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Guiding Aquatic Reptile (Chelonian and Crocodylian) Conservation in the Face of Growing Light Pollution: Lessons From Experience

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ABSTRACT

Life on earth has evolved in response to the spatial, temporal, and spectral properties of natural light. However, with the advent of electricity and artificial lighting, the planet's nocturnal light environment has changed dramatically. This changing light environment is accompanied by altered behaviors in wild organisms, often resulting in drastic impacts on their fitness and population dynamics. Such effects have been demonstrated in a wide range of organisms, from plants to animals. However, there is a gap in our knowledge regarding freshwater reptiles. While extensive studies on sea turtles show alarming impacts of light pollution on their survival and recruitment, little is known about the effects on their freshwater counterparts and other aquatic reptiles, particularly crocodylians. Yet, these species face high extinction risk from anthropogenic stressors. The current lack of knowledge of their responses to the growing global pervasiveness of light pollution is a barrier to their effective conservation. Moreover, their responses could translate into ecosystem-level alterations through top-down effects, as have been observed for other species. Here, we synthesize the existing knowledge of the responses of aquatic reptiles, particularly freshwater crocodiles and turtles, to light pollution and discuss existing mitigation strategies to safeguard these species against the new threat. Knowledge gaps and existing mitigation strategies need to be addressed to promote species conservation in the face of the novel stressor, including in developing countries.

1 | Introduction

Reptiles represent a diverse class occupying a variety of habitats from arid regions to remote islands. Their diversity, however, is not uniform across habitats. The primarily aquatic turtles and crocodylians, for example, are represented by only 351 and 24 species, respectively, compared to the over 9000 species of squamates (Cox et al. 2022). Despite their lower diversity compared to terrestrial forms, they are integral parts of aquatic systems. By being ectotherms, they produce higher biomass per unit energy consumed than endothermic vertebrates and, hence, are important in providing energy for higher trophic levels (Pough 1983; Vitt and Caldwell 2009).

Incidentally, aquatic reptiles also represent the most threatened groups within reptiles, with around 60% and 50% of turtles and crocodylians threatened with extinction, respectively (Cox et al. 2022). About 10% of all known turtle species are classified as Critically Endangered (Buhlmann et al. 2009), and 30% of all crocodylian species are classified as Critically Endangered by the IUCN (Somaweera et al. 2020).

Freshwater reptiles may even be the most threatened group of species (Collen et al. 2014), with freshwater megareptile populations having declined by 72% between 1970 and 2012 (He et al. 2019).

The Indo-Gangetic Plains, in particular, which are recognized as hotspots for freshwater turtle diversity (Buhlmann et al. 2009), are facing a growing number of threats owing to the ever-increasing human population and urbanization. Often recognized threats include habitat degradation, overexploitation, and pollution by chemical contaminants (Cox et al. 2022; IUCN 2024; Sah, Baroth, and Hussain 2020; Sah et al. 2024). Another novel contaminant, artificial light at night (ALAN) associated with light pollution, has been growing in the area, given its intricate connection with human population growth and urbanization (Tripathi et al. 2022). Light pollution has been observed to affect aquatic systems across various levels of biological organization, especially in coastal and freshwater systems close to human settlement where ALAN is most pronounced (Davies et al. 2014; Smyth et al. 2021; Hölker et al. 2023), but little is so far known about its impact on freshwater reptiles including freshwater turtles and crocodylians.

Much of our knowledge about the effects of light pollution on aquatic species relates to the marine environment where it has been observed to affect numerous aquatic species including sea turtles, estuarine fish, and other associated predators such as seabirds (Becker et al. 2013; Dimitriadis et al. 2018; Rodríguez et al. 2017; Christoforou et al. 2023), while less is known about effects on freshwater organisms (Hölker et al. 2023). In particular, our understanding of the responses of freshwater reptiles to light pollution is poor, which remains a hurdle in their effective conservation.

The aim of this review was to synthesize our current knowledge of the effects of artificial light at night on larger aquatic reptiles, especially on freshwater crocodiles and turtles, and to highlight research gaps and priorities. Aquatic reptiles are facing multiple threats of anthropogenic origin, and light pollution is likely to worsen the situation. We start by highlighting the ecological roles of aquatic reptiles to justify the need to conserve them; then, we present the current knowledge on light pollution in aquatic and freshwater environments and then move to discuss the recorded as well as expected responses of aquatic reptiles to artificial light and the potential consequences of the responses. Next, we highlight current research gaps and priorities regarding effects of light pollution on freshwater reptiles. Finally, we draw attention to possible strategies for mitigating negative effects of light pollution by examining efficient strategies employed on sea turtles, discussing their potential for the conservation of freshwater reptiles as well.

2 | Aquatic Reptiles: The Need for Conservation

As previously mentioned, aquatic reptiles play various important roles in the ecosystem and their decline could have repercussions for their ecosystems. In many aquatic habitats, freshwater turtles can have a high stock biomass compared to other vertebrates and even other reptiles, especially on sea islands (Iverson 1982). Their mean maximum biomass varies with habitat and feeding habits, with herbivores achieving the highest values and carnivores the lowest (Iverson 1982). Turtles, therefore, can contribute greatly to a system's secondary productivity (Lovich et al. 2018). They also play important roles as both predators and prey, given their variety of feeding habits, ranging from herbivorous to omnivorous to carnivorous. Some species regulate grazer populations, as has been demonstrated for *Malaclemys terrapin*. Their absence can facilitate the growth of grazing species, such as the marsh periwinkle *Littorina irrorata*, which may result in turning productive habitats into barren mudflats (Silliman and Bertness 2002). Freshwater turtles can also increase nutrient inputs into ecosystems, such as ponds, through sediment dispersal and excretion and thereby provide conducive conditions for lower trophic levels such as phytoplankton (Wilbur 1997; Lindsay et al. 2013). Scavenging turtles are in turn important to riverine systems, playing an essential role in cleaning up the environment by feeding on organic matter, including carcasses (Sinha 1995).

Turtles also contribute to transfer of nutrients and energy between systems, such as between the marine and terrestrial ecosystems. For instance, loggerhead turtle nests have been recorded to transfer a mean of about 688 g of organic matter, 18,724 kJ of energy, 151 g of lipids, 72 g of nitrogen, and 6.5 g of phosphorus per nest to the beach. These are either transferred to predators, decomposers, detritivores, and plants of the ecosystem or lost as metabolic heat or gases. Only a fraction is returned to the ocean as hatchlings (Bouchard and Bjorndal 2000).

Crocodylians are among the largest inhabitants of freshwater ecosystems (Somaweera et al. 2020). Although they are primarily found in freshwater habitats such as rivers, lakes, and swamps, two species *Crocodylus porosus* and *Crocodylus actus* inhabit coastal habitats. Crocodylians are important indicators of ecosystem health, as well as of successful restoration (Fujisaki et al. 2012; Waddle et al. 2015; Brandt et al. 2016; Vashistha et al. 2021). As apex predators, they exert top-down effects on ecosystems. For instance, American alligators reduce the abundance of mesopredators, which increases the survival of a keystone grazer, *L. irrorata* (Nifong and Silliman 2013). Crocodylians also link terrestrial and aquatic ecosystems through trophic interactions with species in both habitats, thus transferring energy and nutrients between these systems (Adame et al. 2018; Somaweera et al. 2020). For example, alligators facilitate the movement of nutrients between wetlands, and creek-river ecosystems through ontogenic habitat shifts (Subalusky, Fitzgerald, and Smith 2009). They also act as ecosystem engineers through their burrowing activities and by being mound nesters, thereby affecting ecological processes and supporting biodiversity (De Miranda 2017; Murray, Crother, and Doody 2020; Strickland et al. 2023).

Their ecological roles and co-occurrence with other species of conservation significance make their conservation important for other species in their habitats as well, qualifying them as umbrella species for conservation programs and policies (Somaweera et al. 2020; Gallegos-Fernández et al. 2023). However, many of these conservation programs do not include mitigation against light pollution, potentially because of how easily the importance of light in governing important processes can be overlooked. The following section discusses how light pollution affects life below water.

3 | Light Pollution: A Growing Threat in Aquatic Reptile Habitats

Life on earth is temporally structured by natural cycles of light and darkness. Daily, monthly, and seasonal light cycles determine behavioral and physiological processes, such as reproduction, foraging, and migration, which ensures that the activities occur at the most suitable times (Kronfeld-Schor et al. 2013; Chi et al. 2017; Russart and Nelson 2018; Sockman and Hurlbert 2020; Bani Assadi and Fraser 2021). The increased use of ALAN—closely linked to human population growth—has altered spatial, temporal, and spectral qualities of natural nocturnal light conditions and, hence, impacted the timing and location of behavioral and physiological processes (Gaston et al. 2013; Hölker et al. 2021). Table 1 provides a glossary of the terms frequently used to describe the properties of light and light pollution.

The geographical extent of ALAN is increased from 5% to 23% of the world's land surface between 2000 and 2014 alone (Falchi et al. 2016) and is expected to further expand with global human population growth (Kyba et al. 2017; Linares Arroyo et al. 2024). Given that the evolution of organisms has occurred under natural light–dark cycles—with the nights being illuminated only by stars and the moon—it stands to reason that any disruption of the natural light environment can act as a disturbance and affect organisms and ecological processes, thus posing a threat to biodiversity (Hölker et al. 2010; Longcore and Rich 2004; Hopkins et al. 2018).

An increasing number of studies are showing that light pollution from ALAN has an impact on wildlife behavior and physiology and thus on population dynamics, community composition, and even ecosystem functions (e.g., Tuxbury and Salmon 2005; Meyer and Sullivan 2013; Perkin, Hölker, and Tockner 2014; Hölker et al. 2015; Zozaya, Alford, and Schwarzkopf 2015; Rodríguez et al. 2017; Maggi et al. 2020; Lao et al. 2020; Manríquez et al. 2021; Knop et al. 2017; Ganguly and Candolin 2023).

3.1 | Light Pollution in Aquatic Environments

While the impact of light pollution on terrestrial habitats has gained most attention, recent research indicates that aquatic habitats are increasingly exposed (Zapata et al. 2018; Jechow and Hölker 2019; Smyth et al. 2021; Hölker et al. 2023). These habitats are imperiled by a range of other disturbances, such as climate change, chemical pollution, noise, and water flow changes, that may interact with light pollution and further exacerbate its negative effects on biodiversity and ecosystem function (Manríquez et al. 2021; Hölker et al. 2023).

Light pollution has been observed to affect numerous aquatic species including aquatic reptiles, their prey, and other associated piscivorous foragers such as seabirds, especially in coastal and freshwater systems close to human settlement where ALAN is most pronounced (Davies et al. 2014; Smyth et al. 2021; Hölker

TABLE 1 | Glossary of terms associated with light pollution and properties of light (adapted from Alaasam et al. 2021).

Term	Definition
Light pollution	Excessive or misdirected artificial light, which disrupts natural environments and negatively affects human health, wildlife, and visibility of stars in the night sky.
ALAN	Artificial light at night emitted into the nighttime environment by humans. The cause of light pollution.
Skyglow	Brightening of the night sky caused by the scattering of artificial light by atmospheric molecules and particles.
Illuminance	Photometric (i.e., tailored to the human visual system) equivalent of irradiance. Luminous flux per unit area is measured in lux (lx), or in lumens per square meter ($lm\,m^{-2}$).
Lux	SI unit of illuminance equal to $1\,lm\,m^{-2}$, and used as a measure of light intensity relative to distance from light source.
Spectral power distribution	Distribution of any radiant or photometric quantity as a function of wavelength, most commonly given in spectral irradiance, ideally provided in nm resolution. For humans, the visible spectrum of light is between 400 and 700 nm.
Spectral tuning	Regulation of characteristics of the spectrum emitted from a light source. In this review, it principally refers to selecting ecologically less impacting wavelengths emitted by a light source.

et al. 2023). For example, artificial light influences benthic organisms by creating more favorable conditions for some species than others and even affecting individual mussel behavior through gaping activity, with further consequences for community composition and ecosystem functions (Davies et al. 2015; Hölker et al. 2015; Christoforou et al. 2023). Fish alter their behavior, such as reproductive (Foster et al. 2016), risk taking (Kurvers et al. 2018), foraging (Becker et al. 2013), and migration (Vowles and Kemp 2021; Pérez Vega et al. 2024), when exposed to light pollution, with potential effects on community structure. Seabird fledglings are, in turn, grounded by nearby ALAN sources, which negatively affects their survival and recruitment (Rodríguez et al. 2017), while sea turtles hatchling misorientate and suffer higher mortality, with negative implications for recruitment (Dimitriadis et al. 2018; Stanley et al. 2020). A changing light environment can also be expected to impact aquatic reptile populations through complex community interactions and bottom-up effects. For example, white LED lights facilitate growth of *Sargassum* species (Huang et al. 2021). *Sargassum* blooms are, in turn, reported to hinder the sea-ward movement of loggerhead turtle hatchlings, reducing the number of hatchlings entering the ocean by up to 22% (Schiariti and Salmon 2022). Similar processes can be expected to affect reptiles in freshwater habitats.

3.2 | The Freshwater Environment Under Threat: The Need for a Focus on Light Pollution

Although research on light pollution in freshwater environments has not yet received the same attention as it does in the context of marine habitats, there is strong evidence of the impact of this stressor on organisms in lakes, rivers, and streams (Moore et al. 2000; Szaz et al. 2015; Ganguly and Candolin 2023; Hölker et al. 2023). Light pollution affects organismal behavior and physiology (Grubisic et al. 2019; Czarnecka et al. 2019), community structure, and ecosystem function (Hölker et al. 2015), both within aquatic systems as well as across the aquatic-terrestrial interface (Meyer and Sullivan 2013; Manfrin et al. 2017).

Freshwater habitats cover less than 1% of the world's surface (Gleick 1998). Nevertheless, these habitats are associated approximately 9.5% of the world's animal species (Balian et al. 2007), and alarmingly, with the steepest biodiversity declines compared to terrestrial and marine habitats; the world's freshwater biodiversity is reported to have declined by 83% since 1970 (WWF 2020). The degree of threat varies across taxa and habitat, with lotic biodiversity being most imperiled (Collen et al. 2014). Freshwater habitats face an ever-growing number of threats, including climate change, species invasions, diseases, harmful algal blooms, habitat modification by hydropower projects, chemical contaminants, engineered nanomaterials, microplastics, light and noise, salinization, and declining calcium levels (Reid et al. 2019). Among these, light pollution has received relatively scant attention (Hölker et al. 2023).

The close association of the growing human population with freshwater accentuates the threats posed by light pollution to the habitats and their biodiversity, especially to lotic habitats (Premke et al. 2022; Hölker et al. 2023). Freshwater megafauna (≥ 30 kg bodyweight), including crocodiles and turtles, face intense threats from multiple anthropogenic activities, including habitat destruction and human-wildlife conflicts arising from the expansion of human activities into their habitats (He et al. 2019). These species are less flexible in coping with environmental changes owing to their complex habitat requirements, slow life history, and low fecundity (He et al. 2017). Moreover, the current knowledge gaps regarding their responses to artificial light pose critical barriers to their effective conservation in the face of a growing human population and urbanization.

4 | Light and Aquatic Reptiles: Perception and Responses

Light plays an important role in guiding the behavior of organisms, and responses of individuals can potentially affect entire communities and even ecosystems. Artificial light has now infiltrated the habitats of aquatic reptiles and affects both these species and other associated organisms, as discussed in previous sections. The roles reptiles play in aquatic ecosystems could potentially be affected by changes in their natural light environment. In Figure 1, we illustrate some of the known effects of light pollution on aquatic reptiles and their potential implications for the different levels of ecological organization and discuss these in detail in subsequent sections.

4.1 | Light: Perception and Cues

Vision plays an important role in an organism's perception of the environment and its subsequent responses. However, vision is not necessarily the only means by which vertebrates sense light conditions (Grubisic et al. 2019). Reptiles have extraoptical photoreceptive senses, such as pineal and cutaneous photoreceptors, that register light conditions (Zimmerman and Heatwole 1990). The parietal, or pineal, eye of many reptiles contains photosensitive cells that mediate the production of melatonin in the pineal gland, which regulates the circadian rhythm, as shown for the turtles *Testudo hermanni* (Vivien-Roels, Arendt, and Bradtke 1979) and *Pelodiscus sinensis* (Tang, Liu, and Niu 2022). In species lacking a discrete pineal gland, such as the crocodile *Crocodylus johnstoni*, a melatonin-mediated circadian rhythm is still observed, indicating the presence of an extrapineal melatonin producing complex (Firth et al. 2010).

Crocodylians sight their aquatic prey before submerging to hunt (Pooley 2016), and their eyes are adapted to low-light conditions through a large number of rods and a retinal tapetum (Whiting and Whiting 2011). Their visual pigments are attuned to longer wavelengths that characterize freshwater and nutrient rich coastal environments, in contrast to marine water bodies that are richer in shorter wavelengths (Lythgoe 1988; Nagloo et al. 2016; Hölker et al. 2023). A similar sensitivity for longer wavelengths is seen in freshwater turtles, which contrasts to the higher sensitivity of sea turtles to shorter wavelengths (Ehrenfeld 1968). Thus, visual perception in aquatic reptiles is optimized for their spectral environments (Hölker et al. 2023).

Both marine and freshwater turtles rely on visual cues for orientation (Ortleb and Sexton 1964), but differ in its use

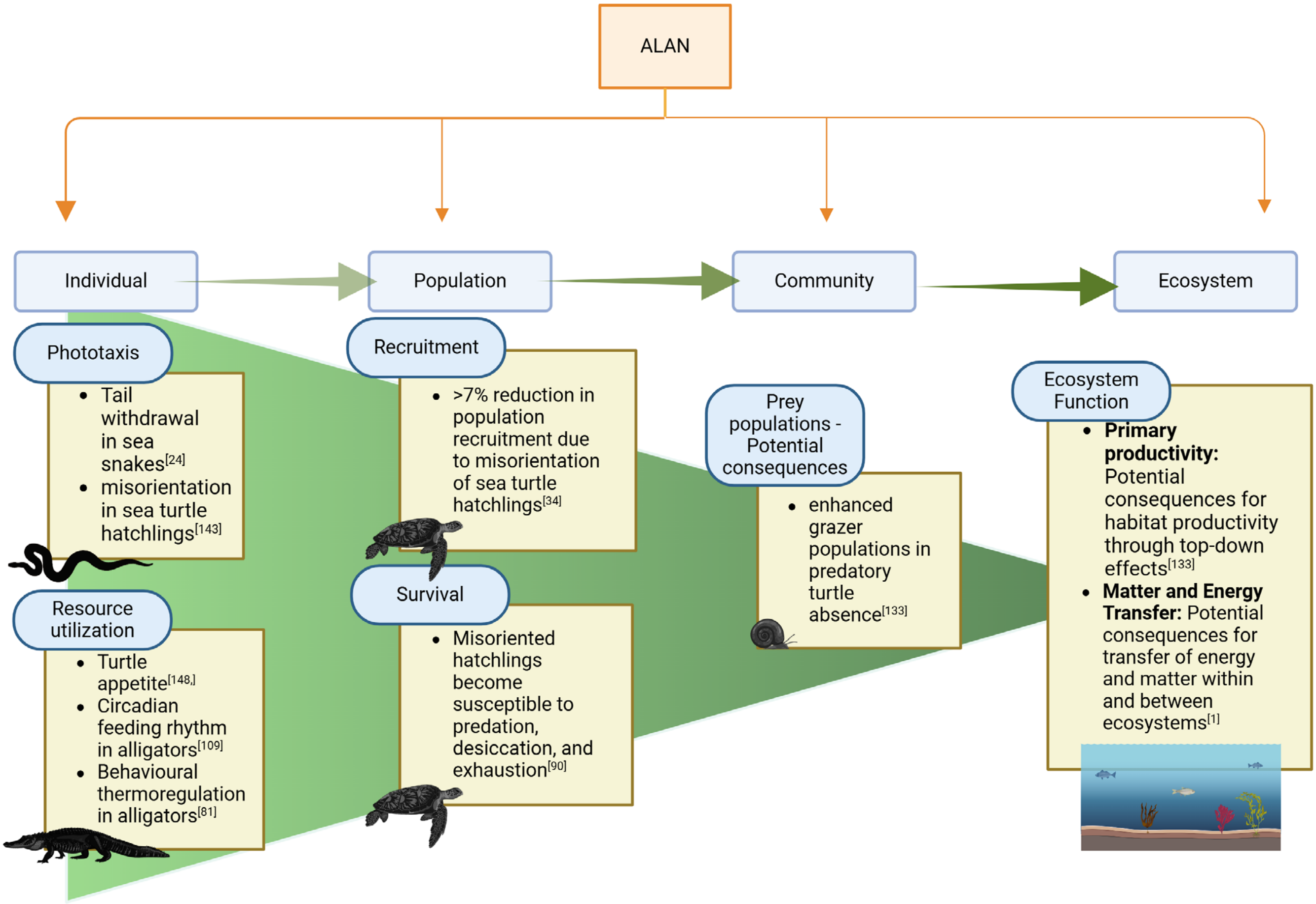

FIGURE 1 | Known effects of ALAN on aquatic reptiles and their potential consequences for ecosystems. Created with Biorender.com.

depending on the habitat. While light reflected from water is known to play an important role in the orientation of sea turtle hatchlings, this may not be the case for freshwater species (Anderson 1958).

4.2 | Behavioral and Physiological Responses to Artificial Light

Light conditions affect the behavior and physiology of aquatic reptiles, thereby influencing their health and fitness. For instance, changes in photoperiod affect appetite, energy metabolism, and endocrinology (particularly melatonin secretion) in the carnivorous Chinese softshell turtle *P. sinensis* (Tang, Liu, and Niu 2022), while increased light intensity reduces its food intake and growth rate (Xianqing et al. 1998). In the herbivorous Green turtle, *Chelonia mydas*, higher nighttime light levels increase again nighttime foraging on seagrass meadows (Taquet et al. 2006), while changes in photoperiod alter the circadian predatory behavior of the American alligator, *Alligator mississipiensis*, even reversing its feeding period (Palmer and Palmer 1994). Thus, ALAN has different impacts on species depending upon their feeding habits and activity patterns, being beneficial to some and detrimental to others.

Thermoregulation is an important physiological process for poikilothermic reptiles, which can be influenced by light conditions. Given that metabolic functions, appetite, and health depend on body temperature (Lang 1979; Spencer, Thompson, and Hume 1998), any alterations in an individual's thermoregulatory processes may have implications for its health and reproduction and, hence, for population dynamics (Krawchuk and Brooks 1998; Jessop et al. 2000; Fernández-Sanz and Reséndiz 2021). Both turtles and crocodiles employ behaviors such as basking and diving to regulate their body temperature, with light functioning as a cue for the behaviors (Chessman, 2020; Lang 1976). For instance, the American alligator, *A. mississipiensis*, uses light as a cue for amphibious behavior, and altered light–dark cycles can consequently alter its diving and basking activities (Lang 1976). Similarly, freshwater turtles engage in nocturnal basking, especially in the tropics and sub-tropics (McKnight et al. 2023), which could be influenced by ALAN. However, limited data exist that explains how such behavioral responses affect the overall health of these species.

4.3 | Impact on Recruitment

Aquatic reptiles face numerous threats with repercussions for their recruitment and population dynamics. The most commonly identified threats include illegal egg collection, predation on eggs and hatchlings by birds, mammals, and other reptiles, degrading of habitats, and various forms of environmental pollution (IUCN 2024). The effects of changing light conditions, and how this may influence these other threats, are, however, often overlooked.

In sea turtles, light conditions influence nesting site selection, with higher nesting density on darker sites (Hu, Hu, and Huang 2018). Individuals also shift to darker nesting sites in response to growing brightness (Behera and Mohanta 2018). Moreover, light pollution affects hatchling orientation and sea-ward movement, as well as their off-shore orientation, which increases mortality and decreases recruitment from 1% to approximately 7% (Truscott, Booth, and Limpus 2017; Dimitriadis et al. 2018). Similar impacts of light conditions on freshwater turtles and their hatchlings may occur and could explain the alarming population declines observed at important nesting sites for both marine and freshwater turtles (Colman et al. 2020; Tripathi et al. 2022). For example, hatchlings of the freshwater turtle *Trionyx* respond positively to light (Anderson 1958), as does the freshwater turtle *Chrysemys picta* (Ortleb and Sexton 1964), both displaying positive phototaxis, while adult *Terrapene* relies on the sun for orientation (Gould 1957), and the yellow mud turtle *Kinosternon flavescens* relies on the sun or the magnetic compass for orientation (Iverson et al., 2009). This variation in the use of similar, light-associated cues and responses may be due to differences among habitats. For example, estuarine turtle hatchlings utilize the same cues as their marine counterparts for movements, but move to higher marsh areas instead of the open water (Coleman et al. 2011).

5 | Research Gaps and Priorities

5.1 | Freshwater Habitats

At present, our knowledge of the extent and impacts of light pollution in aquatic systems largely derives from studies in marine habitats (Navarro-Barranco and Hughes 2015; Brei, Pérez-Barahona, and Strobl 2016; Marangoni et al. 2022). Thus, we lack a clear picture of how the world's freshwater systems, including lakes, rivers, and streams, are faring with respect to this stressor (Hölker et al. 2023). While some studies show that altered light environment affects freshwater invertebrates, fishes, and amphibians (e.g., Bramm et al. 2009; Foster et al. 2016; Dias et al. 2019; Fraleigh, Heitmann, and Robertson 2021; Kühne et al. 2021; Ganguly and Candolin 2023), few studies document the extent and trends of light pollution in freshwater habitats (e.g., Premke et al. 2022; Khanduri et al. 2023; Liu et al. 2024). Considering the geographical isolation of most freshwater habitats, and the degree of endemism of the inhabiting species, research needs to encompass this diversity of freshwater habitats and species. Otherwise, we may underestimate the threat posed by ALAN, which may hurdle effective policy-making for the conservation of aquatic biodiversity (Hölker et al. 2023). Conservation planning also needs to consider the association between human settlements and freshwater habitats, for example, how city boundaries overlap with important and biodiverse inland and coastal systems such as the Everglades, Yangtze and Pearl River Deltas (Jiang et al. 2017; Sklar et al. 2019). The world's protected areas are also growing brighter, with highest occurrence of increasing light pollution at their periphery (Mu et al. 2020). The exposure of freshwater habitats to light pollution may not only directly affect a species but also have consequences for species interaction by promoting the growth of competitors and predators, as has been suggested by Davies et al. (2013) and observed in insect interactions, where ALAN benefits some species by enabling them to prey on others (Sanders et al. 2018). This can ultimately lead to unwanted, novel communities in light-polluted areas (Hölker et al. 2023).

5.2 | Freshwater Reptiles

The growing evidence for impacts of light pollution on freshwater organisms indicates a risk to biodiversity and ecosystem function. Thus, a concerted effort is needed to determine the influence of light pollution on population dynamics and ecological function of species. At present, little knowledge exists about the responses of crocodylians and freshwater turtles to artificial illumination, despite both scientific and anecdotal evidence of altered behavior. Moreover, general knowledge gaps regarding their behavior and ecology (Behera, Singh, and Sagar 2014; Somaweera et al. 2019) accentuate the knowledge gaps pertaining to their responses to novel stressors, including ALAN. The few studies that exist are fragmented and limited, as has become evident in this review. Given that freshwater biodiversity is declining at an alarming rate, the incomplete knowledge of the vulnerability of threatened species to novel stressors is yet another hurdle to their efficient conservation. The nature of their responses, whether adaptive or maladaptive, has the potential to influence their population dynamics and persistence (Tuomainen and Candolin 2010). Thus, empirical studies on the influence of ALAN on the behavior, physiology, and ecological function of threatened species are needed, not only to close existing knowledge gaps but also to ensure their survival in the wild (Hölker et al. 2021).

5.3 | Biological Processes

Our current knowledge of the behavioral response of aquatic reptiles to light is limited to the few studies conducted on appetite of captive and foraging behavior of wild sea turtles, migration and sea-finding behavior of turtles, and only two studies conducted on predatory and thermoregulatory behaviors of alligators. The only records that we could find on crocodylian behavioral responses to light are more than two decades old. Overall, the studies cited in our review have demonstrated that light affects important processes that can modulate both fitness of an individual and recruitment of a species, but there is little evidence of the extent to which these are affected.

For example, we know that light influences appetite and feeding habits in both turtles and alligators (Palmer and Palmer 1994; Taquet et al. 2006; Tang, Liu, and Niu 2022), and in turn influences growth rate in turtles (Xianqing et al. 1998). However, our knowledge of how this affects nutrition, health, metabolism, and reproductive biology is incomplete. We do not yet know how light-induced changes in feeding behavior alter feeding preferences, particularly in predators such as crocodylians, and whether this affects energy expenditure and nutrition.

Similarly, studies have shown that artificial lights can influence nesting site selection in sea turtles (Behera and Mohanta 2018; Hu, Hu, and Huang 2018). However, few studies have addressed how the brightness of nesting sites affects their susceptibility to other threats including floods, erosion, and predators (Stanley et al. 2020).

Lang (1976) demonstrated how reversing the photoperiod can temporarily reverse thermoregulation-associated basking and diving behaviors in alligators. Our knowledge of how this affects the body temperature of individuals is, however, incomplete. We also lack a clear understanding of how changes in light photoperiod, intensity, and wavelength can affect biological processes involved in reproduction in both turtles and crocodylians, even though evidence exists for terrestrial reptiles such as lizards and anoles (Thawley and Kolbe 2020).

Moreover, there are gaps in our knowledge of how a changing light environment can exert bottom-up effects through the ecosystem to impact turtles and crocodylians. For instance, we know that ALAN can affect community composition and assemblages of microorganisms, invertebrates, and fish (Becker et al. 2013; Davies et al. 2015; Hölker et al. 2015). These organisms are an important part of the aquatic food web. Changes in their composition can be expected to affect their consumers, including reptiles. However, there is little information of such ALAN-induced bottom-up effects.

5.4 | ALAN in Developing Countries

ALAN is closely linked to human population growth and urbanization, and hence, nocturnal satellite images are often used as a tool to monitor urban growth (Zhang and Seto 2011; Linares Arroyo et al. 2024). Given the present trends, the world's urban areas are projected to expand by 40% to 67% by 2050 (Li et al. 2019). However, urbanization follows an uneven distribution, with low and middle-income countries demonstrating higher population growth (Sun et al. 2020). This unevenness is reflected in trends in light pollution, with developing countries displaying a growing trend compared to many developed countries where nighttime brightness levels have partly leveled out (Kyba et al. 2017; Sánchez de Miguel et al. 2021) and can thus extend to the effectiveness of conservation measures, such as protected areas, which have been more effective in reducing anthropogenic pressure in countries with higher human development index (Geldmann et al. 2019). The difference in effectiveness of conservation measures can be expected to apply in the context of novel stressors such as light pollution, with the developing world facing a greater magnitude of threats, including to freshwater biodiversity (Vörösmarty et al. 2010). Yet, research on the impacts of urban growth on aquatic ecosystems is concentrated to regions other than the ones most vulnerable to urban expansion (McDonald et al. 2019). Moreover, conservation planning for aquatic systems that support a large human population, such as the Ganges River in India, is complicated by various social, economic, and cultural factors (Hussain et al. 2020). Areas such as the Ganges River provide important habitats for riparian reptiles, including threatened freshwater turtles and crocodylians, and these habitats are experiencing a decrease in dark area (Tripathi et al. 2022). Similarly, light pollution has been projected to increase in protected inland aquatic and associated habitats in Indonesia, including the Lake Toba Geopark, Gunung Batur Geopark, and Sermo Dam (Riza et al. 2023). The population-dense Pearl River in China, which serves as a habitat for freshwater turtles, such as the threatened *Pelochelys cantorii* (Xiaoyou et al. 2019), is also experiencing increasing light pollution (Jiang et al. 2017).

In addition to the existing knowledge gaps and complications related to the conservation of aquatic habitats in developing countries, research pertaining to light pollution is yet to gain emphasis in such regions, especially in the context of ecology and biodiversity conservation. For example, most of the research on the ecological effects of light pollution in Asia is restricted to a handful of countries, primarily China (see also Jiang et al. 2017; Mu et al. 2020). Therefore, there is a need for both the scientific community and policymakers to consider various socio-economic and ecological aspects of ecosystem conservation in developing countries, including how various developmental projects add to nighttime brightness. Research is also needed on what alternatives there are to achieve a balance between the growth of human populations, economy, and industry while maintaining natural light regimes in ecosystems. Dedicated efforts and allocation of funds to the study and mitigation of the impacts of light pollution in vulnerable habitats are needed, as well as the monitoring of the stressor to determine hotspots and safe zones. Such research is urgently needed to promote proactive decisions regarding biodiversity conservation in aquatic habitats (Hölker et al. 2023).

6 | Learning From Sea Turtles: Is There Hope for Mitigation?

As mentioned in previous sections, sea turtles are the most well-studied group of aquatic reptiles in the context of light pollution (Marangoni et al. 2022). This includes not only their responses to ALAN but also potential mitigation measures. Given the current rate of growth of light pollution, it is too risky to wait for new research to fill our knowledge gaps before formulating mitigation strategies (Hölker et al. 2023). The continuing increase in light pollution requires prompt action, and our existing knowledge on how to mitigate effects of light pollution on sea turtles may prove useful in guiding conservation measures for freshwater reptiles.

Numerous studies have identified successful mitigation measures for protecting sea turtles against light pollution (Pendoley and Kamrowski 2016; Marangoni et al. 2022). Several governments have even implemented measures to safeguard sea turtles from ALAN. A good example is the “Keep it low, Keep it long, Keep it shielded” slogan of the Florida Fish and Wildlife Conservation Commission, which has proven that people's awareness of simple solutions can be effective in reversing the harm of excessive nighttime lighting (McDermott 2023). In the following, we will present these and other simple but effective mitigation measures and discuss to what extent they can be transferred to freshwater systems.

6.1 | Light Distribution

Shielding of lights is a simple yet effective way of ensuring safety of sea turtle nesting beaches from artificial light that may cause misorientation (Long et al. 2022). The goal is to only illuminate areas where lighting is required and to prevent light from reaching water surfaces or other sensitive habitats (Hölker et al. 2023). For example, when lamp shades were installed on moonlit nights, more green turtle hatchlings were able to find the sea (Yen et al. 2023). Low-fixed light sources that reduce light trespass are another possibility, such as embedded lights on roads (Bertolotti and Salmon 2005). Vegetation that acts as a natural light barrier can in turn shield turtles from the light (Karnad et al. 2009), but effects on plants and associated organisms (insects, birds, etc.) need to be considered (Grubisic, Haim, et al. 2018; Grubisic, van Grunsven, et al. 2018).

6.2 | Illuminance (Radiance) and Wavelength

Sea turtle hatchlings are extremely sensitive to light pollution. Disorientation of hatchlings and, to a lesser extent, adult females of the Australian flatback turtle (*Natator depressus*) was observed on nesting beaches where skyglow was visible up to ~50 km from the light source. The disruptive effect was slightly reduced by the moon (Shimada et al. 2023). The in-water orientation of Olive Ridley sea turtle hatchlings (*Lepidochelys olivacea*) varies with increasing light illuminance (radiance), with thresholds depending on the wavelength of the light (Cruz et al. 2018). For instance, green light has been found to misorient hatchlings at intensities above 5 lx, yellow light above 10 lx, and red light above 39 lx (Cruz et al. 2018). Furthermore, white light (at 37 and 4 lx) had a stronger effect on the sea-finding behavior in green turtle hatchlings than yellow light (at 15 and 2 lx), while light illuminance had no effect on sea-finding behavior at both colors (Yen et al. 2023). Thus, both illuminance and wavelength must be considered when planning wildlife-friendly lighting. Longer wavelengths have been shown to be comparatively safe for sea turtle hatchlings, and light emitting diodes (LEDs) with wavelengths of about 620 nm have been recommended for lighting along beaches used by turtles as nesting sites (Long et al. 2022). However, it is debated whether spectral tuning is effective for protecting freshwater animals, given that many aquatic taxa use the entire visible spectrum (Hölker et al. 2023), for instance, the Green Turtle *C. mydas* (400–600 nm) (Granda and O'Shea 1972). Other species differ in sensitivity, such as the Red-Eared Slider *Trachemys scripta* that is most sensitive to longer wavelengths (orange, red). Thus, transferring spectral recommendations from marine to freshwater systems may be less straightforward.

6.3 | Dark Sites/Infrastructures and Buffers

Protected areas are usually less exposed to light pollution given policy interventions that facilitate the abatement of light pollution (Mu et al. 2020; Sung 2022; Yan and Tan 2023). Thus, dark sites or infrastructures could be an effective extension of the same principle (Sordello et al. 2022). Protection and maintenance of dark sites has consequently been recommended for sea turtles (Tuxbury and Salmon 2005), and can be an effective way of conserving light-naïve habitats and their biodiversity (Peregrym, Pénzesné Kónya, and Falchi 2020). In addition to dark sites, buffer zones where no light is allowed may be effective mitigation strategies, as sea turtles can be affected by artificial lights (skyglow) as far as 18–50 km away (Hodge, Limpus, and Smissen 2007; Shimada et al. 2023). A study on industrial light found that sea turtle hatchlings were not affected when the lighting was more than 500 m away, but that a buffer zone of at least 1.5 km is needed as built areas are typically lit by numerous luminaries (Pendoley and Kamrowski 2016).

Considering the affinity of turtles with other reptile groups, such as crocodylians (Field et al. 2014), the above-stated mitigation measures may be applied to the conservation of other aquatic species. In Figure 2, the above-mentioned strategies are summarized, as well as the specifics that may need to be adjusted to suit freshwater species.

7 | Conclusions

Aquatic and especially freshwater habitats and biodiversity are threatened by multiple anthropogenic stressors. Recently, light pollution has emerged as a novel stressor that alters the spatial, temporal, and spectral qualities of the light environment, which affects the physiology and behavior of the inhabitants, with potential consequences for community composition and ecosystem function. Reptiles play important roles in freshwater ecosystems by regulating community composition and ecosystem processes, yet are one of the most threatened groups of species imperiled by multiple stressors driven by anthropogenic activity. A growing number of studies show that artificial light at night affects their physiology and behavior through impacts on movements, appetite, thermoregulation, and endocrine responses, which, in turn, can have consequences on their health and fitness. Light plays an important role in a reptile's perception of and response to its environment and can have far-reaching consequences for both the species and the ecosystem it inhabits. Thus, the potential impacts of light pollution on these species need to be better understood to inform conservation decisions for aquatic reptiles and their habitats. This is even more important given the scarcity of data regarding the response of crocodylians to light, these being some of the world's most threatened species.

Yet, the impact of light pollution is given little priority in research or conservation policy (Hölker et al. 2021). This is particularly true in developing countries, where social, economic, cultural, and demographic factors make biodiversity conservation even more difficult. Under these conditions, the existing knowledge gaps pertaining to the impact of light pollution on the behavior and biology of threatened reptiles further complicate the task of conserving biodiversity and ecosystems. These knowledge gaps require immediate attention from both the scientific community as well as policymakers and other stakeholders to enable the formulation of effective conservation strategies in the face of an ever-changing environment. Learning from measures that have proven effective for related taxa, such as sea turtles, could be useful in setting up initial measures to protect aquatic reptiles against light pollution. Simple but effective initial measures include adjusting the correct height, color, intensity, and shading of lights. Their implementation requires the understanding and willingness of people to participate in the conservation of species from a stressor that they may not perceive as a potential threat. Therefore, the current situation, especially in developing countries, requires both dedicated research to reduce light pollution and raising public awareness.

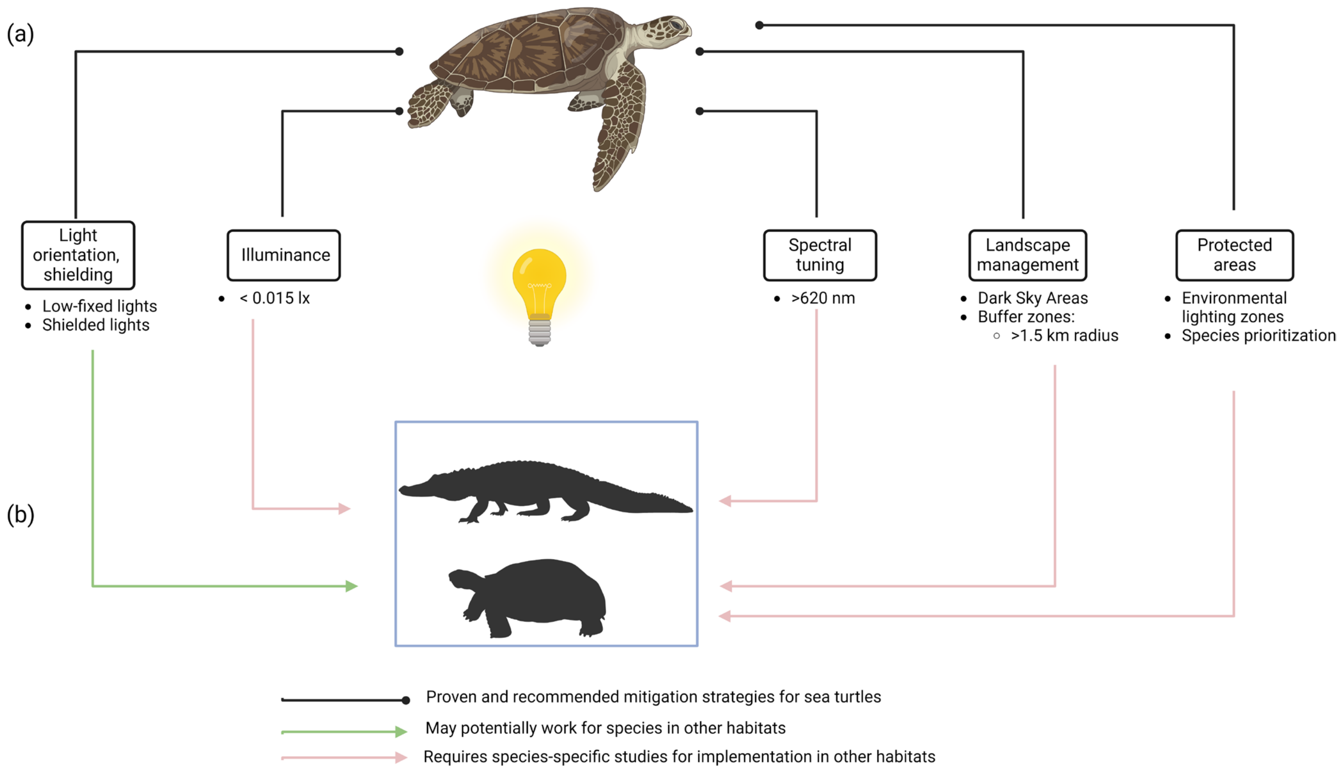

FIGURE 2 | Strategies implemented for mitigation of effects of light pollution on sea turtles (a), and their potential application to the conservation of other aquatic reptiles (b): Distribution of lights aimed to reduce light trespass and skyglow (Long et al. 2022; Yen et al. 2023), regulation of Intensity taking into consideration both indirect and direct illumination (Dimitriadis et al. 2018), selection of longer wavelengths (Long et al. 2022), protection of light-naïve habitats through protected/dark sky areas and infrastructure (Tuxbury and Salmon 2005), and enhancing existing protected areas by prioritizing both species and their light sensitivity, and engaging local communities (Kamrowski et al. 2015; Jägerbrand and Bouroussis 2020). Created with BioRender.com.

Author Contributions

Megha Khanduri: conceptualization (equal), investigation (equal), visualization (equal), writing – original draft (equal). **Franz Hölker:** supervision (equal), writing – review and editing (equal). **Ruchika Sah:** investigation (equal), supervision (equal), writing – review and editing (equal). **Syed Ainul Hussain:** funding acquisition (equal), investigation (equal), project administration (equal), resources (equal), supervision (equal), writing – review and editing (equal). **Ruchi Badola:** funding acquisition (equal), investigation (equal), project administration (equal), resources (equal), supervision (equal). **Ulrika Candolin:** conceptualization (equal), investigation (equal), resources (equal), supervision (lead), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Related WIREs Articles

How dark is a river? Artificial light at night in aquatic systems and the need for comprehensive night-time light measurements

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