219] because of the importance of sleep in the winter months. Individual animals have a greater energy expenditure during the breeding season [199, 219] therefore, a lack of sleep in the winter season may have negative effects on the following breeding months [219].

2.6 Photosynthesis

Photosynthesis is a process which requires carbon dioxide and water to convert solar energy into glucose which is then used for biochemical reactions in plants and other photosynthesising organisms [196]. This mechanism produces oxygen and is vital for all aerobic life on earth. Green plants absorb natural light for photosynthesis at wavelengths of about 400-700nm, with peak absorption at the blue and red regions of the spectrum [200] which includes most emissions from artificial lights. Photosynthetically active radiation levels (any wavelength between 400 and 700nm that organisms use for photosynthesis, Fig.2) are much lower in ALAN compared to sunlit conditions; $0.5\mu\text{molm}^{-2}\text{s}^{-1}$ and $100\text{-}2000\mu\text{molm}^{-2}\text{s}^{-1}$ respectively [99] and so the effects of light pollution on photosynthesis are expected to be low (although this has not been studied in detail). However, the broad wavelength that plants, and other non-plant autotrophs, use for photosynthesis highlights that almost all artificial lights have the capability of affecting this process, whether that be detrimental or not.

Much like animals, plants require a routine of light and dark during a 24-hour period to maintain healthy growth [22] and to ensure key mechanisms function correctly such as seed germination, flower development, and leaf abscission, all of which require the correct intensity, duration, and wavelength of light [11, 35, 173]. Circadian rhythms in plants have been studied in *Arabidopsis* and are generated by clock-controlled genes with specific hormones and chemicals regulating the biological rhythms, including auxins and calcium [107, 183, 288].

The presence of ALAN encourages photosynthesis to occur at times when it usually stops or slows down [22], e.g., during the night. This is often utilised by growers within greenhouses to enhance speed of growth and size of commercial plants [11], which can impact the phenology of their growth and flowering and thus, potentially having negative impacts on herbivores and pollinators within the ecosystem outside of greenhouses [22]. White LEDs (broad emission spectra) are heavily used around the world, and these are known to overlap with the photosynthesis action spectrum [11]. These will therefore, trigger photosynthesis when close to plants [11].

Light pollution may have large effects on photosynthesis in environments that are principally dark, such as caves, and such effects may be very localised to the sources of light. Cave environments are one of the few places where it has been shown that artificial light pollution affects the ecology of the ecosystem [99]. Tourists are led into caves where there are arrangements of artificial lights for safe movement. This activity creates large

communities of ‘lampenflora’ [60, 154, 192, 201, 250] which are organisms that are completely reliant on the artificial sources of light for energy [30]. They include four major groups; fungi, algae, ferns, and mosses, which for example, are found in the Waitomo caves in New Zealand [99, 132]. These photosynthetic organisms may disturb the trophic interactions within the cave ecosystems, which can decrease the numbers of existing organisms. Lampenflora also produce weak acids which can erode geological limestone formations [48] and have a negative impact on tourism to these cave habitats through a loss of geological attractions and visitor numbers. Furthermore, wavelengths from artificial light can reflect from the walls of the cave and so lampenflora communities are able to grow not only in the entrance of caves, but also deep within the formations where tourists cannot reach [20] which highlights how these communities can affect the whole cave environments. These predictions provide parallels with the idea that organisms can be affected by light pollution even when they are miles away from the source due to residual amounts of skyglow [89, 150], meaning species that live in rural areas away from cities are still at risk.

High light intensities damage the photosynthetic apparatus in plants by disrupting the rate of electron transport, oxidation/reduction, and yield in photosystem two [16, 103, 123, 238, 270], important in the breaking of water molecules into oxygen, hydrogen (protons) and electrons [222]. This can cause a reduction in the efficiency of photosynthesis and thus, decreases the resulting growth yield and biomass of the plants [17, 270]. However, plants respond and adapt (to an extent) to fluctuating light intensities and frequencies [299] and so, damage to their photosynthetic apparatus might be minimal in the presence of ALAN. For example, the aquatic moss *Fontinalis* adapts to high light intensities (i.e., when exposed to sunlight) by reducing its number of chloroplasts [104]. Similar results have been found in the shrub *Phlomis fruticosa* L., (*Lamaiceae*) where chloroplast number is also reduced in the presence of high light intensities [151], and also in the cyanobacterium *Synechocystis* which contain high-light-inducible polypeptides that allow this species to adapt to fluctuations in intensity [116]. It has been shown that short-term exposure (one minute) to low artificial light intensities (quantum flux density of $120 \mu\text{E m}^{-2}\text{s}^{-1}$) on cucumber leaves (*Cucumis sativus* L.) does not cause irreparable damage and are able to recover from this exposure within 60-80 minutes under dark conditions [56], highlighting that some species do have a level of resistance to light stress. Conversely, long-term exposure (up to five hours) to higher light intensities ($650 \mu\text{E m}^{-2}\text{s}^{-1}$) caused irreversible damage to the chlorophyll and generated photoinhibition [56] which means the plants could no longer use solar energy for photosynthesis. The previously mentioned experiments were carried out in vitro and so may not give an accurate representation of plant responses in the wild, nor the light intensities of modern streetlights, therefore, future studies would be more valid when combining both lab and field data. Further, it would be useful to predict and test the ‘threshold values’ of light intensity required to irreversibly alter mechanisms in plants, and animals, such as photosynthetic apparatus and circadian rhythms.

In addition to light pollution affecting photosynthesis in plants, marine organisms that rely on this chemical process can also be impacted. Coral reefs are some of the most biodiverse ecosystems in the world, providing habitats and food for 25% of marine species [161, 254]. Coral relies on the mutualistic interaction with zooxanthellae, a group of dinoflagellates, for growth and survival [158]. These dinoflagellates are photosynthetic and provide essential nutrients to the coral and are used in building their skeletons made from calcium carbonate [158]. Levy *et al.* (2020) and Ayalon *et al.* (2019) investigated the effects of ALAN on the Red Sea coral species: *Sylophora pistillata*, *Turbinaria reniformis*, *Acropora eurystroma*, *Pocillopora damicornis*, and found that ALAN inhibited photosynthesis in the coral zooxanthellae and increased oxidative stress, which is linked to coral bleaching [12, 161]. Coral reefs are already at risk of mass global decline via global warming through increased water temperatures and bleaching events [185, 255]. The additional stressor of ALAN may be another factor that could drive some of the world’s reefs to extinction and it’s vital that further research is carried out to preserve these vital ecosystems.

Photosynthesis in plants is also dependent on the external temperature [38, 245, 267], water availability [245], salinity [1], and pH [165] and so, plants in different locations and habitats (e.g., aquatic vs. terrestrial) around the world may be affected by the addition of light pollution in different ways. Future studies could use induction kinetics to measure chlorophyll fluorescence [163] on a large range of plant species under ‘normal’ intensities (current ambient environment without the presence of direct artificial light/LED) of artificial light pollution to build-up a more detailed understanding of photosynthetic damage to light stress. In addition to this, subsequent research should investigate the effects of different colours of LED lights on photosynthetic pigments. For example, in the context of treating polluted water, using red LED (others tested were blue, yellow, white, LED/incandescent lamps) was the most effective way of maximising the biomass of the bacteria and for maximising pigment

production, and was the most effective at treating the water and removing the chemical oxygen demand of the *Rhodospseudomonas* strain [304]. Although this is not in the context of ecological light pollution, this study highlights how different colours and sources of light have the ability to affect the photosynthetic process in organisms in different ways and therefore, should be monitored in the future for potential development of mitigation strategies.

3. An introduction to polarisation vision in animals

Along with the amplitude and wavelength, light waves also have an oscillating magnetic and electrical vector (E-vector) component [Fig.1], and this is what is important for polarisation [131, 178]. Unlike the wavelengths for colour vision, animals that can see the polarisation of light tend to have photoreceptors sensitive to wavelengths of around 500nm underwater and 380nm on land [178]. Direct light travelling from the sun generates waves with E-vectors distributed in multiple directions which are perpendicular to the light beam and its direction of travel, this creates uniformly distributed orientations of waves and thus, the light is unpolarised [178, 287]. However, if this light beam passes through a dichroic filter or is scattered, some of the E-vectors are absorbed, some are reflected, or some are dispersed which induces polarisation of light [178]. Polarised light [Fig.5] is common in nature and examples of sources which produce this include clear skies (celestial polarisation) and the surface of water [94, 287, 290] which are both “*large-field polarisation*” [179]. Other sources include waxy leaves [178, 197] and body parts of animals such as shiny carapaces as seen in stomatopod crustaceans which can produce communication signals in polarisation [94].

The specific structure of eyes that are capable of polarisation vision differs between species. As a general principle, for eyes to be sensitive to the polarisation of light they require the photoreceptors to have at least two rhabdomeric microvillar orientations to differentiate between the different angles or degrees of polarisation [24, 177], and these microvilli must be parallel over the whole length of the rhabdom [109, 289]. Behavioural experiments and neuroanatomical studies carried out on a range of insects, including monarch butterflies and dung beetles, have shown that the central complex of the insect brain contains specialised neurones that are responsible for the input and output of polarisation information [83].

3.1 Small field polarisation

Although most vertebrate eyes, including humans, are not sensitive to polarisation [178], many other invertebrates use this source of light for a multitude of behaviours, and this has been studied considerably in insects and crustaceans. For example, many crustaceans rely upon polarised light [125] more so than colour vision because the aquatic environment has a narrow spectral range [179]. Some crustaceans use polarisation vision for communication [180] such as stomatopods which use the polarised structures on their carapaces to communicate with other individuals of the same species, [40, 44, 94, 98, 177] perhaps important for sexual signalling and the identification of conspecifics [177, 243].

Cephalopods such as mourning cuttlefish, *Sepia plangon*, have acute sensitivity to polarisation, which is important in camouflage, intraspecific communication [247, 269, 287], and important for foraging behaviour; the cuttlefish *Sepia officianlis* selectively hunts silver polarising fish over ones that are not polarised [246]. Octopuses (*Abdopus aculeatus*, *Octopus cyanea*) use polarisation for object detection and recognition and have a wide range of sensitivity to angles of polarisation ranging from 1 to 53 degrees [268]. *Papilio*, a genus of butterfly, has sensitivity to horizontally and vertically polarised light which contributes to colour discrimination and facilitates foraging and breeding behaviour [134]. Polarisation is also used in breeding behaviour. For example, dragonflies (Odonata) utilise horizontal polarisation vision to differentiate between ‘dark’ and ‘bright’ water sources to lay their eggs and breed [25].

3.2 Large field polarisation

Many diurnal insects, such as bees, use the celestial polarisation pattern for navigation [109, 122, 197, 225, 226, 284, 302]. The dung beetle, *Scarabaeus zambesianus*, uses the celestial polarisation pattern to roll its dung along straight paths which enables them to avoid competition from other individuals [57-59, 287]. Similar

behaviours have been studied in ants which use the celestial polarisation pattern to calculate their route and number of steps needed to return to their nest [146, 297, 298].

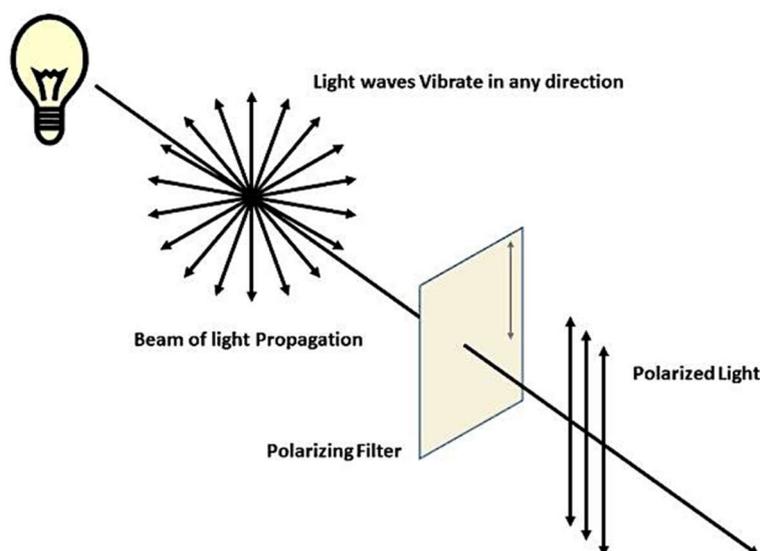


Fig 5. Schematic showing the difference in the waves of unpolarised versus polarised light after travelling through a filter. The polarised light in this instance is linear in the vertical direction. Unpolarised light waves travel in all directions whereas, polarised light travels in one direction parallel to the electric field (see Fig.1). Obtained from Kochiashvili et al. 2018 [141].

3.3 The potential effects of light pollution on polarisation vision and an introduction to polarised light pollution

In addition to the terms ‘ecological’ and ‘astronomical’ light pollution [168] is “*polarised light pollution*”. This can occur when light that is not usually polarised, such as sunlight, interacts with anthropogenic objects which causes it to become artificially polarised, such as by reflecting off buildings and roads [124]. It can also occur when artificial sky glow reduces the natural solar and lunar polarisation cues in the urban night sky [149]. This is caused by the low value of polarisation in skyglow mixing with polarised scattered light from the sun or moon which causes the degree of polarisation to decrease, meaning polarisation-based navigation mechanisms used by insects may become ineffective [149]. ALAN can reduce visibility of the night sky via “*astronomical light pollution*” [221]; one-third of the global human population cannot see the milky way at all due to light pollution [89]. This means that animals also have reduced visibility to moonlight which may disrupt the polarisation signals from celestial objects that certain animals use, such as the dung beetle, *Scarabaeus zambesianus*, [57-59, 287] which may interfere with navigation and orientation.

The use of LEDs is increasing around the world and there are some developments in this technology such as gallium-nitride-based (GaN) LEDs, which are themselves polarised [182] and may interfere with the polarisation cues produced by objects, such as the surface of water bodies which can disrupt behaviours such as finding oviposition sites, as seen in the dragonfly [25]. It has been shown that GaN LEDs are more energy efficient for specific technologies, such as liquid-crystal displays, and enhance both contrast and intensity of illumination [75], both of which improvements are due to the polarising nature of these LEDs [182]. This means that although GaN LEDs are currently very specialised and are not used widely, they may become more common in the future therefore, research into the effects of these (and other future developments of LEDs) on polarisation mechanisms in animals should be communicated with electrical engineers and other people in the lighting industry alike to perhaps minimise their prevalence and keep their use to a small number of specialised devices.

Light produced from LEDs can penetrate the surface of water and has effects on animal behaviour, which is seen in fishing practices that use bright LEDs to attract fish to the nets such as the Japanese squid fishery [264] and the Korea hairtail fishery [5]. This might affect the polarisation signals that some animals use underwater for foraging, mating, and object discrimination behaviours (depending on the degree and plane of polarisation). This

is an important area for future research to ascertain what light sources are the least detrimental to aquatic animal behaviour.

Other forms of polarisation pollution can have detrimental effects on behaviour, for example, aquatic insects that are in search for linear polarised light are attracted to artificial sources of polarisation, such as asphalt roads, which causes insects to be trapped in these areas, as seen in the stonefly, *Perla abdominalis* [81]. It is possible to predict that other behaviours may be affected by this kind of pollution, especially in terrestrial animals, such as insects, that use polarisation signals for migration, foraging and breeding, and may also affect marine animals if the artificial polarised light sources are near aquatic habitats. However, such predictions have not been studied and detrimental behaviours have not yet been quantified, and so this is an important area for future research.

4. Conclusion

Light pollution is widespread and is increasing globally every year which is putting stress on many organisms. The specific effects of light pollution are determined by species type, sex of individuals, and ecosystem functioning and affects most, if not all, organisms. These effects can be highly detrimental and include the disruption to sleeping patterns and circadian rhythms - which are essential to control many important behaviours - , the confusion of visual systems, and the alteration of photosynthetic mechanisms. We have also proposed the possibility that light pollution might also disturb polarisation cues which animals use for different functions such as communication and orientation.

Light pollution has generally been a lesser-known environmental stressor to the scientific community until very recently, and it is this which makes resolving this issue even harder; all the light sources are already out there in our communities. We suggest that for us to conserve vulnerable species and to reduce light pollution, more research is required about species effects whilst simultaneously testing new ways of lighting our communities and ways of improving our existing light sources. With this in mind, and using the information from our previous sections, we have identified five key areas of research and associated methodologies to be carried out in the future; how photosynthetic mechanisms are altered (with a focus on coral reefs), the plasticity of organisms' visual systems and behaviour when exposed to light stress (to predict whether animals can adapt to changing light levels), the wider implications of light pollution - not only at the individual level, but also at the wider ecosystem level, experimental studies on polarised light pollution, and improvements in the specificity of current monitoring systems to investigate the levels and type of light pollution and its associated effects. This will hopefully enable realistic mitigation strategies and may include changes to the colours of existing lights, the timing of lights switching on and off during the day, or a total change to the current artificial light sources in vulnerable areas and habitats.

A 'world atlas' of artificial light was first created in 2001 to quantify the amount of light pollution around the world using high-resolution satellite images [49, 89]. A second world map utilised modelling and software packages to monitor other indicators of light pollution including effects on celestial polarisation by counting the number of visible stars in the night sky [50]. Although light pollution around the world is now being quantified, the levels and type of light pollution and its associated effects on the surrounding habitats still need to be continuously monitored for mitigation strategies to be proposed. Such monitoring and research require an interdisciplinary approach, should include lab and fieldwork experiments, and should utilise scientists from a range of fields, including engineering, ecology, biochemistry, physics, and biology. This is essential to educate both the scientific community and the public about the extent and associated impacts of light pollution on the world's organisms, contributing towards effective conservation and preservation of many different species. Therefore, we propose the idea of a worldwide light pollution association which would bring scientists together from many fields and would create annual reports on both the on-going quantification of light pollution and the associated effects on different organisms around the world. These annual reports should also propose strategies to reduce any negative effects on organisms and should be communicated with local governments and authorities.

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