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Effects of artificial light at night on fishes: A synthesis with future research priorities

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Abstract

Nearly all organisms rely on natural fluctuations of light as cues for synchronizing physiological processes and behavioural actions associated with foraging, growth, sleep and rest, reproduction, and migration. Consequently, although artificial lighting sources have provided a plethora of benefits for humans, they can lead to disruptions for wild organisms. With one quarter of the human population living within 100 km of coastlines, there is great potential for artificial light at night (ALAN) to influence the physiology, behaviour and fitness of fishes. Through a review of the literature (n = 584 publications focused on the effects of ALAN on individual organisms or ecosystems), we illustrate that most papers have concentrated on terrestrial species (59%) compared with aquatic species (20%) or a mixed approach (21%). Fishes have been underrepresented in comparison with many other taxa such as birds, insects and mammals, representing the focus of less than 8% of taxa-specific publications. While the number of publications per year focusing on fishes has generally been increasing since the mid-2000s, there has been a downturn in publication rate in the last few years. To understand where research related to ALAN in fishes has been focused, we partitioned studies into categories and found that publications have mostly concerned behaviour (41.0%), abundance and community structure (24.4%), and physiology (22.8%), while the longer-term effects on fitness (6.9%) are lacking. We synthesize the research completed in fishes and outline future priorities that will help ascertain the short- and long-term consequences of this relatively novel stressor for fish health and persistence.

KEYWORDS
artificial light at night, behaviour, community structure, fitness, light pollution, physiology

1 | INTRODUCTION

The benefit of artificial lighting for humans has led to an increase in the duration, distribution and brightness of light at night, as well as the quality of light emitted as the colour spectrum is explored (Smith, 2009). It is estimated that the extent of the Earth's artificially lit landscape has been increasing by 2.2% each year, with the level of brightening in already-lit areas increasing at this same rate (Kyba et al., 2017). Until just 100 years ago, the sun, stars and moon were the only significant sources of light present in the biosphere. Natural variations in these light sources provide plants and animals with a reliable cue for daily and seasonal physiological responses, the regulation of reproduction, migratory timing, leaf-out and loss and many other biological activities and behaviours (Gaston et al., 2013; Longcore, 2010). Indeed, virtually all organisms have developed an internal circadian rhythm (i.e. biological clock) that allows them to anticipate the shift from day to night and perform necessary actions accordingly (Stevens et al., 2013).

The widespread increase in artificial light at night (ALAN) has caused a diversity of organisms to experience a new anthropogenic stressor, the consequences of which are not yet fully understood (Zapata et al., 2019). However, research has been accumulating that indicates even relatively low levels of light can disrupt normal physiology and behaviour (Ouyang et al., 2018). For example, newly hatched sea turtles have an innate response to orient in the direction of the greatest light to make it safely to the sea, which traditionally has been the moon's glow, but in many coastal areas is being replaced by artificial lighting on land (Tuxbury & Salmon, 2005). In birds, the timing of egg laying in females and the mating songs produced by males are affected by streetlights as they unintentionally mimic changes in day length (Kempenaers et al., 2010). Additionally, many birds depend heavily on the night sky since both directional and temporal cues are used to guide them during migration, which can be disrupted by artificial light (Cabrera-Cruz et al., 2018). In nocturnal species, such as bats, ALAN may displace individuals from inhabiting certain areas, making them more vulnerable to predation (Stone et al., 2012). A recent meta-analysis illustrated that exposure to ALAN has broad implications across species, showing marked changes to the onset of daily activity for diurnal species, disruption to hormone levels and alterations to life history traits (e.g. number of offspring; Sanders et al. 2021).

Although the impact of ALAN on terrestrial taxa has garnered a fair degree of attention, there is comparatively less research on aquatic ecosystems (Davies et al., 2014; Zapata et al., 2019). Considering that more than 25% of the Earth's population lives within 100 km of a marine or freshwater coastline, aquatic ecosystems can be highly susceptible to the effects of ALAN (Small & Nicholls, 2003). Sources of direct lighting on coastlines range from temporary lighting, which includes ships and light fisheries, to more permanent sources of light, which include home lights, resort lights, residence lights, streetlights found in towns, cities, harbours and docks, and a multitude of other fixtures (Davies et al., 2014). The light that is emitted by these sources can expand out into the waters as the scattered light emitted is reflected by the clouds, further altering the lightscape as "skyglow" (Davies et al., 2014). The intensity of lighting can range from approximately 10–60 lux for common streetlight fixtures to 100–300 lux for stadium-level floodlighting and indoor lighting (Gaston et al., 2012; Rich & Longcore, 2006; Sanders et al. 2021). As a result, shallow waters in urban and suburban locations can often experience light intensities at night that vary from 0.03 to 2.5 lux (e.g. due to skyglow; Perkin et al., 2014) up to 150–200 lux in more strongly lit areas such as harbours (Bolton et al., 2017). In comparison, full moonlight on a clear night gives an illumination level of 0.1–0.3 lux and on a cloudy night radiates just 0.00003–0.0001 lux (Rich & Longcore, 2006). Although the effects of ALAN may be more visually obvious in terrestrial environments, both marine and freshwater aquatic ecosystems should be further explored given they are also readily exposed (Davies et al., 2014; Perkin et al., 2011).

With more than 35,000 species (WWF, 2021), fishes represent the largest and most diverse group of vertebrates (Ravi & Venkatesh, 2008). Most species rely on visual cues for some combination of prey localization and capture, avoidance of predators, mate finding and reproductive activities, recognition of conspecifics, habitat selection, navigation and utilizing refugia (Hammerschlag et al., 2017). Considering that the attenuation of light through the water column is relatively low, fish visual systems have evolved to optimize light use in their respective ecosystems (Bowmaker, 1995). Water acts as a monochromator (i.e. it transmits a narrower band of wavelengths than are present at input) and maximum transmission of light occurs at approximately 460 nm (blue light); however, this value can change depending on the purity of the water (Bowmaker, 1995). For example, turbidity causes a shift in the spectrum towards red light, around 600 nm, due to greater absorption of shorter (bluer) wavelengths of light (Bowmaker, 1995). The sensitivity of rods and cones to specific wavelengths of light is determined by the presence of visual pigments, and those of fishes have some of the largest ranges of wavelength sensitivity of all vertebrates, with peak sensitivities from 350 nm (near ultraviolet) to 635 nm (far red; Bowmaker, 1995). The retinae of fishes are also unique in comparison with other vertebrates in that they can continue to grow over the lifetime of the fish through the addition of new neurons or stretching of existing tissue (Fernald, 1988). These adaptations in visual systems highlight the importance of light reception in fishes overall, and the potential for light of different intensities or spectral qualities to have different consequences depending on the underlying environmental conditions, the fishes being affected and their stage of development.

Fishes also possess light-detecting cells that are not involved in vision but instead gather information for a variety of neural systems, including allowing entrainment of circadian rhythms (i.e. ensuring biological clocks remain synchronized with real-world time; Gerkema et al., 2000). This aspect of light detection is essential for ensuring appropriate daily changes in behaviour and physiology related to locomotion, activity and rest, and foraging (Kopperud & Grace, 2017) and is dependent on the light–dark cycle (Menaker 1969). Along with daily rhythms, light-regulated biological clocks are also necessary for seasonal changes, such as the timing of reproduction (Maitra et al., 2006). As a result, changes to the light environment such as the amount of light available, its quality and the timing at which it occurs further have the potential to profoundly alter the behaviour, physiology, health and fitness of fishes through disruption of circadian and circannual processes.

Human impacts on aquatic ecosystems and fish populations are well documented in both freshwater habitats (e.g. pollution, invasive species, habitat alteration; Barbarossa et al., 2021; Dudgeon et al., 2006; Reid et al., 2019) and estuarine and coastal marine habitats (e.g. pollution, overexploitation, habitat alteration; Crain et al., 2009; Kennish, 2002). Human activity tends to be concentrated in areas that surround (e.g. streams, rivers, small lakes, estuaries) or are adjacent to (e.g. littoral areas of large lakes, coastal areas of oceans) shorelines. Globally, freshwater and marine fishes are experiencing marked declines due to human activity (Arthington et al., 2016; Gordon et al., 2018), including populations that regularly use nearshore habitats or enter them at key life-history stages. For example, pollock (*Pollachius virens*, Gadidae) have declined from inshore habitats on the coasts of Atlantic Canada, and the management and protection of these ecosystems are important to maintaining their potential to supply historically depleted adult stocks (McCain et al., 2016). Many populations of river herring (*Alosa pseudoharengus*, Clupeidae and *Alosa aestivalis*, Clupeidae, collectively), which are anadromous and rely on coastal streams for spawning and rearing, have reached historic lows in population size and are in need of a full ecosystem approach to restoration (Hare et al., 2021). Similar patterns have been observed in the Hudson River estuary (New York, USA), where striped bass (*Morone saxatilis*, Moronidae) are showing declining abundances and the American shad (*Alosa sapidissima*, Clupeidae) population is at an all-time low (Nack et al., 2019). Given the declining population trends in many fishes living in nearshore areas and their dependence on vision for day-to-day activities, developing a more holistic understanding of threats such as ALAN should be beneficial to managing commercially, recreationally and culturally valuable fisheries as well as targeting conservation efforts for imperiled populations.

Using a structured search of the primary literature, we quantitatively determine the extent to which researchers have explored the environmental issue of ALAN in fishes, in comparison with other taxa. We quantify whether ALAN research in fishes has been increasing over time and which categories of research (behaviour, physiology, community structure, morphology and fitness) have been most commonly investigated. Along with a summary of the status of the literature, we provide suggestions for expanding the research conducted in fishes, with special attention to documenting conservation implications. By identifying current gaps in the literature, this synthesis provides a roadmap to further our understanding of how the emerging stressor of ALAN is affecting a group of species of great commercial, recreational and cultural importance.

2 | TRENDS IN ALAN RESEARCH

To form a database of ALAN publications, we conducted a search in the global search engine Web of Science (Core Collection) on 18 September 2019 using the following key terms: "unnatural light"; "artificial light at night"; "night-time light"; "light pollution"; "artificial light"; "outdoor light"; "night sky pollution"; "global light emissions"; "artificially lit habitats"; "artificially lit environment"; "street light"; "artificial illumination"; "artificial glow"; "anthropogenic light"; "artificial night light"; ALAN. We further refined the search by excluding Web of Science categories that were unrelated to wildlife biology (e.g. applied physics, political science and oncology). Our full search string with all exclusions can be found in the Supporting Information (Part 1; Table S1). We completed an additional search with the same terms and exclusions on 29 January 2021 that was limited to the date range of "September 2019 – present" to update the database. In the first search, we obtained 3,549 publications which we then manually coded to form a database that only pertained to the biological effects of any form of artificial light (i.e. focused on plants, animals or whole ecosystems, or reviews of any combination of these). The second search yielded 670 papers that were manually coded by CLM. We acknowledge that we used a single search engine to obtain our results, and we therefore could have missed papers on ALAN that were published in highly specialized or local journals, articles that were not in English and/or publications that would be considered grey literature (e.g. government reports, theses; Mongeon & Paul-Hus, 2016). In the Life Sciences, we anticipate this could lead to a loss of up to 7%–8% of journal articles (Vieira & Gomes, 2009). However, we do not anticipate that certain taxonomic groups would be more likely to be excluded in the Web of Science Core Collection based on the search engine's journal coverage compared with others (e.g. Scopus). Further, our analysis did not require the comparison of the literature across disciplines or languages. As a result, we are confident that our results still provide a robust snapshot of the current state of the research on ALAN in fishes and in comparison with other taxa.

All publications considered to fall within our criteria of pertaining to the biological effects of artificial light were further categorized. We recorded (1) taxa of focus (or multi-taxa if the paper pertained to more than one major taxonomic group; or non-taxonomic if the publication reviewed overall effects of artificial light on entire ecosystems or from a global perspective); (2) whether the paper focused on aquatic or terrestrial ecosystems/species or both; (3) whether the paper dealt with artificial light in the context of pollution or other contexts (e.g. lighting in aquaculture facilities, the use of light for attraction in fisheries, light for commercial growth of plants). If a publication pertained to fishes (whether independently or as part of a multi-taxa approach, and in any setting—wild, laboratory or aquaculture), we further recorded: (4) species studied; (5) whether the study was completed in an aquaculture setting; (6) the focus/foci of the research (behaviour, physiology, fitness, morphology, community structure). Fitness was considered to be an organism's ability to survive and/or produce offspring. Although the effect of light on fish growth, behaviour and reproduction has also been studied in the context of improving aquaculture production (see review by Ruchin, 2021), we focus our review on publications specifically designed to study light pollution as they will have greater applicability to the light levels and ecological conditions experienced by wild fishes.

After manually removing papers that did not pertain to the effects of light on living organisms, we retained a database of 957 publications. We determined that 584 of these specifically discussed artificial light at night as a stressor (i.e. as light pollution), while the remaining papers covered other related topics such as normal function or ecology under natural light–dark cycles or the use of artificial lighting in industry (e.g. aquaculture facilities, greenhouses) or for behavioural guidance. Of the 584 ALAN papers, 60 took a non-taxonomic approach in that they discussed global, full ecosystem, or large-scale effects on biodiversity, most of them being reviews or meta-analyses. The publications with a taxonomic focus on light pollution (*n* = 524) covered a variety of taxa including birds (29%), insects (17%), mammals (17%), reptiles (9%), fishes (8%), other invertebrates (7%), multiple taxa (often bats and insects; 5%), plants (4%), amphibians (3%) and other organisms (algae, fungi, microorganisms; 1%; Figure 1). Studies on terrestrial organisms (59%) were more common compared with aquatic (20%) or mixed systems (21%).

Of the five taxonomic groups with greater than 40 publications pertaining to ALAN, birds, mammals, insects and reptiles have shown a general trend of increasing numbers of publications over time, although there are fluctuations from year to year in the total number of papers (Figure 2a). Mammals, insects and reptiles have shown a flatter climb in publication rate compared with birds (Figure 2b). Further, fishes have shown a decline in the number of papers published each year since 2016 (Figure 2a), having only reached a maximum of 6 publications in a single year.

The 8% (*n* = 41) of total publications focusing on fishes (Table S1) covered a number of major research topics (Figures 3 and 4) including behaviour (41.0%), abundance and community structure (24.4%), physiology (22.8%), fitness (6.9%) and morphology (4.9%).

3 | BEHAVIOUR

3.1 | Swimming activity

Swimming activity represented the most common metric investigated of the potential effects of ALAN on behaviour. Swimming is important to fulfilling many biological needs in fishes, such as acquiring food, avoiding predators, mating and/or caring for offspring and making seasonal migrations (Beamish, 1978). As a result, any ALAN-induced changes to general activity level are expected to have consequences for fish survival and/or reproduction, either directly through disruption of an associated behaviour or through changes in energy expenditure that then place limitations on the resources

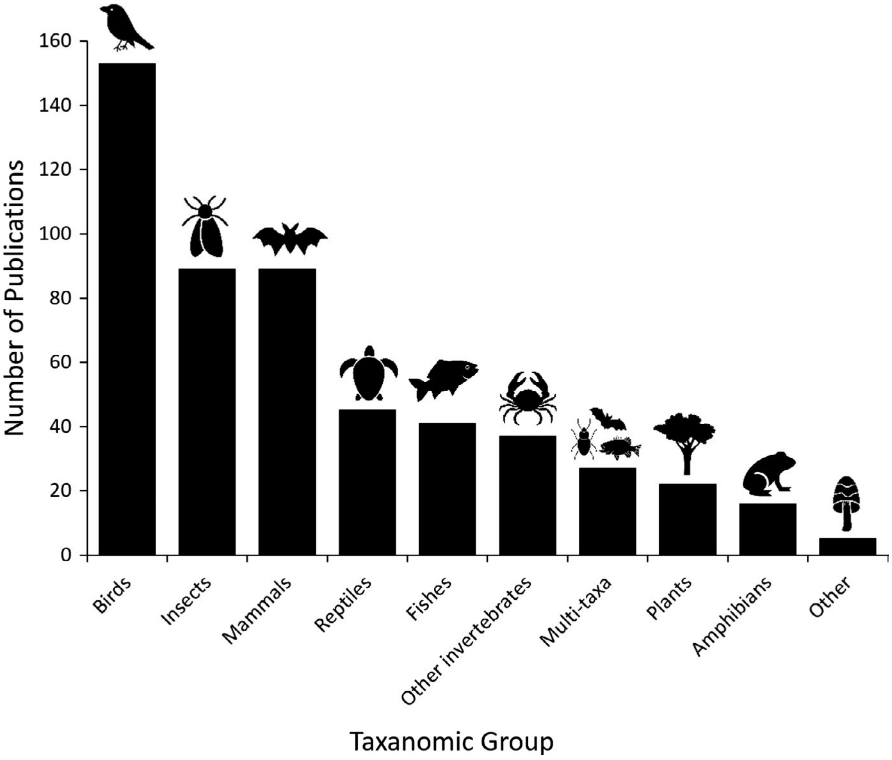
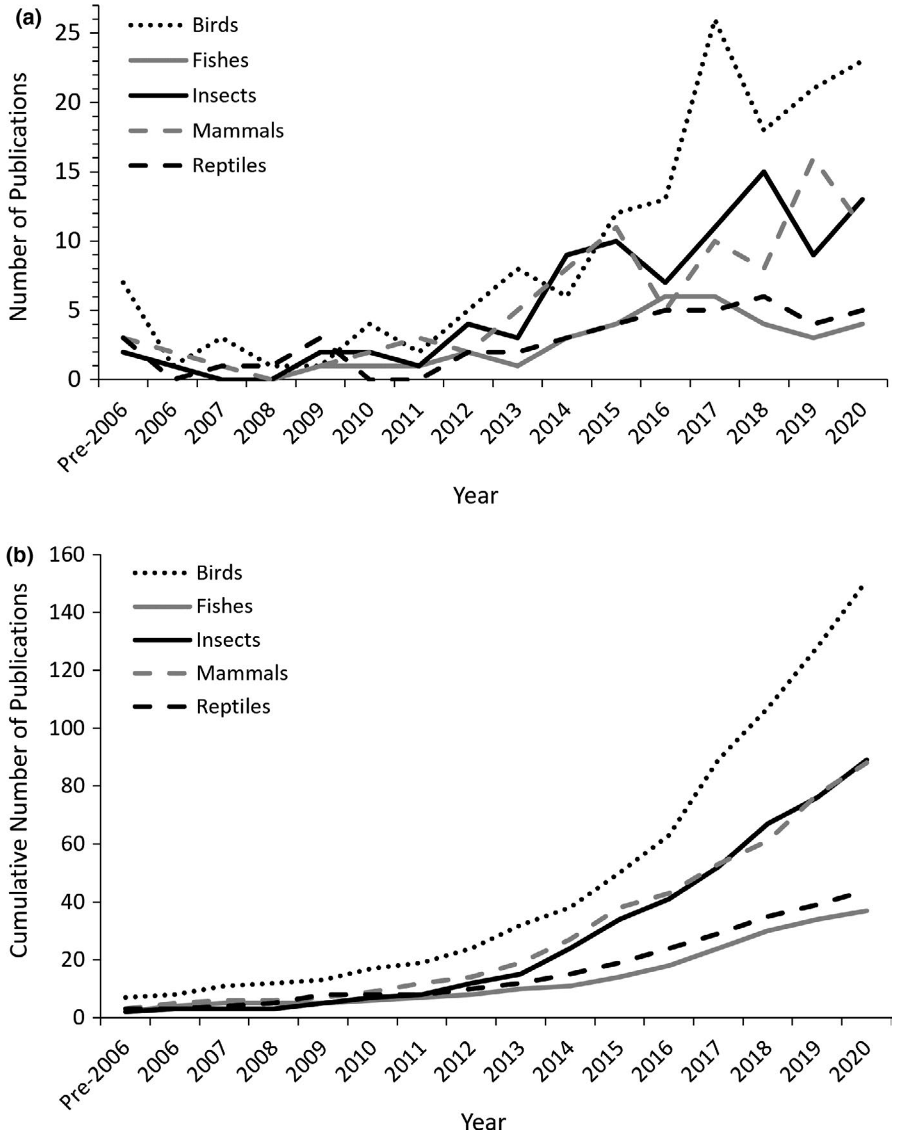


FIGURE 1 Number of publications in the primary literature focused on artificial light at night divided by major taxonomic group (1965–2021)

FIGURE 2 (a) Number of publications and (b) cumulative number of publications by year focused on artificial light at night in the five taxonomic groups with the largest total number of publications



available for reproduction or maintenance activities. Using accelerometer biologgers, Foster et al. (2016) found that nest-guarding male smallmouth bass (*Micropterus dolomieu*, Centrarchidae) exposed to two different types of ALAN in their natural habitat—low intensity dock-lighting (median 2.6 lux) and higher intensity simulated traffic lights (median 40.4 lux)—increased their total activity level in comparison with controls living in unaltered habitats. Fish experiencing the intermittent (traffic) lighting treatment showed the greatest increase in activity levels and the largest fluctuations in activity level between night and day, with implications for energy budgets during this crucial stage of reproduction (Foster et al., 2016). Indeed, there is some evidence that increases in swimming activity associated with light pollution could lead to increased energetic demand. Following a 10-day period of ALAN (70 lux) exposure, overall activity of wild-caught rockfish (*Girella laevifrons*, Kyphosidae) increased, with fish exposed to light showing greater activity across their entire 24-hr cycle compared with control fish (Pulgar et al., 2019). Further, while control fish showed peak activity levels at mid-day coinciding with expected change in the tide, light-exposed fish lost this circadian and circatidal pattern (Pulgar et al., 2019). Given that the increased activity in light-exposed fish was also paired with higher oxygen consumption (see Section 4.0 on Physiology below), these results further illustrate that ALAN has the potential to increase the energetic cost of living (Pulgar et al., 2019) with potential for carryover consequences to fitness.

To our knowledge, only two studies have documented the influence of ALAN on the activity of fish within communities in natural waterways, finding noticeable differences compared with unlit reaches or times. Bolton et al. (2017) reported that the installation of LED lighting in a wharf led to fishes being more active on lit nights compared with normal night-time conditions, as determined by analysis of underwater sonar footage (DIDSON). Becker et al. (2013) similarly investigated the activity of fish in a lit estuary using the same technology, finding that large fish worked to maintain their position in the lit area, a potentially energetically costly activity due to the swimming requirements necessary to compete with the current flows. These results further reinforce the potential for ALAN to alter the energetic budgets of a variety of fish species, with consequences for the functioning of entire communities if predator–prey relationships, reproduction, recruitment or species distribution is affected (Zapata et al., 2019).

We also have only limited information on how swimming activity may respond to different wavelengths of light. Lin et al. (2021) exposed the cyprinid *Ptychobarbus kaznakovi*, Cyprinidae to red, yellow, green and blue light of various illuminance levels (15–120 lux) and found that swimming activity was higher in the lit areas of arenas across all wavelengths in comparison with dark areas; however, the greatest increases were seen under yellow and red light. These results indicate that wavelength may be an important consideration for lighting along waterways and that there may also be potential applications for excluding or guiding fish as part of recovery efforts (Lin et al., 2021). There is also some evidence that different types of standard lighting sources could have various impacts on fish swimming behaviour, but whether these effects are related to the spectral quality of light still requires investigation. For example, swimming speed of juvenile rudd (*Scardinius erythrophthalmus*, Cyprinidae) was higher under halogen light (5.4 lux) compared with high pressure sodium (8.2 lux), while not differing from metal halide (7.1 lux), perhaps due to visual conditions/visibility (Tałanda et al., 2018). Therefore, the type of light source over a waterway could have consequences for the level of disruption to fish behaviour and it will be necessary to conduct more research to understand how the spectral characteristics of different light sources (particularly LEDs which are more energy-efficient and offer unlimited opportunities for tailoring spectral quality) may change the responses of different fish species.

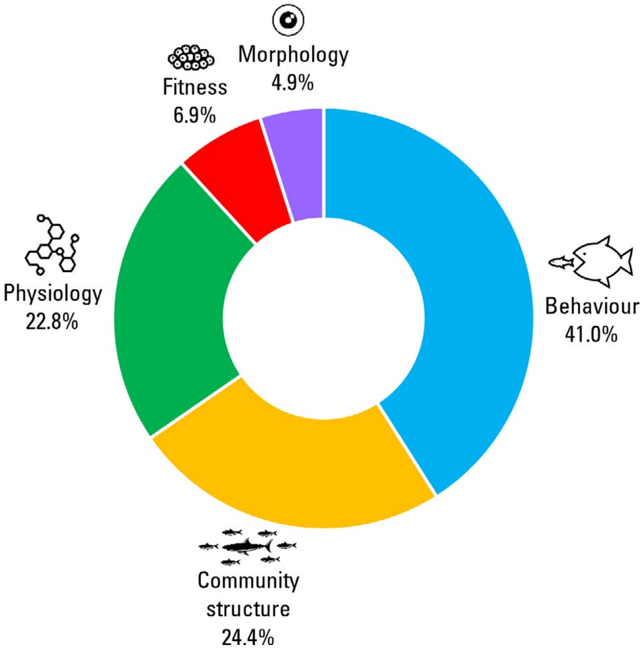


FIGURE 3 Proportion of major research topics covered in publications on the effects of artificial light at night on fishes (*n* = 41)

Finally, there are examples where ALAN did not influence the activity of the fish under investigation. For example, Trinidadian guppies (*Poecilia reticulata*, Poeciliidae) experiencing 10 weeks of ALAN (either bright at 5,000 lux or dim at 0.5 lux) did not show differences in activity level compared with fish kept on a normal light-dark cycle (Kurvers et al., 2018). In addition, juvenile bonefish (*Albula vulpes*, Albulidae) exposed to eight hours of simulated constant streetlighting (48 lux) or intermittent car headlights (80 lux) overnight showed no subsequent differences in overall activity, number of freeze events or burst swimming events compared with controls (Szekeres et al., 2017). The overall complement of studies on activity level has investigated a range of brightness levels and it is currently unclear whether there is a minimum threshold where behaviour may be affected, or how a species' life history, daily pattern of activity, developmental stage or habitat type may influence their behavioural sensitivity to ALAN. However, given that light-intensity thresholds for physiological effects appear to exist (see Section 4.0), it is feasible that behavioural thresholds will also be evident, and that they may be low (e.g. near 1 lux; Sanders et al., 2021). Based on patterns

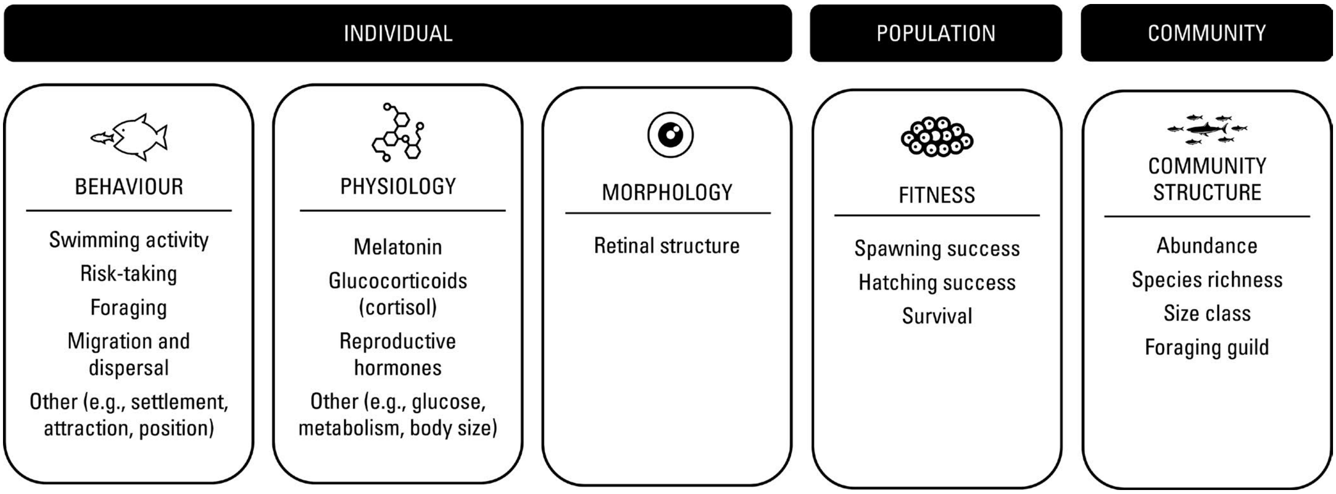


FIGURE 4 Summary of the major research topics investigated in artificial light at night publications focused on fishes, including subtopics within each major category

documented across species in a recent meta-analysis (Sanders et al., 2021), species or life stages with lower mobility to find refuge, lower behavioural flexibility and/or a nocturnal activity pattern could experience greater negative consequences. There is a pressing need for studies that simultaneously document behavioural changes and the associated consequences for energy expenditure, as well as the downstream influence of those changes on fitness.

3.2 | Foraging

Many species of fishes show diel rhythms of feeding activity (Helfman, 1993). Thus, ALAN can induce changes in foraging by either providing more or improved feeding opportunities (e.g. by increasing attraction of prey to light or improving forager vision) or increasing the risk of predation during feeding. For example, using a visual foraging model (VFM) based on experimentally determined reaction distance and capture success under various light levels, Mazur and Beauchamp (2006) showed that a nocturnal piscivore (cutthroat trout; *Oncorhynchus clarkii*, Salmonidae) experiencing urban light pollution (1–20 lux) gained greater access to vertically migrating prey fishes. Low-level ALAN in the laboratory also increased the consumption of invertebrate prey (gammarids) by Eurasian (also known as European) perch (*Perca fluviatilis*, Percidae) compared with dark nights, with fish being similarly effective predators during illuminated nights (2 lux) as they were in dusk conditions (10 lux; Czarnecka et al., 2019). Interestingly, the inclusion of woody debris did not provide an effective refuge for invertebrate prey under illumination, only under darkness, indicating that habitat complexity may not always mitigate the influence of ALAN on prey communities (Czarnecka et al., 2019). In a more natural setting, Tabor et al. (2004) investigated the ability of cottids (*Cottus* spp., Cottidae) to prey on sockeye salmon (*Oncorhynchus nerka*, Salmonidae) fry under four light intensities in artificial streams. As light intensity increased, cottids preyed on a larger number of fry, likely because fewer fry were emigrating from the lit areas. While cottids consumed approximately 5% of fry in dark conditions, 45% of fry were consumed in the brightest light conditions (5.4 lux). Further, Nelson et al. (2021) found that predation risk of Chinook salmon smolts in the wild increased with increasing ALAN intensity (0–70 lux at the surface), but only 3–5 hr after sunset. ALAN therefore has the potential to alter predator-prey dynamics to favour visual predators, increase predation on small-bodied species and therefore potentially lead to downstream changes in abundance of certain species.

In a community context, Bolton et al. (2017) showed that adding ALAN to a wharf led to greater predation of sessile invertebrates by fishes compared with dark nights, with levels of predation similar to those observed in daytime. In turn, the assemblage of sessile invertebrates changed under ALAN, indicating that this stressor has the potential to cause cascading effects through ecosystems. Bolton et al. (2017) also found evidence that fish were beginning to forage earlier on lit nights. More work is needed to determine whether acquisition of extra food resources can compensate for potential losses to rest and recovery that could result from extending total foraging time, for example through the measurement of body condition (Bolton et al., 2017). Other potential mismatches between evasiveness of prey and visual conditions for predators under ALAN could further accentuate alterations to predator-prey dynamics. Tałanda et al. (2018) measured the reaction distance of juvenile rudd as well as the evasiveness of their prey, *Daphnia*, under various light sources. While *Daphnia* were able to reliably gain information on the predation threat posed by fish under halogen lights (likely due to the spectrum being similar to that of sunlight), evasiveness was lower under metal halides, resulting in less capacity to escape predation. These types of disruptions to predator–prey interaction can have downstream consequences for entire ecosystems, for example if prey items are important for water quality and algae control (Tałanda et al., 2018).

Larger-scale *in situ* experiments will be necessary to account for full assemblages of predators and prey to determine how ecosystem functioning and water resource management may be impacted by various forms of ALAN (Tałanda et al., 2018). *In situ* experiments, or more complex laboratory designs, will also allow researchers to measure the behaviour of foraging individuals that are under their own predation pressure by piscivores, leading to a clearer picture of how ALAN will influence predator-prey dynamics in natural systems. Many studies investigated behavioural responses to short-duration ALAN, while aquatic systems are often facing ongoing changes to the lit environment. As a result, longitudinal studies that monitor how behaviour may change under longer-term light pollution will be helpful to understanding any persistent behavioural effects (Czarnecka et al., 2019). Finally, although ALAN may appear to create a benefit to some species by increasing access to prey, there is still potential that physiology and reproduction are simultaneously being altered (see sections below). Species, populations or individuals able to flexibly adjust their foraging activity to take advantage of opportunistic increases in prey under ALAN would be predicted to benefit from increased light intensity, with prey species facing increased risk of predation with increasing brightness. However, whether the benefits outweigh potential costs still requires investigation, in particular by observing fish over their full-day cycle (i.e. diel changes in foraging and energy intake) and across seasons.

3.3 | Movement, migration and dispersal

Migration and dispersal are important aspects of the life cycle of many fishes as it allows for territory establishment and exploration of temporally productive areas that increase fitness (Lennox et al., 2016). Often, natural lighting acts as a cue to initiate migratory behaviour and artificial lights can therefore disrupt this process (Lennox et al., 2016). For example, wild Atlantic salmon (*Salmo salar*, Salmonidae) smolts exposed to street lighting (14 lux) migrated from their natal stream at random times, compared with those under natural conditions which timed their migration with sunset (Riley et al., 2012). Riley et al. (2015) further experimentally documented that the dispersal of Atlantic salmon fry was delayed by 1.4 to 2.2 days under streetlight intensities as low as 1 lux (up to 8 lux) in the laboratory and similar results were unsurprisingly found under higher light intensities of 12 lux (Riley et al., 2013). In addition, the timing of dispersal is altered under lit conditions, with the mean time of fry dispersal taking place 5.5 hr after dusk under 1 lux, compared with 4 hr under dark control conditions (Riley et al., 2015). The distribution of dispersal times was also wider under 1 lux compared with darkness, with significantly more fish dispersing during daylight hours (Riley et al., 2015). Tabor et al. (2004) were also able to delay the migration of sockeye salmon fry in an 8-m section of shoreline through the installation of low-level light sources (0.1 lux). The subsequent removal of ALAN caused the fry to leave the shoreline (Tabor et al., 2004). As dispersal is a critical life stage leading to establishment and defence of territories, disruption of its timing could have implications for survival, particularly if nocturnal dispersal no longer affords protection from predators or if altered timing leads to a reduction in available energy reserves (Riley et al., 2013, 2015).

3.4 | Risk-taking behaviour

Behavioural traits associated with personality, such as risk-taking (or boldness), have been linked to survival and reproductive success in natural environments in fishes (e.g. Biro et al., 2003; Wilson et al., 2010). As a result, any effects of ALAN on the ability of fish to assess risk could result in altered predation outcomes or disruptions to energy balance, with potential fitness consequences. However, research on this category of behavioural response is limited. Becker et al. (2013) found that small fish showed a greater tendency to form schools on lit nights in an estuary, and this behaviour was viewed as an anti-predatory response to increased risk under ALAN. In a captive choice environment, zebrafish (*Danio rerio*, Cyprinidae) were not deterred by bright light (1000–1500 lux) but spent less time close to a crossing tube and more time in the upper layer of the tank in dimmer light (300–750 lux), which was interpreted as a sign of lower anxiety and lower perceived predation risk in lower light levels (Sabet et al., 2016). Further, Trinidadian guppies exposed to 10 weeks of ALAN (bright light: 5000 lux; dim light: 0.5 lux) emerged quicker from their refuge compared with control fish, with the brightest treatment leading to the greatest reduction in emergence time (Kurvers et al., 2018). Fish exposed to bright light also spent less time near walls and more time in the open compared with control fish (Kurvers et al., 2018). Both of these traits would likely increase risk and individuals may have increased their activity at night under ALAN, thereby taking on metabolic costs that would need to be replenished during daytime (i.e. if fish were hungrier and therefore took on greater risk to forage; Kurvers et al., 2018). Although this study suggests that diurnal behaviour following ALAN exposure can be disrupted, future studies should investigate a greater range of brightness levels to determine whether levels more closely resembling those found near coastlines could alter risk-associated behaviours. Further, documenting behavioural responses across the day and in relation to a hierarchy of lux levels will reveal if there is a dose-dependent relationship.

3.5 | Other behavioural responses

Apart from the more common behaviours discussed above, there were a number of additional studies that investigated responses to ALAN based on other aspects of behaviour. For example, Berge et al. (2020) found that fish and microzooplankton communities showed a near-instantaneous response to ALAN from a ship down to 200 m in depth and up to 200 m away, changing position in the water column via alterations to swimming behaviour in response. Given how little understanding we have of transient sources of light pollution, such as those associated with fishing or other vessels, this study indicates that this source of ALAN could have consequences for entire communities, at least for a short duration. ALAN may also affect other large-scale group behaviours within a single species. Bogue (*Boops boops*, Sparidae) were observed forming massive nocturnal juvenile shoals (biomass exceeding 1 ton at peak) in the shallow littoral zone; however, these were only recorded in anthropogenically modified habitats (both structural modifications and presence of light pollution; Georgiadis et al., 2014). Through visual observations of shoal micro-distributions between lit and shaded areas, Mavraki et al. (2016) determined that shoals favoured darker regions. As a result, the fish may be attracted on the large scale to lit, protected bays but then hide in shaded locations at the local scale, likely for predator avoidance. Finally, O'Connor et al. (2019) allowed convict surgeonfish (*Acanthurus triostegus*, Acanthuridae) to make a settlement choice in the laboratory between darkness and lit habitat (LED, 250 lux), with larvae showing a significant preference for dark habitat. Exposure to lower-level ALAN (20–25 lux) also caused larvae to make a quicker choice in response to visual stimulus (conspecific or heterospecific fish) compared with control larvae (O'Connor et al., 2019). While these individual investigations do not allow broad conclusions to be made, they still provide information on how ALAN can potentially alter behaviour in general and open avenues for future study of phototaxis at various life stages, whether ALAN can mask lunar cues important to reproduction and/or settlement (O'Connor et al., 2019), and how transient forms of ALAN influence fish species.

4 | PHYSIOLOGY

4.1 | Melatonin

Fish possess a light-sensitive organ called the pineal gland that produces and releases melatonin in response to varying light levels (Ekstrzm & Meissl, 1997). Melatonin is considered the key driver of biological rhythms that synchronize physiological processes with behavioural actions such as shoaling, locomotor activity, feeding or vertical migration (Brüning et al., 2018). Disruption of circadian rhythm and the loss of melatonin patterns can further interrupt reproduction, resulting in significant fitness implications. Levels of melatonin oscillate following photoperiodical changes with release being suppressed by light; levels are high during the night and low during the day (Brüning et al., 2018).

Almost all studies in fishes have shown a decrease in the production of melatonin when fish are exposed to ALAN. Khan et al. (2018) demonstrated the depression and loss of overall rhythmicity of melatonin in zebrafish serum, whole brain, retina and ovary in response to continuous light (300 lux) of relatively short duration (1 week) as well as over longer periods of one month and one year, in comparison with normal light–dark conditions (12-h light, 12-h dark). Further, some species show different responses depending on the spectrum of light tested. For instance, common roach (*Rutilus rutilus*, Cyprinidae) showed equivalent melatonin depression across three colours of light (blue, red, green) as well as to white light (Brüning, Hölker, et al., 2018), while in European perch, melatonin levels were least suppressed under blue light (Brüning et al., 2016). The magnitude of this suppression is expected to be biologically relevant (i.e. night-time levels are suppressed below natural daytime levels, and there is often an associated loss of overall rhythm in melatonin secretion; Brüning et al., 2016). A decrease in melatonin levels has been observed during exposure to levels of light as low as 1 lux and increasing the lux level has little to no effect (Brüning et al., 2015, 2016; Brüning, Hölker, et al., 2018). As a result, there is likely a threshold level of ALAN near 1 lux that can alter circadian rhythm by causing melatonin suppression in some fishes, and this light level is similar to that experienced below walkway lighting in aquatic environments (Brüning et al., 2016). Even lower light intensities, such as those associated with skyglow (0.01–0.1 lux), have been found to suppress night-time melatonin levels after periods as short as 10 days in Eurasian perch in captivity (Kupprat et al., 2020).

In a more natural experiment where European perch and roach were held in net cages within drainage channels, light levels of 15 lux at the surface produced by streetlights did not lead to differences in melatonin levels compared with fish experiencing natural light conditions (half-moon; up to 0.02 lux; Brüning, Kloas, et al., 2018). The authors outline that changes to melatonin rhythm could have been masked by individual differences, differences in sampling times between cages or due to low levels of light from the moon (Brüning, Kloas, et al., 2018). Given the other findings on these species and others in captivity, it is clear that more wild studies are needed. Such investigations should be performed in areas with similar abiotic and biotic properties between control and lit environments to ensure that the effect of ALAN can be disentangled from the effects of other conditions. Overall, the limited data available in fishes suggests that even low levels of light pollution may affect the circadian rhythm and melatonin release, particularly for freshwater fishes.

4.2 | Cortisol

The glucocorticoid hormone cortisol is a commonly measured indicator of stress in fish, and it influences several processes such as growth, osmotic regulation, immunological function and energy metabolism (Mommsen et al., 1999). In many species, cortisol also exhibits a circadian rhythm (Sánchez-Vázquez et al., 2019). If ALAN represents an unexpected stressor or energetic challenge, cortisol levels could be expected to differ in comparison with controls; however, the results of studies investigating this question in fishes have been mixed. Despite the changes to melatonin levels described above across light regimes (1, 10 and 100 lux) for European perch, Brüning et al. (2015) found no evidence that ALAN led to differences in overall cortisol levels or rhythm (with a peak occurring in the morning). Likewise, in a study on juvenile bonefish, Szekeres et al. (2017) found that whole-body cortisol showed no significant response to ALAN relative to controls. However, glucose was elevated 8 hr after exposure to both of two types of light pollution: constant streetlighting (48 lux) and intermittent car headlights (80 lux). Fish under the constant streetlight treatment also experienced higher levels of blood glucose than those under intermittent lighting (illuminated for 1 min every 10 min). This rise in glucose is similar in magnitude to what is experienced in adults during catch-and-release angling, and likely indicates that there was indeed a rise in cortisol, but it was transient and therefore not captured by sampling 8 hours post-treatment (Szekeres et al., 2017).

In contrast to the above investigations, Newman et al. (2015) did document elevated cortisol levels in dispersing Atlantic salmon fry exposed to ALAN (1–8 lux). However, this pattern was only found to be marginally significant when sampling water from flow-through incubators over a period of 1 month (analysis of Polar Organic Chemical Integrated Samplers from a full population of fish in each incubator). Water cortisol concentrations of individual fry sampled from containers (after 30 min) did not show differences between light-exposed and control treatments (Newman et al., 2015). As a result, ALAN may not be interpreted as a stressor for dispersing fry, or individuals may have become acclimated to the light levels. The authors were unable to test whether length of exposure or age influenced cortisol levels of individual fry, but further investigations with larger sample sizes could clarify these questions and be pertinent to managers (Newman et al., 2015).

In all cases, experiments were completed in a laboratory setting that lacks many environmental and ecological inputs, such as refuges, predators and prey (Brüning et al., 2015). It is therefore unclear whether the addition of ALAN to a more natural setting, or over longer periods of time, may lead to alterations in cortisol secretion. The release of cortisol may be transient, meaning more studies sampling fish at other intervals (e.g. minutes to 1–2 hr) following interaction with artificially lit environments are necessary to fully understand the influence of ALAN on stress physiology (Szekeres et al., 2017).

4.3 | Reproductive hormones

Gametogenesis is dictated by a cascade of hormones with gonadotropin-releasing hormone (GnRH) stimulating release of luteinizing hormone (LH) and follicle-stimulating hormone (FSH) from the pituitary, and thereby leading to the production of sex steroids (Brüning, Kloas, et al., 2018). This hormone cascade is controlled by daily fluctuations in photoperiod, along with other factors such as temperature, and can therefore be hypothesized to be affected by ALAN (Brüning, Kloas, et al., 2018). Brüning et al. (2016) found that mRNA expression of luteinizing hormone and follicle-stimulating hormone was suppressed by white light levels as low as 1 lux in female European perch. Conversely, there were no differences in gonadotropin expression in male perch exposed to ALAN in comparison with control fish, perhaps due to the timing of the reproductive cycle and maturation of gonads occurring earlier in males than females. Other wavelengths of light (blue, green, red) did not influence the mRNA expression of gonadotropins in either sex; however, the authors speculate that the timing of this part of the experiment likely occurred too early in the season and thus the reproductive cycle had not yet begun. Brüning, Hölker, et al. (2018) similarly did not find that either white or coloured light impacted the mRNA expression of gonadotropins in roach in a laboratory setting, again potentially due to a time of year effect on the reproductive axis (i.e. the study was completed outside of a photolabile period for this fish species). These findings highlight the importance of considering seasonality, among other contexts, when interpreting the effect of anthropogenic change on physiology. Indeed, in a follow-up study in a natural setting, Brüning, Kloas, et al. (2018) found a reduction in both mRNA expression of gonadotropins (luteinizing hormone and follicle-stimulating hormone) and circulating sex hormones (17β-oestradiol and 11-ketotestosterone) in European perch and roach under streetlighting (13.3–16.5 lux at the surface).

Although the research into the effect of ALAN on the reproductive hormone axis of fishes is limited, the available evidence indicates that light pollution has potential to disrupt hormonal rhythms, particularly if species exhibit a photolabile period associated with onset of gonadogenesis, with downstream consequences for fitness and population dynamics (Brüning, Kloas, et al., 2018). The work thus far has only been completed in two freshwater species, illustrating the vast potential for understanding how this emerging stressor influences reproductive physiology in natural settings across species, seasons, habitat types and geographic areas.

4.4 | Other physiological traits

Additional investigations into the physiological effects of ALAN have included a variety of metrics. For example, Pulgar et al. (2019) exposed juvenile wild-caught rockfish to the same level of ALAN commonly found in its coastal intertidal habitats (~70 lux). After 10 days, fish displayed higher oxygen consumption compared with controls, likely as a result of higher activity levels. This potential change in overall energetic balance can increase the metabolic cost of living and could lead to changes in mass over longer exposure periods (Pulgar et al., 2019). Indeed, Atlantic salmon fry exposed to simulated streetlighting (12 lux) were smaller at dispersal compared with control fish under a natural light–dark cycle (Riley et al., 2013). ALAN has also been shown to lead to desynchronization of a number of clock-associated genes over timespans of weeks to months and to upregulation of genes that ultimately lead to tumorigenesis, with the confirmation of ovarian tumour formation through histology in wild-caught zebrafish after one year of exposure (300 lux; Khan et al., 2018).

Overall, research on the physiological consequences of ALAN for fishes has been limited to a small subset of traits in a few species. Given the vast toolbox of physiological measurements available to assess stress, immune and energetic responses to anthropogenic change (Madliger et al., 2018), there is much greater potential to document whether and how fish cope with this stressor. As with behaviour, physiological monitoring has the power to provide information on the mechanism underlying threats and therefore imparts the ability to design better-targeted solutions. Greater scope in physiological monitoring (both the number and type of metrics) will broaden our understanding of the time periods (e.g. time of night, season or life stage), environmental conditions, and species that will be most affected by ALAN, and therefore how to best put mitigation strategies in place.

5 | ABUNDANCE AND COMMUNITY STRUCTURE

Because ALAN can alter the availability and distribution of resources, influence risk landscapes by changing predatory–prey interactions and interfere with dispersal and movement patterns, there is potential for the restructuring of community composition (Zapata et al., 2019). Such changes could include differences in relative abundance of particular species, species richness and diversity, and the spatial distribution of taxa in light-polluted compared with dark environments (Zapata et al., 2019). Research on these types of ALAN-induced effects have been relatively limited; we found only 12 publications related to abundance and/or community composition in fishes, many of which focused on predator–prey interactions. In some cases, the sources of ALAN were quite bright in comparison with non-lit environments. Keenan et al. (2007) investigated the lit environment near offshore petroleum platforms in the Gulf of Mexico and recorded 10–1,000 times more light (based on irradiance profiles) present near platforms in comparison with control sites in open water. They then modelled the 3-D light field and estimated that platforms could represent enhanced foraging environments, providing both sufficient light to visually locate and capture prey and by attracting positively phototaxic prey for species such as Atlantic herring (*Clupea harangus*, Clupeidae), damselfishes (Pomacentridae) and Japanese scad (*Decapterus maraudsi*, Carangidae). In a field study, when quantifying the actual abundances of fish near artificial lighting systems on oil platforms using baited remote underwater video, Barker and Cowan (2017) found that more fish were observed near-lit platforms, but fish were leaving surface waters during the night, possibly due to increased predation pressure caused by artificial lighting. Likely, artificial lighting was decreasing the relative safety many fish experience under darkness by increasing the visibility of prey from predators below (Barker & Cowan, 2017). Other sources of bright, localized light, such as what would be associated with intensive salmon aquaculture, have also been shown to drastically change species composition and abundance within illuminated areas. Using purse seine surveys, McConnell et al. (2010) observed greater than 100 times more Pacific herring (*Clupea pallasi*, Clupeidae) in an artificially lit area created to mimic an aquaculture facility (15–36,000 lux depending on distance from the source light), along with greater abundance of threespine stickleback (*Gasterosteus aculeatus*, Gasterosteidae), Pacific sand lance (*Ammodytes hexapterus*, Ammodytidae), soft sculpin (*Psychrolutes sigalutes*, Cottidae) and larval great sculpin (*Myoxocephalus polyacanthocephalus*, Cottidae) compared with nights where the area was not illuminated. These types of light sources therefore not only have the potential to change natural predator–prey relationships, but also may increase the interactions between wild and farmed fishes, with implications for disease transmission (McConnell et al., 2010).

Dimmer sources of light in aquatic environments have also been found to influence community dynamics. For example, while Nelson et al. (2021) found that predator densities were not related to ALAN 1–3 hr after sunset, the density of piscivorous fishes was greater with ALAN 3–5 hr after sunset. Becker et al. (2013) determined there was a size-dependent response to artificial light in an estuary near a floating restaurant, with increased abundance of small shoaling fish (<100 mm) when the area was lit. As a response to increased foraging opportunities, large predatory fish (>500 mm) also increased in abundance in the illuminated area. By creating more optimal conditions for visual predators, these light-related changes have the potential to lead to unnatural top-down regulation of fish populations (Becker et al., 2013). Bolton et al. (2017) found similar results where predation risk was amplified for marine species exposed to a newly installed source of ALAN (~160 lux) under a wharf. Overall, ALAN increased the abundance of small- and medium-sized fish. While the abundance of predatory fish was lower under ALAN, they showed more predatory behaviour in comparison with darkness (Bolton et al., 2017). As an anti-predator response, many shoaling fish formed large aggregations, which highlighted that they were aware of their increased vulnerability to predation when entering the area of artificial light (Becker et al., 2013; Bolton et al., 2017). As outlined above, given that darkness acts as a refuge for many prey species and allows them to perform important activities such as rest, spawning and foraging, ALAN is likely decreasing the ability of fish to accomplish these important behaviours as they must expend more energy actively protecting themselves from predation (Bolton et al., 2017).

The response to ALAN may also be graded, with greater changes in abundance as the brightness of the light increases. Tabor et al. (2017) found that the addition of light led to greater abundances of subyearling salmonids (Chinook salmon *Oncorhynchus tshawytscha*, Salmonidae; Coho salmon *Oncorhynchus kisutch*, Salmonidae; and Sockeye salmon *Oncorhynchus nerka*, Salmonidae; combined), with the greatest number of fish caught in light treatments of 50 lux, an intermediate number at 5 lux and the fewest under darkness. Such nocturnal phototaxic behaviour could lead to higher predation risk for young salmonids (Tabor et al., 2017). Still, other communities may be less susceptible to the effects of ALAN. For example, Martin et al. (2021) installed a submersible light (leading to brightness of 75.700 μE m^{-2} s^{-1} immediately under the light) in seagrass habitat in Florida, USA. While they recorded that the community structure of fishes differed between day and night, they observed no changes in patterns due to ALAN. Future study is necessary to determine whether this was due to the short duration of light (30 hr). Similarly, Perkin et al. (2014) installed streetlights in forested streams of coastal British Columbia, Canada, and found that the abundance and growth rate of cutthroat trout did not differ between lit (0.81 lux) and control reaches (<0.00167 lux), even though drift of aquatic invertebrates was 50% less in lit compared with dark areas. Again, the authors suggest that future research should determine whether longer-term exposure to light (i.e. months to years) or its presence in other seasons leads to different results before concluding that ALAN does not influence stream ecosystems.

The relative paucity of research available on this topic has likely partially stemmed from the difficulty in observing fish communities at night in darkness (i.e. to obtain control conditions) without creating artefacts (Hammerschlag et al., 2017). Direct sampling has obviously contributed important information, though it is important to acknowledge that alternative capture techniques can lead to bias in the size and age of fishes sampled. The availability of acoustic camera technology (e.g. DIDSON) has the potential to allow further data collection on how ALAN influences abundance and behaviour of fishes simultaneously (Martin et al., 2021). In addition, all the studies to date in fishes have dealt with a single source of light, and it will be informative to determine how multiple sources of light and dispersed light such as skyglow may impact coastal community structure (Becker et al., 2013). More studies are also warranted that compare not just lit communities to dark controls, but also to daytime conditions to begin separating the influence of ALAN from the structural aspects of urban environments (Becker et al., 2013). Finally, the effect of different levels of structural diversity, and therefore potential refuges from light, will be necessary in fully understanding how ALAN affects various habitats (Perkin et al., 2014).

6 | FITNESS

There has been limited research on the fitness-related effects of ALAN for fishes, likely partly due to the logistical difficulties of studying reproduction in the field. However, there is an expectation that light-induced changes in behaviour and physiology (see above) could, in turn, influence survival (e.g. through increased predation risk) or ability to reproduce (e.g. by altering parental behaviours, interfering with egg hatching). In some cases, the effects of ALAN on reproduction have been clearly documented. For example, Fobert et al. (2019) found that exposure of common clownfish (*Amphiprion ocellaris*, Pomacentridae) to low levels of ALAN similar to light-polluted near-shore areas (26.5 lux surface; 10–15 lux bottom) did not influence frequency of spawning or fertilization success. However, eggs incubated in ALAN conditions did not hatch, compared with 86% hatching success in controls (Fobert et al., 2019), illustrating a detrimental impact of light pollution on reproductive success. Possibly, ALAN masks a darkness cue that is integral for hatching to occur (Fobert et al., 2019). In contrast, Brüning et al. (2011) found more mixed and species-specific results for the effect of ALAN on hatching, although the light regime of 3,500 lux is arguably less biologically relevant. For roach and bleak (*Alburnus alburnus*, Cyprinidae), time to 50% hatch was longer under constant illumination compared with controls, whereas chub (*Leuciscus cephalus*, Cyprinidae) hatching was accelerated. Continuous light conditions also extended the full hatching period (time to 100% hatched) in Eurasian perch and roach (Brüning et al., 2011). The ecological relevance of delayed hatch requires further investigation; while earlier hatched larvae may have access to greater food resources and gain advantages for growth (e.g. Durham & Wilde, 2005; Phillips et al., 1995), they are also often smaller at hatch and can experience higher mortality (e.g. Raventós & Macpherson, 2005; Simonin et al., 2016). Despite the brightness of the light used in this experiment, Brüning et al. (2011) showed that ALAN can interrupt potential cues associated with hatching, likely through alteration of the signals sent to the pineal gland and retina, which, in turn, control a hatching enzyme that determines time to hatch (Helvik & Walther, 1992).

Research investigating the effect of ALAN on survival is also very limited. O'Connor et al. (2019) found that wild-caught convict surgeonfish larvae under ecologically relevant ALAN (20–25 lux) for 10 days had higher growth rates and attained greater body masses, but experienced higher post-settlement mortality rates than controls (26% and 4%, respectively). In addition, in a predator–prey trial using a pair of nocturnal predators (clearfin lionfish, *Pterois radiata*, Scorpaenidae), larvae that had been exposed to the 10-day ALAN treatment experienced higher predation rates than control fish, in some trials as high as 9:1 (O'Connor et al., 2019). In a different fitness-related investigation, Riley et al. (2013) exposed Atlantic salmon fry to broad-spectrum streetlight conditions in a laboratory setting and recorded no difference in survival prior to dispersal compared with controls. The authors did, however, outline that the period between emergence of fry and establishment of feeding territories is critical to wild salmonid population dynamics. The authors documented a 3-day delay in fry dispersal under ALAN conditions (see Behaviour Section 3.0), which could have strong implications for fitness in the wild, indicating the need for such *in situ* experiments (Riley et al., 2013).

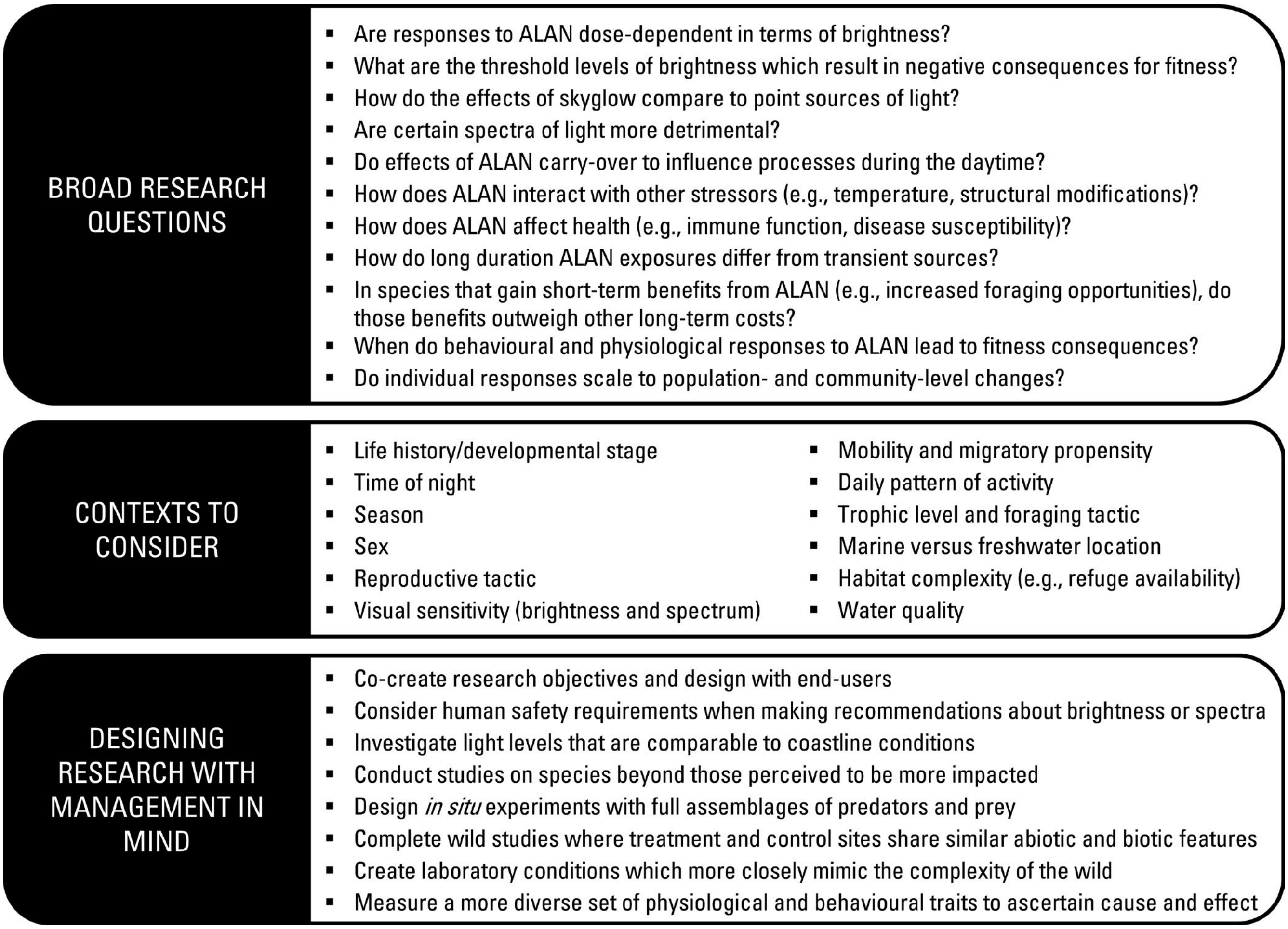
While some studies have therefore documented an effect of ALAN on fish survival and reproductive success, the impact this could impart on population or community dynamics is not yet known. In some species that disperse long distances, the effects could be particularly far-reaching by influencing recruitment dynamics. There is a need to better understand habitat selection during settlement, as some larvae may be attracted to lit areas, as well as post-settlement survival in habitats of varying brightness (Fobert et al., 2019). It is evident that ALAN may influence species differently based on life history, but the exact mechanisms remain unclear. For example, it may be expected that pelagic spawners whose eggs are carried offshore or species with eggs that hatch during the day may be less impacted; however, ALAN could cause signal-masking and induce hatch at the wrong time of day or night, disrupting optimal timing that may be essential for survival of embryos and/or larvae (Fobert et al., 2019). Future research that takes place in the field is essential to include potential costs (e.g. predation risk) and benefits (e.g. access to prey resources) to fully understand the consequences of ALAN for wild populations (Fobert et al., 2019).

7 | MORPHOLOGY

The effect of ALAN on morphology appears to be the topic least explored in fishes. Grace and Taylor (2017) documented developmental changes in the retinas of elopomorph fish in concert with changes in average light environment, with dramatic divergence among taxa that leads to specialized visual capacities. The authors detail that further work is necessary to determine whether the ability to change retinal structure over development will impart a capacity for resilience under scenarios of light pollution, or whether ALAN will instead be detrimental for individuals that must move between dark- and light-polluted locations (Grace & Taylor, 2017). At a finer scale, Kopperud and Grace (2017) measured retinomotor movement in juvenile Atlantic tarpon (*Megalops atlanticus*, Megalopidae) in relation to light–dark cycles. Constant light levels abolished the normal pattern of retinomotor movements in both cones and rods, indicating that light exposure at unexpected times may disrupt vision and therefore predator avoidance and ability to capture prey (Kopperud & Grace, 2017). This limited evidence suggests that there are implications for ALAN to alter retinal development and function, and there would be great benefit in studying such effects under the levels of light often found in coastal environments.

8 | RECOMMENDATIONS AND CONCLUSIONS

We found a total of 41 publications (published as of January 2021) investigating the consequences of ALAN on behaviour, physiology, abundance and community structure, fitness, and morphology in fishes. Based on our synthesis, Figure 5 provides a summary of research gaps, and biotic and abiotic contexts that are important to consider when studying the effects of ALAN on fishes, and suggestions for improving the management applications of ALAN research. Clearly, ALAN can induce physiological and behavioural changes at relatively low intensities (e.g. 1 lux), but we are still lacking information on the consequences of these effects for fitness and higher levels of organization (i.e. ecosystem effects). The threshold values of brightness that impact behaviour, physiology and performance may also differ between species, and these should be compared



BROAD RESEARCH QUESTIONS

- Are responses to ALAN dose-dependent in terms of brightness?
- What are the threshold levels of brightness which result in negative consequences for fitness?
- How do the effects of skyglow compare to point sources of light?
- Are certain spectra of light more detrimental?
- Do effects of ALAN carry-over to influence processes during the daytime?
- How does ALAN interact with other stressors (e.g., temperature, structural modifications)?
- How does ALAN affect health (e.g., immune function, disease susceptibility)?
- How do long duration ALAN exposures differ from transient sources?
- In species that gain short-term benefits from ALAN (e.g., increased foraging opportunities), do those benefits outweigh other long-term costs?
- When do behavioural and physiological responses to ALAN lead to fitness consequences?
- Do individual responses scale to population- and community-level changes?

CONTEXTS TO CONSIDER

- Life history/developmental stage
- Time of night
- Season
- Sex
- Reproductive tactic
- Visual sensitivity (brightness and spectrum)
- Mobility and migratory propensity
- Daily pattern of activity
- Trophic level and foraging tactic
- Marine versus freshwater location
- Habitat complexity (e.g., refuge availability)
- Water quality

DESIGNING RESEARCH WITH MANAGEMENT IN MIND

- Co-create research objectives and design with end-users
- Consider human safety requirements when making recommendations about brightness or spectra
- Investigate light levels that are comparable to coastline conditions
- Conduct studies on species beyond those perceived to be more impacted
- Design *in situ* experiments with full assemblages of predators and prey
- Complete wild studies where treatment and control sites share similar abiotic and biotic features
- Create laboratory conditions which more closely mimic the complexity of the wild
- Measure a more diverse set of physiological and behavioural traits to ascertain cause and effect

FIGURE 5 Summary of future research questions, contexts that should be considered or directly investigated when conducting ALAN research in fishes, and suggestions for how to generate research with stronger management applications

with light conditions quantified in a greater diversity of underwater areas to make stronger predictions of ALAN's influence on aquatic environments (Kurvers et al., 2018; O'Connor et al., 2019). Working towards a community ecology approach that considers the interactions between species and trait distributions will be necessary to understand effects of ALAN on broader ecosystem functions (Sanders & Gaston, 2018).

Ultimately, it is difficult to make long-term conclusions from the information presented herein, as most studies have been conducted in short-term artificial environments. To determine the effects of ALAN on fishes within the constraints of competition, predation and resource limitation, adequately conceptualizing the complexity of natural settings is required. As such, further work in the wild (including use of large mesocosms) or more natural laboratory settings will be necessary. *In situ* studies will be particularly important for quantifying how ALAN can generate both potential benefits (e.g. increased access to resources) and costs (e.g. predation; Fobert et al., 2019). A number of technologies are increasing the potential to collect data in wild settings including DIDSON cameras and predation event recorders, as well as acoustic telemetry (e.g. bridge lighting has been shown to attract free-swimming acoustically tagged Chinook salmon smolts; Celedonia et al., 2011). The vast diversity of life-history strategies found across fishes requires examination of how ALAN could differentially impact species or developmental stages due to visual sensitivity, habitat complexity, water quality, marine versus freshwater environments, foraging tactic, personality type, nocturnal versus diurnal lifestyle, life stage and other factors. It will also be beneficial to conduct studies in more natural settings to determine the additive effects of ALAN coinciding with other natural and anthropogenic stressors, such as changing temperature regimes, structural modifications to shorelines, nutrient inputs and chemical stressors (Perkin et al., 2011, 2014). Further, much of the research in fishes has investigated direct lighting sources; however, skyglow poses a more widespread and persistent threat. Although research on skyglow is increasing (e.g. The LakeLab Experiment, Leibniz-Institute of Freshwater Ecology and Inland Fisheries), continued information on how it affects fishes will be necessary for well-informed conservation planning.

Conservation efforts concerning ALAN in other taxonomic groups with larger research bases demonstrate that effective management strategies can indeed be developed. For instance, research on sea turtles has resulted in laws passed in Florida coastal areas to restrict lighting placement adjacent to nests (Salmon, 2003). Reducing the intensity of ALAN at existing illuminated structures also represents a feasible management strategy. For example, new low intensity LEDs were installed on the Sundial Bridge in Redding, California (USA) to reduce the perceived negative effects of ALAN on migrating juvenile salmon (Hacker, 2019). It may be possible to eliminate overall input of light into heavily affected systems by preventing the amount directed into the sky (e.g. by using covered lights or other shielding), by shortening periods of lighting (e.g. through time limits or motion sensors) (Czarnecka et al., 2019; Gaston et al., 2013; Nelson et al., 2021), using dimmers (McNaughton et al., 2021), or by employing LEDs that tailor spectral quality (Becker et al., 2013). As more research amasses across taxa, the potential for solutions that balance considerations of human safety in built landscapes with the well-being of wildlife (Longcore et al., 2018) should only increase.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are publicly available on Zenodo: https://doi.org/10.5281/zenodo.5780239.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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