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Casting a light on the shoreline: The influence of light pollution on intertidal settings

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Light pollution is becoming prevalent among other coastal stressors, particularly along intertidal habitats, arguably the most exposed to anthropogenic light sources. As the number of light pollution studies on sandy beaches, rocky shores and other intertidal habitats raises, commonalities, research gaps and venues can be identified. Hence, the influence of light pollution on the behavior and ecology of a variety of intertidal macro-invertebrates and vertebrates are outlined by examining 54 published studies. To date, a large majority of the reported effects of light pollution are negative, as expected from the analysis of many species with circadian rhythms or nocturnal habits, although the severity of those effects ranges widely. Experimental approaches are well represented throughout but methodological limitations in measurement units and standardization continue to limit the proposal of general conclusions across species and habitats. In addition, studies targeting community variables and the explicit influence of skyglow are heavily underrepresented. Likewise, studies addressing the interaction between light pollution and other natural and anthropogenic stressors are critically needed and represent a key venue of research. The nature of those interactions (synergistic, additive, antagonistic) will likely dictate the impact and management of light pollution in the decades ahead.

KEYWORDS

light pollution, sandy beaches, rocky shores, tidal flats, species responses

Introduction

Natural ecosystems are facing an unprecedented increase in the number of human-related stressors (Halpern et al., 2008; Bellard et al., 2012). So, it is critical to identify what aspects of the species' behavior and ecology are being altered and what changes can be expected in the short- and long-term (Griffen et al., 2016). An examination of the published evidence also helps to identify research gaps and venues, particularly in emerging fields of study (Dicks et al., 2014). Arguably, one of such fields is the influence of artificial light pollution at night (hereafter light pollution). Compared to other equally pervasive stressors, light pollution has only recently gathered considerable attention

(Davies and Smyth, 2017) despite its fast growth worldwide (Sánchez de Miguel et al., 2021). Historically, most research on light pollution has focused on terrestrial settings and species (Vaz et al., 2020), while studies on aquatic systems (Baz et al., 2022) and on marine systems have lagged behind (Longcore and Rich, 2004). Among the latter, intertidal settings are of interest because they are already exposed to a wide range of other stressors (Gunderson et al., 2016), and are arguably the most directly exposed to the main sources of light pollution.

Our review focuses on the influence of light pollution upon the behavior and ecology of marine intertidal species. We define intertidal settings broadly to include soft- (sandy beaches, sandy and muddy flats, saltmarshes) and hard-bottoms (rocky shores, tide pools and man-made structures), and to encompass a diverse range of invertebrates and vertebrates, and the nature of their use of the intertidal (permanent or seasonal). Even though light pollution effects may emerge from exposure to discrete light sources or the more diffuse and widespread skyglow (Kyba et al., 2015; Cox et al., 2022), most studies with intertidal species have focused on the former type of pollution. This is reflected in the results of this review. Nonetheless, our goals are threefold: (i) to establish commonalities on species' responses to light pollution, (ii) to identify gaps emerging from those studies, and (iii) to propose key venues of research in relation to other co-occurring stressors. The geographic scope of our review is outlined in Table 1 and Figure 1 and includes 54 published articles (as of July 1st, 2022). These were searched using keywords such as "light pollution" "intertidal" and other relevant descriptors from databases (e.g., Academic Search Complete, BioOne), peer-reviewed and reputed sources, and cross-referencing.

Sandy beaches and resident invertebrates

A wide range of light pollution (0.005–200 lx) has been directly or indirectly measured in sandy beaches by thirteen articles nearly equally split in laboratory and field studies. Often referred to as semi-terrestrial species, talitrid amphipods were among the first model-species used in the study of circadian rhythms (see Scapini et al., 2005) and light pollution. Among them, *Talitrus saltator* was the first to be used to assess the influence of skyglow changes on the species' orientation across the intertidal (Torres et al., 2022). *T. saltator* on beaches in Wales and Tunisia, *Orchestoidea tuberculata* in Chile, *Americorchestia longicornis* in Canada and *Platorchestia smithi* in Australia have all been used to measure responses to more direct sources of light pollution. Locomotor activity, a variable intuitively expected to be sensitive to light pollution, has been measured across most studies but has offered inconsistent results. While the activity of three of these species was drastically reduced in the presence of high (200 lx;

Bregazzi and Naylor, 1972) or mid-level light pollution (60 lx; Luarte et al., 2016; Lynn et al., 2021a), it remained only slightly altered in other cases (Fanini et al., 2016; Dhouha et al., 2019). The same can be said about burrowing isopods such as *Tylos europaeus* in Tunisia, *T. spinulosus* in Chile and *A. bipleuria* in Australia. While activity declined in the former two species, it remained unaltered in the latter one (Fanini et al., 2016). As suggested by Dhouha et al. (2018), these responses seem to be dictated by the strength of the stressor (light intensity), although there are also methodological differences, which in the case of Fanini et al. (2016) entailed the application of a recreation index (McLachlan et al., 2013) as a proxy of light pollution.

Various other behavioral and life history traits have been measured in beach amphipods, isopods and coleopteran insects (*Phalerisida maculata*), and their outcome is more consistent with respect to light pollution stress. Abundance declined in response to light pollution in *T. spinulosus* (Duarte et al., 2019), and in response to an urbanization index used as a proxy of light pollution (Legendre and Legendre, 1998) in *P. maculata* (Gonzalez et al., 2014). Similarly, light pollution was detrimental to feeding rates in *O. tuberculata* (Luarte et al., 2016) and *A. longicornis* (Lynn et al., 2021a) and closely related variables such as food absorption efficiency in *A. longicornis* (Lynn et al., 2021a), RNA:DNA ratios in *P. maculata* and in *T. spinulosus* (Quintanilla-Ahumada et al., 2021, 2022) as well as growth rates in *O. tuberculata* (Luarte et al., 2016). Although the trends are consistent across species, there have been exceptions: Not all the differences between controls and light pollution treatments have been significant. Only two studies have addressed the effects of light pollution on sandy beach communities located in Wales (Garratt et al., 2019) and Uruguay (Orlando et al., 2020). While species diversity increased with light pollution in some sites (Garratt et al., 2019) it declined in others (Orlando et al., 2020). Garratt et al. (2019) also documented a handful of other responses to light pollution stress: an increase in overall biomass, a change in species composition but a lack of effects on overall abundance and dominance.

Sandy beaches and seasonal vertebrates

Seasonal vertebrates such as loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), and flatback turtles (*Natator depressus*) are among the species that have gathered the most public awareness about light pollution impacts (Mazor et al., 2013; Pendoley and Kamrowski, 2016). Seventeen studies to date, most of them field-oriented, have addressed the influence of a wide range of light pollution (0.01–480 lx) on the nesting and hatching of turtles. Studies on the behavior of female turtles attempting to nest have measured light pollution with different methodologies, from direct *in situ* measurements

TABLE 1 Habitat and type of animals studied, target species, location (country), study setting (L, laboratory; F, field), light pollution intensity reported (in lux unless otherwise specified; n.d.: unclear), measured response, light pollution influence and reference (#).

Habitat/animals	Species	Country	Setting	Light (lx)	Measured response	Light pollution influence	#	
Sandy beaches/	<i>T. saltator</i>	Tunisia	L	140	Activity	No influence	1	
	<i>T. europaeus</i>					Significant reduction		
Inverts	<i>T. saltator</i>	Wales	L	200	Activity	Activity suppression	2	
	<i>T. saltator</i>	Wales	F	Skyglow	Orientation	Changes in skyglow alter orientation	3	
	<i>T. saltator</i>	Tunisia	L	5–140	Survival/activity	Mild reduction/light-dependent	4	
	<i>O. tuberculata</i>	Chile	L/F	60	Activity feeding/growth rate absorption efficiency	At least 50% reduction 2x/3x reduction No difference	5	
	<i>A. longicornis</i>	Canada	L/F	60	Activity/feeding rate absorption efficiency growth rate	Alteration/2x reduction 3x reduction Mild reduction	6	
	<i>P. smithi</i>	Australia	F	Index	Activity	Mild reduction	7	
	<i>A. bipleura</i>							
	<i>T. spinulosus</i>	Chile	L/F	120	Abundance/size activity rhythm	5x reduction/reduction Reduction and alteration	8	
	<i>T. spinulosus</i>	Chile	L	0–100	RNA:DNA Abs. efficiency/Growth	Dose response (decline) Dose response (rise)/No effect	9	
	<i>P. maculata</i>	Chile	L	60–120	RNA:DNA	10–20% Reduction	10	
<i>P. maculata</i>	Chile	F	Index	Abundance	Decrease with urbanization level	11		
Sandy beaches/	45 species	Wales	F	0.005–5.12	Species composition Species richness/biomass Dominance/total density Species abundance	Altered by light intensity Enhanced (interact w/org. matter) No change Variable (some up, some down)	12	
	35 Species	Uruguay	F	Satellite	Species richness	Significant reduction	13	
	<i>C. caretta</i>	FL/United States	F	0.5–480	Nesting density	Significantly reduction	14	
	<i>C. mydas</i>	Costa Rica						
	Turtles	<i>C. caretta</i>	Australia	F	n.d.	Hatchling sea-finding	Significantly disruption	15
		<i>C. caretta</i>	Greece	F	0.01–0.08	Hatchling orientation	Significantly disruption	16
		<i>C. caretta</i>	FL/United States	F	n.d.	Hatchling orientation	Impairing after long exposure	17
		<i>C. caretta</i>	Israel	F	Satellite	Nesting density	Significant reduction Significant reduction	18
		<i>C. mydas</i>				Nest persistence		
		<i>D. coriacea</i>	FL/United States	F	Satellite	Nesting density	Significant reduction	19
<i>C. caretta</i>								
<i>C. mydas</i>								
<i>C. caretta</i>	FL/United States	F	1.9–29.2	Hatchling orientation	Significant disruption	20		

(Continued)

TABLE 1 (Continued)

Habitat/animals	Species	Country	Setting	Light (lx)	Measured response	Light pollution influence	#
	<i>D. coriacea</i>	Gabon	F	n.d.	Hatchling/sea-finding	Disruption with bright light	21
	<i>C. mydas</i>	Guadeloupe	F	14.5 (%)	Nesting activity model forecast	Significant reduction extinction within 80 year.	22
	<i>E. imbricata</i>						
	<i>D. coriacea</i>						
	<i>C. caretta</i>	FL/United States	L	4.6–4.9 × 10 ¹¹	Hatchling orientation	Significant disruption	23
	<i>C. mydas</i>			Photons/cm ² /s			
	<i>N. depressus</i>	Australia	F	250–500 W	Hatchling	Significant disruption when lights nearby (<200 m)	24
	<i>C. mydas</i>				Sea-finding ability		
	<i>E. imbricata</i>	Barbados	F	n.d.	Hatchling survival	At least 50% reduction	25
	<i>N. depressus</i>	Australia	F	Rad. octagons	Hatchling sea-finding	Significant reduction	26
	Various species	Guadeloupe	F	Satellite	Nesting activity	Significant reduction	27
	Various species	FL/United States	F	n.d.	Hatchling	Significant disruption	28
					Sea-finding ability	Disruption	
	<i>C. caretta</i>	FL/United States	F	n.d.	Nesting density	Preference for shaded areas	29
	<i>C. caretta</i>	Cabo verde	F	Various	Nesting behavior	20% Less nesting attempts	30
					Predation risk (ghost crab)	Risk increase	
Rocky shores/ inverts	<i>B. balanoides</i>	Wales	L	50–100	Phototaxis settlement behavior	Light avoidance by cyprids	31
	<i>B. crenatus</i>					Shade-seeking by <i>B. Balanoides</i>	
	<i>E. modestus</i>						
	Various species	Denmark	F	n.d.	Phototaxis behavior	Light seeking in 82% of larvae	32
	<i>B. balanoides</i>	Canada	F	212–16	Settlement rates	Late settlement rate reduction	33
	<i>J. cirratus</i>	Chile	F	95–16	Settlement rates	Late settlement rate reduction	34
	<i>N. scabrosus</i>						
	<i>H. panicea</i>	Japan	L	80 W	Larval release	Increase of density with light	35
	<i>H. sanguineus</i>	Japan	L	0.5	Larval release	Timing and rhythm disruption	36
	<i>H. elegantissima</i>	CA/United States	L	25 μ Einsteins × m2 × s2	Expansion activity	Expansion of tentacle activity constant/added risks	37
	<i>N. lapillus</i>	United Kingdom	L	~25	Behavior	Less refuge seeking at waterline More complex response to prey and predator's cues	38
					risk perception		
	<i>N. lapillus</i>	United Kingdom	L	0–50	Interaction with full moon	Interaction with moon at high lux	39
	<i>C. concholepas</i>	Chile	L/F	330–490	Prey search/self-righting	Lower/2–3x slower 2x increase/4–5x lower in lit areas	40
					Metabolism/density		

(Continued)

TABLE 1 (Continued)

Habitat/animals	Species	Country	Setting	Light (lx)	Measured response	Light pollution influence	#
	<i>L. obtusata</i> <i>L. fabalis</i>	United Kingdom	L/Model	Light spectrum	Snail conspicuousness	Broader spectrum raises conspicuousness in color morphs	41
	<i>G. laevifrons</i>	Chile	L	70	Activity metabolic rate/weight	Increased probability and freq. 20% increase/no change	42
Tidal Flat/	<i>T. tetanus</i>	Scotland	F	n.d.	Foraging	Increased foraging time but no effect on physiological factors	43
Salt marsh	<i>N. granulata</i>	Argentina	F	~40	Predation Cannibalism/density	44–61% Reduction 30% increase/5x increase	48
	<i>N. granulata</i>	Argentina	F	0–6	Feeding rate/concealment Burrow maintenance	Reduction/reduction Increase	49
	<i>N. granulata</i>	Argentina	F	2–6	Spatial aggregation	Increase	50
Estuary	Various species	S. Africa	F	n.d.	Fish diversity	Larger fish/numbers under light	51
	Various species	Australia	F		Fish predation rates Prey communities	Increase of predation rates Alteration prey communities	52
Coral reef	<i>A. ocellaris</i>	Australia	L	~30	Egg fertilization/spawning Hatching success	No changes Significantly reduced	53
	<i>A. chrysopterus</i>	Polynesia	F	4.3	Survival rates Growth rates	36% Reduction 44% reduction	54
Birds and others	6 Shorebirds	Portugal	F	0.18–0.71	Choice of site Foraging/prey intake	Increase in visual predators Increase/Increase in 4 spp.	44
	<i>C. n. nivosus</i>	CA/United States	F	Satellite	Plover density/roosting	Reduction in roosting density	45
	<i>P. leucocephalus</i>	FL/United States	F	n.d.	Foraging, patch preference	Significant reduction near lights	46
	<i>H. ulvae</i>	France	L	n.d.	Crawling activity/feeding	Significantly reduction	47

References: ¹Dhouha et al. (2019); ²Bregazzi and Naylor (1972); ³Torres et al. (2022); ⁴Dhouha et al. (2018); ⁵Luarte et al. (2016); ⁶Lynn et al. (2021a); ⁷Fanini et al. (2016); ⁸Duarte et al. (2019); ^{9/10}Quintanilla-Ahumada et al. (2022, 2021); ¹¹Gonzalez et al. (2014); ¹²Garratt et al. (2019); ¹³Orlando et al. (2020); ¹⁴Witherington (1992); ¹⁵Berry et al. (2013); ¹⁶Dimitriadis et al. (2018); ¹⁷Lorne and Salmon (2007); ¹⁸Mazor et al. (2013); ¹⁹Hu et al. (2018); ²⁰Witherington and Bjorndal (1991); ²¹Bourgeois et al. (2009); ²²Brei et al. (2016); ²³Tuxbury and Salmon (2005); ²⁴Pendoley and Kamrowski (2016); ²⁵Harewood and Horrocks (2008); ²⁶Kamrowski et al. (2014); ²⁷Strobl et al. (2016); ²⁸Witherington and Martin (2000); ²⁹Salmon et al. (1995); ³⁰Silva et al. (2017); ³¹Crisp and Ritz (1973); ³²Thorson (1964); ³³Lynn et al. (2021b); ³⁴Manriquez et al. (2021); ³⁵Amano (1986); ³⁶Saigusa and Kawagoye (1997); ³⁷Shick and Dykens (1984); ³⁸Underwood et al. (2017); ³⁹Tidau et al. (2022); ⁴⁰Manriquez et al. (2019); ⁴¹McMahon et al. (2022); ⁴²Pulgar et al. (2019); ⁴³Dwyer et al. (2013); ⁴⁴Santos et al. (2010); ⁴⁵Simons et al., 2022; ⁴⁶Bird et al. (2004); ⁴⁷Orvain and Sauriau (2002); ^{48/49}Nuñez et al. (2021a,b); ⁵⁰Quiñones-Llópez et al. (2021); ⁵¹Becker et al. (2013); ⁵²Bolton et al. (2017); ⁵³Fobert et al. (2019); ⁵⁴Schligler et al. (2021).

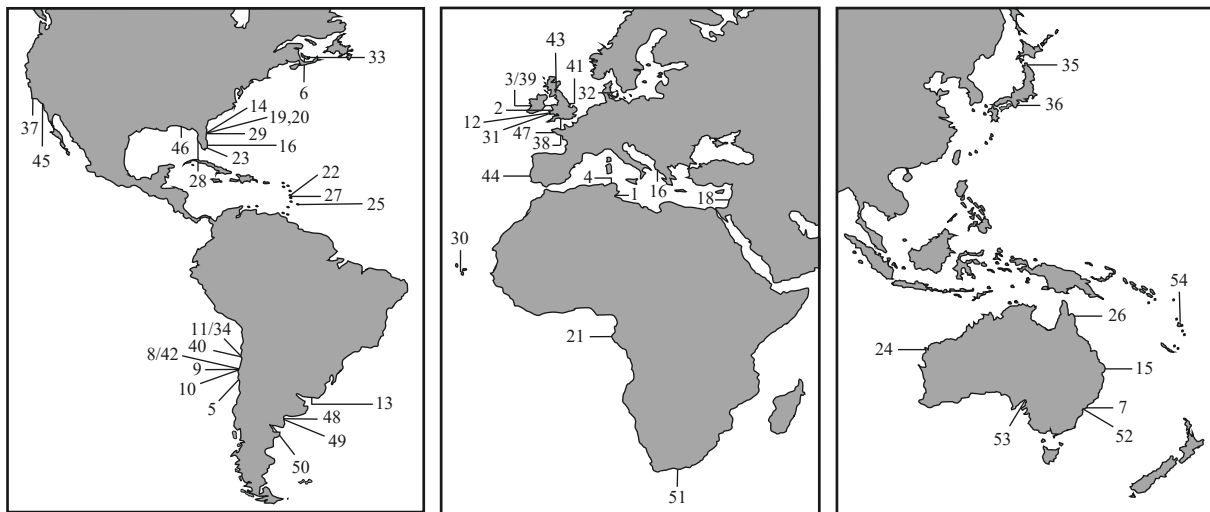


FIGURE 1

Outline maps of the main geographic regions where the study of light pollution on (macro) intertidal organisms has taken place this far. The maps are for illustrative purposes only, so locations are all approximate and not necessarily at scale. Numbers refer to the 54 studies listed and detailed in [Table 1](#).

(Witherington, 1992; Mazor et al., 2013) to satellite imagery (Strobl et al., 2016). These studies have shown rather consistent responses to light pollution: leatherback, green and hawksbill turtle nests have declined in lit areas (Strobl et al., 2016; Silva et al., 2017; Hu et al., 2018). While some species avoided illuminated beaches (Brei et al., 2016), others such as leatherback turtles nesting in Israel used these sites less persistently (Mazor et al., 2013). Furthermore, some females took longer to choose and complete their nests in lit than in dark beaches (Silva et al., 2017). Numerical models have also predicted that permanent light exposure may cause local-scale extinction in some species within 80 years (Brei et al., 2016). Light color (Silva et al., 2017) or source (mercury vs. low pressure sodium; Witherington, 1992) have been also suggested to influence the effects of light pollution on nesting. These should be carefully considered when attempting the management of this source of stress (Gaston et al., 2012).

The second main impact of light pollution is upon turtle hatchling success (Witherington and Martin, 2000; Lorne and Salmon, 2007). Although light pollution remains detrimental, the precise effects are less consistent than those described above. Light pollution disrupts orientation and/or local survival of small hatchlings emerging in sandy beaches of Australia, Greece and Florida, United States (e.g., Witherington and Bjørndal, 1991; Salmon et al., 1995; Lorne and Salmon, 2007). For example, in loggerhead hatchlings exposed to this stressor in Greece, nearly 50% were led astray from a direct path to the water (Dimitriadis et al., 2018). Such effects are mitigated by the distance to light sources or the presence of physical shields (Pendoley and Kamrowski, 2016) or by the influence of full moons (Tuxbury and Salmon,

2005; Berry et al., 2013; Kamrowski et al., 2014). Similar results were found for leatherback hatchlings in Gabon (Bourgeois et al., 2009), which in the presence of light pollution, could not use natural cues such as backshore silhouettes to orient themselves. Regarding another stressor, predation, Silva et al. (2017) found that ghost crab's activity and predation on loggerhead turtle nests was exacerbated under light pollution in beaches of Cabo Verde (NW Africa). In contrast, Harewood and Horrocks (2008) found that predation on hatchlings crawling over the beach was unaltered, but these authors also suggested that disoriented hatchlings incurred on a harmful waste of energy, that later imposed limitations to their ability to swim.

Rocky shores and related hard-bottom species

These studies (12) have used a wide range of light pollution intensities (0.5–490 lux), mainly on experimental studies conducted in laboratory settings. These studies were preceded by seminal articles focusing on the influence of natural light levels (e.g., moon cycles) on the establishment of barnacles (e.g., Thorson, 1964; Crisp and Ritz, 1973). They were followed by recent studies addressing the differential influence of light pollution on the settlement of acorn barnacles (*Semibalanus balanoides*) in Atlantic Canada (Lynn et al., 2021b) and *Jellhius cirratus* and *Notochthamalus scabrosus* in northern Chile (Manríquez et al., 2021). In both studies, early settling stages (cyprids) were only mildly affected by light pollution, whereas

late settling stages (spats) suffered a significant reduction in density with respect to (naturally dark) controls. The literature offers two other examples of light pollution's detrimental effects at even earlier life stages: Light pollution stress delayed the release of larvae in the sponge *Halichondria panicea* (Amano, 1986) and a prominent crab species (*Hemigrapsus sanguineus*) (Saigusa and Kawagoye, 1997) both in Japan.

Established stages (juveniles-adults) have reacted rather consistently to light pollution. In an artificially built jetty in California, light pollution changed the diel activity of sea anemones (*Anthopleura elegantissima*; Shick and Dykens, 1984). This prompted these anemones to keep expanding their tentacles into the night hours, which at low and high tide conditions exposed them to higher desiccation and predation risk, respectively. Avoidance of light pollution by slow moving marine snails has been reported in the UK (dogwhelks; *Nucella lapillus*; Underwood et al., 2017) and Chile (large predatory "locos," *Concholepas concholepas*; Manríquez et al., 2019). In dogwhelks, light exposure caused a reduction in their response to predator's olfactory cues, and has also been shown to interact with natural moonlight cycles on the foraging rates of this species on acorn barnacles (Tidau et al., 2022). Light pollution also slowed down the ability of locos to up-right their bodies from an upside-down position, a key antipredator ability in this species (Manríquez et al., 2019). Another anti-predator strategy (camouflage) has been assessed on *Littorina obtusata* and *L. fabalis* in the UK (McMahon et al., 2022). Testing the light spectra perceived by three predators of these snails, these authors concluded that light pollution makes some littorinid's color morphs more conspicuous, removing the benefits originally provided by camouflage. The influence of light pollution on a direct indicator of stress, metabolic rates, has been also measured in the locos referred above and small tide-pool rockfish (*Girella geofrancis*; Pulgar et al., 2019). In both species, light pollution increased metabolic rates, adding energy costs and demands in both species. In the case of the snails, this was accompanied by reduced feeding rates while avoiding lit areas (Manríquez et al., 2019), whereas in the rockfish light pollution altered circadian and circatidal rhythms (Pulgar et al., 2019).

Estuarine and vegetated bottoms used by shorebirds and other species

Tidal flats and vegetated bottoms are used as stopovers by many shorebirds (Murray and Fuller, 2015) which become exposed to the same light pollution sources outlined above. Still, most light-related studies continue to focus on urban skylights altering the orientation of migratory birds (Cabrerá-Cruz et al., 2018), on the mortality of seabirds at or near

colonies (Oro et al., 2005) or on seabird collisions with light-emitting structures (buildings, platforms or wharves; Jones and Francis, 2003). Reports on this stressor's effects directly linked to the intertidal zone are more limited (ten, primarily field-oriented are listed here), and for shorebirds they stem from the study of foraging at daylight vs. night hours (e.g., Rojas et al., 1999). For example, a study of the common redshank (*Tringa tetanus*) in estuarine flats in Scotland showed that birds exposed to light pollution turned to sight-based foraging and fed well into the night hours (Dwyer et al., 2013). Similarly, among six shorebirds in Portugal, visual foragers used light pollution to their advantage and ended up feeding longer and heavier in lit areas (Santos et al., 2010). Tactile foragers faced a disadvantage and where feasible they switched to visual foraging. Simons et al. (2022) also found that Western snowy plovers (*Charadrius nivosus*) in California were less likely to roost in areas exposed to light pollution due to higher predation risk.

Bird et al. (2004) reported light pollution effects on nocturnal beach mice on tidal flats of Florida, United States: These mice foraged less and reduced food patch preference in areas closer to light sources. Similarly, Orvain and Sauriau (2002) studying mud snails (*Hydrobia ulvae*) on French mud flats found a reduction in snails' crawling activity (and growth) in response to light. The impact of light included reduced survival rates, as this stressor entailed enhanced predation rates on the snails by their visual predators. The influence of light pollution on a more mobile invertebrate, the burrowing crab *Neohelica granulata* has been reported in saltmarsh habitats from Argentina (Nuñez et al., 2021a,b). Using tethering and cage experiments, these authors showed that juvenile crab survival decreased by 30–60% when exposed to light pollution, while the abundance of adult crabs increased up to five times (Nuñez et al., 2021a). Light exposure also reduced crab feeding rates and increased burrow maintenance (Nuñez et al., 2021a). The effects of light pollution on the activity and spatial distribution (aggregation) of this key bioturbator species were also found to be site (context) dependent (Nuñez et al., 2021b; Quiñones-Llopiz et al., 2021).

Additional studies have addressed the influence of light pollution on fish living in borderline habitats, defined here as shallow subtidals closely connected to the intertidal. Since these are not tidal habitats, the studies below illustrate impacts but are not meant to be a comprehensive list (see Bassi et al., 2022 for studies on light pollution and fish). Becker et al. (2013) found that shallow water fish diversity in a South African estuary changed in the presence of light pollution: Large predatory and small shoaling fish aggregated near light sources at night. Given that they were primarily visual predators, these authors suggested that this would enhance feeding rates on nearby prey. Likewise, Bolton et al. (2017) studied fish predation and behavior under a wharf in Australia and found that light pollution reduced fish abundance but increased their predation rates on sessile invertebrates. Also in Australia, but in coral

reefs habitats, [Fobert et al. \(2019\)](#) found that the reproductive success (egg hatching) of a clownfish (*Amphiprion ocellaris*) was reduced under light pollution. Another study from coral reefs in the French Polynesia examined the long-term effects of light pollution on juvenile anemonefish (*Amphiprion chrysopterus*; [Schligler et al., 2021](#)) and found that this stressor reduced fish survival and growth. While light pollution has positive effects on some species, these benefits often extend across trophic levels to their own predators, a balance (or unbalance) that warrants further study.

Commonalities, gaps, venues, and co-occurring stressors

To date, a large majority of the reported effects of light pollution is negative. To some degree, this is related to the targets of most of these studies, which have included species with marked circadian rhythms (e.g., talitrid amphipods), nocturnal habits (e.g., foraging shorebirds), or tradeoffs involving visual predators (e.g., rocky shore snails). The severity of these effects ranges widely, from mild responses to the complete suppression or disruption of animal activity. From the literature reviewed, a first important gap has been identified already: The limited number of studies focusing explicitly on community-level effects, which to date include only [Garratt et al. \(2019\)](#) and [Orlando et al. \(2020\)](#). A second gap is the virtual absence of studies explicitly assessing the response of intertidal organisms to the influence of skyglow, or the brightening of the night sky resulting from the reflection and large-scale scattering of light emissions (see [Kyba et al., 2015](#)). Skyglow is often mentioned, but with one exception ([Torres et al., 2022](#)), most studies continue to focus on discrete light emissions (either direct sources or their reflection). A third outstanding gap is the virtual absence of studies addressing the combined effects of light pollution and other stressors (see [Miller et al., 2017](#) for examples in terrestrial insects). Exceptions include a few studies referred above: [Orvain and Sauriau \(2002\)](#) and [Garratt et al. \(2019\)](#) found that the effects of light pollution on community biomass and mud snails, respectively, were modulated by the availability of organic matter in the habitat. Similarly, the influence of light pollution on dogwhelk foraging ([Tidau et al., 2022](#)) and sea turtle hatchlings (a few studies) interacted with natural moonlight cycles. These studies mark the beginning of the examination of potential synergistical effects (see [Halfwerk and Slabbekoorn, 2015](#)) between light pollution and other natural or anthropogenic stressors and should likely escalate in complexity as new research becomes available.

Research on light pollution has not been free of limitations. Experimental approaches are well represented, but a standardization of methodologies and more consistent

light intensities are needed to allow more meaningful comparisons among experiments. The use of lux units has allowed studies across species and habitats in intertidal and terrestrial habitats (e.g., [Grunst et al., 2022](#)). However, species' spectral detection ranges change among distinct types of organisms ([Dominoni et al., 2020](#)) and lux measurements do not necessarily capture those differences. Alternative units and methodologies further dissecting light characteristics and species perception ranges need to be consistently applied to describe this stressor's impacts ([Gaston et al., 2012](#)). Likewise, more dose-response analyses are needed to better understand the reaction of species to current and predicted light-stress scenarios (see [Quintanilla-Ahumada et al., 2022](#)). At the landscape scale, the use of remote sensing tools is growing in popularity and applicability ([Hu et al., 2018](#)). However, as in other habitats (e.g., [Raap et al., 2017](#)) and disciplines, a combination of rigorous exploratory and experimental approaches is likely to provide the best prospects for understanding how species respond to light pollution. With regards to the interplay between light pollution and other natural and anthropogenic stressors, it remains to be seen whether additive, non-additive or antagonistic effects predominate in these interactions. Their nature will likely dictate the impact and management of light pollution in the decades ahead.

Author contributions

KDL and PQ conceived and conducted the review of existing literature and drafted and edited the full manuscript. Both authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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