Science of the Total Environment 990 (2025) 179906

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

The disruption of a symbiotic sea anemone by light pollution: Non-linear effects on zooxanthellae and molecular indicators

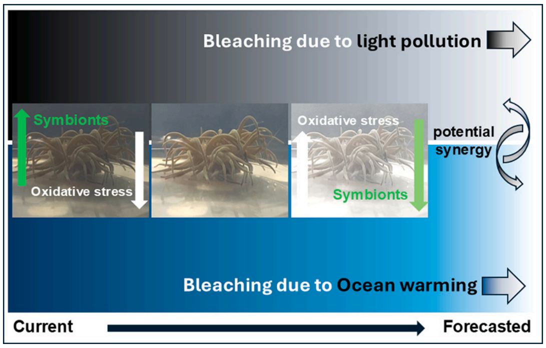
K. Devon Lynn[a], Ana Queirós[b,c], Elizabeth Talbot[b], Thomas Mesher[b], Christine Pascoe[b], Pedro A. Quijón[a,*]

[a] Coastal Ecology Laboratory, Department of Biology, University of Prince Edward Island, Charlottetown, PE, Canada
[b] Marine Ecology & Biodiversity, Plymouth Marine Laboratory, Plymouth, Devon, UK
[c] Faculty of the Environment, Science & Economy, University of Exeter, UK

HIGHLIGHTS

- Light pollution is a pervasive stressor affecting coastal species worldwide.
- Light pollution effects on a widespread symbiotic sea anemone are strong.
- Two light intensities cause bleaching and contrasting responses in zooxanthellae.
- Directly inverse responses are found in oxidative stress molecular indicators.
- Light pollution bleaching may act synergically with ocean warming bleaching.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Diez Salvador

Keywords:
Snakelocks anemone
Northeast Atlantic
Rocky shore
Bleaching
MARLAN

ABSTRACT

Artificial Light at Night (ALAN) is a pervasive stressor that may affect coastal organisms, particularly sessile forms associated with photosynthetic symbionts. We examined the effects of ALAN upon the symbiotic snakelocks anemone (*Anemonia viridis*)'s relationship with photosynthetic zooxanthellae, as well as molecular indicators of oxidative stress and metabolism. Anemones were exposed to natural daylight/night or either mild or strong ALAN intensities for four weeks, before quantifying zooxanthellae, superoxide dismutase (SOD) enzymes, and respiration rates. In comparison to natural conditions, anemones exposed to ALAN showed significantly higher and lower zooxanthellae counts, under mild and strong ALAN, respectively. In turn, SOD concentrations were lower and much higher when exposed to mild and strong ALAN, respectively, with no change in respiration rates. Concurrent bleaching suggests that ALAN is harmful to this, and possibly other species associated with symbiotic microalgae. And while we didn't measure heat stress, such bleaching may potentially act synergistically with other larger-scale forms of bleaching associated with rising ocean temperatures.

---

* Corresponding author.
E-mail address: pquijon@upei.ca (P.A. Quijón).

https://doi.org/10.1016/j.scitotenv.2025.179906
Received 18 February 2025; Received in revised form 7 June 2025; Accepted 11 June 2025

1. Introduction

Worldwide drivers of change in natural systems are increasingly anthropogenic in origin (Bellard et al., 2012; Davies and Smyth, 2018). One of these stressors, still underrepresented in the literature particularly from marine systems, is Artificial Light at Night (ALAN) (Longcore and Rich, 2004; Davies et al., 2014). ALAN sources are expanding globally (Sanchez de Miguel et al., 2021) and along coastlines to include numerous ports, marinas, vessels, lighthouses, piers, breakwaters, and lighting networks associated with roads and coastal cities (Longcore and Rich, 2004; Davies et al., 2020). In fact, ALAN is becoming pervasive, with biologically relevant light pollution affecting nearly 76 % of the seafloor nearby well-lit cities. Moreover, ALAN has potentially wider effects than those already measured (Smyth et al., 2022), and known to alter physiological, behavioral, reproductive, and ecological traits (see Stanley et al., 2015; Ludvigsen et al., 2018; Manríquez et al., 2021a; Duarte et al., 2019, 2023; Lynn and Quijón, 2022; Miranda-Benabarre et al., 2024). Initial apprehension about ALAN effects was driven by the perception that most light is filtered out by the water column. However, some of its wavelengths are now known to penetrate depths of up to 100 m (Davies and Smyth, 2018).

Along the coastline, ALAN studies have often focused on the response of mobile organisms (Lynn and Quijón, 2022) even though sessile species, including those living in association with micro-algal symbionts (sponges, corals, sea anemones), are equally, if not more vulnerable to light effects (Davies et al., 2014; Hiddink et al., 2014). Some of these species play key ecological roles (see Hatcher, 1997; Pawlik and McMurray, 2020; Bedgood et al., 2023), so their alteration may signal changes for entire coastal communities (Anthony, 1997). Sea anemones, for example, are widespread across latitudes (Muller-Parker and Davy, 2001), and their behaviour seems to be dictated almost entirely by local environmental cues (Batham and Pantin, 1950; Anthony, 1977; Wahl, 1984; Glon et al., 2020): from changing currents and light levels, to temperature, salinity, food and various tactile stimuli (Hall and Pantin, 1937; Batham and Pantin, 1950; North, 1957; Shumway, 1978; Anthony, 1997). Potential susceptibility to ALAN makes symbiotic sea anemones interesting study models, and possibly suitable indicators of the influence of light pollution on the shoreline.

Snakelocks anemones (*Anemonia viridis*) are widespread along Northeast Atlantic rocky shores (Wood, 2013; Savage et al., 2022). Populations of this species live from the intertidal to about 10 m deep (Tezcan and Gozer, 2015), and in Plymouth and the southwestern England coastline, are often found in tide pool habitats (Wood, 2013). Their exposure to ALAN raises a question about the potential effects of this stressor on its physiology and condition, so our focus was two-fold: i) we assessed the influence of ALAN on the symbiotic relationship between the anemone and its zooxanthellae (*Symbiodinium* sp.), which are prevalent in these and other sea anemones (Shick and Dykens, 1984; Colombara et al., 2017); and ii) we assessed the effects of ALAN on the anemone's physiological condition as measured by respiration rates and the molecular indicator of oxidative stress Superoxide dismutase (SOD; Leutenegger et al., 2007; Main et al., 2010). Our working hypothesis was that these three response variables are altered by ALAN, and we tested its consequences in laboratory mesocosm trials lasting four weeks.

2. Materials and methods

2.1. Collection and maintenance of sea anemones

Specimens of *Anemonia viridis* (hereafter anemones) were collected near the mid-high tide levels from tidal pools located at Wembury Beach, Devon, UK (N 50.3178, W 4.0845). Anemones were 2–3 cm in basal width and were collected by hand using silicone spatulas and careful mechanical removal, before being transferred to seawater tanks in the Plymouth Marine Laboratory (PML). The anemones were placed in individual 14 L tanks within the PML's Marine Artificial Light at Night Research Facility (see Queirós et al., 2022), https://www.pml.ac.uk/science/publications/Plymouth-Marine-Laboratory-Light-Pollution-Resea) and allowed to attach to petri dishes arranged in the tanks to facilitate respirometry analyses later in the trials (see below). The tanks were supplied with ~36 ppt, ~15 °C filtered (10 μm) seawater collected from Plymouth Sound in the previous week, just south of Plymouth, UK, with pumps (Eheim CompactON 2100) from 600 L header tanks ensuring continuous recirculation of oxygenated seawater. Tidal simulation (synchronized with local tide times) was accomplished by stoppage of the pumps and gradual drainage of the tanks during low tide, by use of the tidal simulator integrated into the MARLAN (Queirós et al., 2022). However, the anemones were never allowed to be air exposed, mimicking the conditions recorded in their natural habitat. Anemones were starved for a 96-h acclimation period in preparation for the experimental trials.

During the four-week trials, anemones were fed freeze-dried brine shrimp every third day with manual removal of food and fecal debris from the tanks the day after feeding. The MARLAN simulates a tidally dynamic underwater seascape, which affects both sunlight, moonlight and ALAN conditions experienced within experimental tanks, with sunlight and ALAN being attenuated at high tide (Queirós et al., 2022). Specifically, daylight conditions were synchronized with local diel times and light mimicked by a 500-lux white light source which switched to a 167-lux light during local high tide conditions, which resulted in a 13:11 Day:Night photoperiod at that time of year. During night hours, anemones maintained in natural conditions (controls or CTRL), were kept in complete darkness at night, while the anemones exposed to ALAN were subjected to one of two light conditions at night: either mild (10 lx; AL-10) or severe (50 lx, AL-50) white light exposure. These intensities were within the range of ALAN intensities reported by Davies et al. (2020) in this and other regions. They are also well within the range used for ALAN dose-response studies using other intertidal organisms (see Quintanilla-Ahumada et al., 2022). Those light conditions were attenuated with the tidal cycle to circa 30 % of their level at low tide. Replicated controls ($n = 10$) and ALAN treatments (each with $n = 6$) were run simultaneously.

2.2. Tissue collection and zooxanthellae density

At the end of the four-week trials, sea anemones were carefully taken from their tanks and used in respirometry trials (see below) before a small (0.01 g, wet weight) biopsy was extracted from approximately the same position in both their tentacles (zooxanthellae) and their basal musculature (SOD and proteins). Tissue samples were placed in filtered seawater and frozen at −20 °C before assays were done. The anemones were then returned to the tidal pools from where they were originally collected at Wembury Beach.

To quantify zooxanthellae, tentacle tissue samples were individually homogenized in Calcium-free seawater plus 0.5 mM EDTA for 10 s using a Bel-Art ProCulture Cordless Homogenizer. Then the solution was pipetted into a haemocytometer for counting using an Olympus BH-2 compound microscope, following the protocols by Shick and Dykens (1984).

2.3. SOD concentrations and respiration rates

For enzyme analysis (SOD), basal musculature tissue was homogenized in ice-cold PBS then centrifuged at 10,000 ×g at 4 °C for 20 min. The supernatant was then collected and frozen at −80 °C according to the recommendations of the Invitrogen Superoxide Dismutase (SOD) Colorimetric Activity Kit (Thermo Fisher Scientific, Prod. #EIASODC, lot # 23SD012D) that was used. The collected supernatant was then thawed and processed according to kit protocols, with the exception of buffer dilution which was set at a 1:1 ratio instead of the 1:4 ratio recommended by the kit due to lack of SOD recognition at the higher dilution. Samples were read at 450 nm using a BMG Labtech CLARIOstar microplate reader. SOD concentration was then calculated according to the kit protocol. Measurement of SOD enzyme concentration has been shown to be an indicator of oxidative stress in response to environmental changes in other studies involving sea anemones (see Shick and Dykens, 1984; Shick et al., 1991; Leutenegger et al., 2007; Main et al., 2010; Lynn et al., 2024). In parallel, total proteins were also quantified in a similar manner by using collected basal musculature homogenate with a Pierce BCA Protein Assay kit (Prod # 23227, lot # YH374060) to ascertain total protein concentration. Superoxide dismutase (SOD) concentration was then standardized by total protein concentration.

Anemones taken from the control and each ALAN treatment at the end of the four-week experimental trial were moved to sealed cylindrical 3.5 L acrylic respirometry chambers. These chambers had a stage installed at the bottom, above magnetic stirrers, to ensure consistent oxygen distribution in the seawater. Due to equipment restrictions and differences in the attachment abilities of the anemones, the number of replicates was limited to $n = 4$ per treatment. Anemones were allowed to acclimate for 1 h before oxygen readings were taken using a World Precision Instruments Oxymini Fibre Optic oxygen meter and oxygen sensitive foils attached to the inner wall of the chambers, calibrated using a one-point calibration procedure, per manufacturer guidance. Oxygen readings were taken in sets of 6 readings (one every 10 s) every 10 min for 1 h. All readings were taken on the same day and recorded as μmol/L, to be then converted to μmol/g/h using anemone weights.

2.4. Data analysis

Each response variable measured (zooxanthellae counts, SOD, and respiration rates) were compared among controls (CTRL) and the two ALAN treatments (AL-10 and AL-50) using one-way ANOVAs. Assumptions of normality and equal variance were tested for each analysis using the Shapiro-Wilk and the Brown-Forsythe tests, respectively, with no violations detected. Differences deemed significant ($p < 0.05$) were further assessed among individual treatments using Holm-Sidak *a-posteriori* tests.

3. Results

3.1. Symbiont cell count

Sea anemones exposed to control conditions (CTRL) averaged (mean ± S.E.) 24 × 10^4 ± 3.6 cells ml^{-1} zooxanthellae in their tentacle tissues (Fig. 1A). By comparison, those exposed to AL-10 nearly doubled the number of zooxanthellae (47 × 10^4 ± 4.7 cells ml^{-1}), whereas those exposed to AL-50 were drastically lower (half the concentration measured in CTRL: 12 × 10^4 ± 1.1 cells ml^{-1}; Fig. 1A). Among-treatment differences were significant (ANOVA $p < 0.001$; Table 1), with *a-posteriori* tests $p \leq 0.020$ in all pairwise comparisons.

3.2. SOD concentrations and respiration rates

Average SOD enzyme concentrations measured in the tissues of CTRL anemones (44 ± 8.8 U mL^{-1}) nearly doubled the concentration measured under AL-10 conditions: ~21 ± 3.3 UmL^{-1}; Fig. 1B). By comparison, SOD enzyme concentrations were several times higher in anemones exposed to the more intense AL-50: ~136 ± 6.9 U mL^{-1} (Fig. 1B). Differences were significant (ANOVA $p < 0.001$; Table 1) among all treatments (*a-posteriori* tests $p \leq 0.049$ in all pairwise comparisons).

Anemones exposed to CTRL and mild AL-10 intensities showed very similar oxygen consumption rates (averages of ~11 ± 2.8 μmol O_2 g^{-1} h^{-1}, in both; Fig. 1C). Meanwhile anemones exposed to the more intense AL-50 intensity showed an average of nearly 38 % higher oxygen consumption rates (~15 ± 0.8 μmol O_2 g^{-1} h^{-1}, Fig. 1C), but these differences were not significant (ANOVA $p = 0.323$; Table 1). No anemone mortality was recorded during the four weeks of the experimental trials.

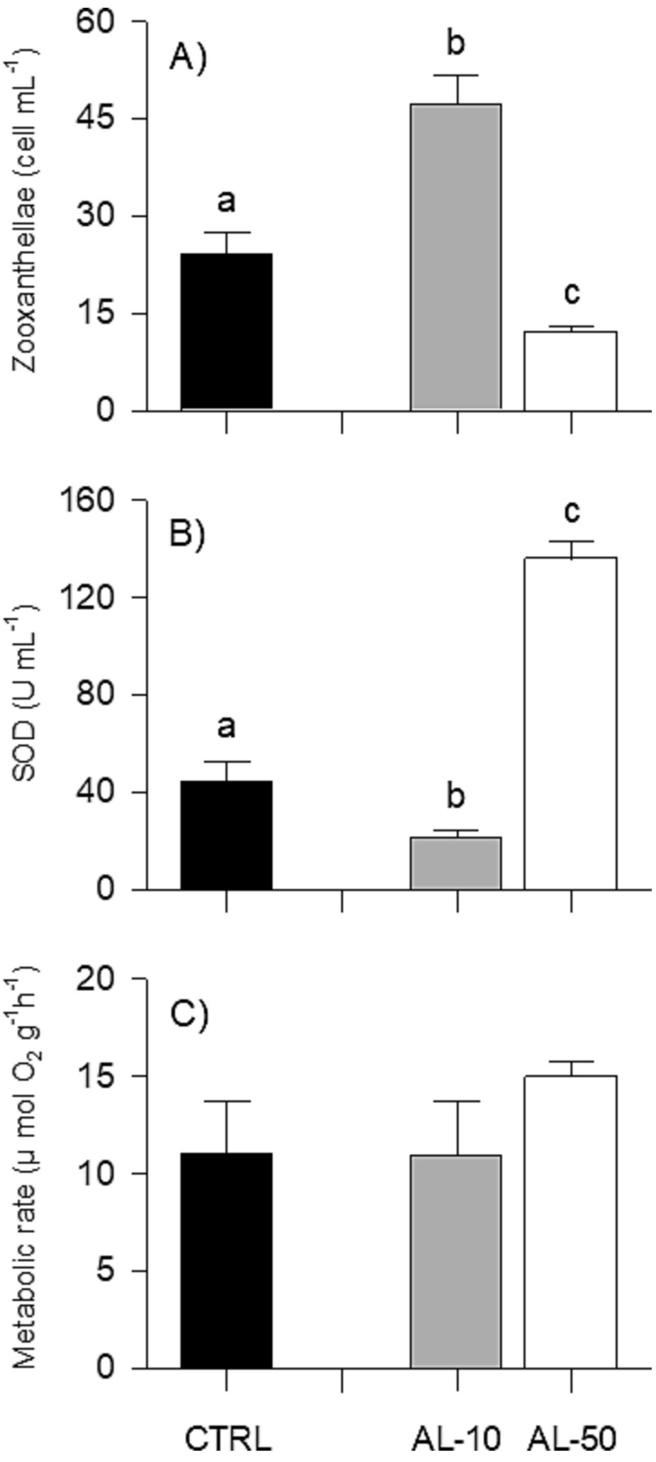


Fig. 1. A) Mean (+S.E.) counts of zooxanthellae symbionts in the tentacle tissues of the snakelocks anemone (*Anemonia viridis*), under natural day/night conditions (control: CTRL), and under the exposure of two ALAN intensities: 10 and 50 lx (AL-10 and AL-50, respectively). B) SOD concentrations in basal tissues, and C) metabolic rates. When present, different small-case letters above the bars stand for significant differences ($p < 0.05$) among light treatments.

4. Discussion

Most research on ALAN effects continues to focus on mobile vertebrates such as sea turtles, shorebirds, or fish (Dwyer et al., 2013; Hu et al., 2018; Pulgar et al., 2019, 2023) and mobile invertebrates such as crustaceans and mollusks (Underwood et al., 2017; Manríquez et al.,

Table 1

Summary of separate one-way ANOVAs comparing the variation in zooxanthellae numbers, metabolic rates and SOD enzymes measured in snakelocks anemones (*Anemonia viridis*) exposed to natural light/dark conditions (controls) and two ALAN intensities (10 and 50 lx). Significant *p*-values are presented in bold.

Response variable	ANOVA output					
	SV	DF	SS	MS	F	P
Zooxanthellae	Between groups	2	3839.271	1919.636	20.238	**<0.001**
	Residual	19	1802.183	94.852		
SOD	Between groups	2	45,925.22	22,962.61	49.411	**<0.001**
	Residual	19	8829.843	464.729		
Metabolic rates	Between groups	2	42.453	21.226	1.284	0.323
	Residual	9	148.781	16.531		

2021a; Lynn et al., 2021a; Duarte et al., 2019, 2023; Miranda-Benabarre et al., 2024). However, some studies have started to switch that focus to prominent sessile organisms (Manríquez et al., 2021b; Lynn et al., 2021b, 2024). This study contributes to that latter venue by documenting ALAN sharp effects on two important life history features of the snakelocks anemone: its relationship with zooxanthellae and a molecular indicator of stress (SOD). These results support our working hypothesis and suggest a harmful influence of ALAN on the physiology and ecology of this species. As discussed below, such influence is associated with bleaching events which may contribute or possibly act synergically with the effects of other (much better-known) bleaching events caused by global warming (Pryor et al., 2021).

4.1. Changes in zooxanthellae counts

Exposure to a mild light intensity (10 lx; see Quintanilla-Ahumada et al., 2022) caused an increase in the number of symbionts that is consistent with the results of Kinzie et al. (1984). These authors showed an increase in *Symbiodinium* zooxanthellae following exposure to various light spectra, including the white lights used here. Such response reversed at a higher ALAN intensity (50 lx), resulting in a drastically lower number of symbionts, even below control levels. These results align with Verde and McCloskey (2002), who showed that zooxanthellae growth rate increased with light intensity up to a threshold and declined thereafter. Although those authors manipulated daylight intensities, rather than ALAN intensities, their conclusions likely apply to our results. They proposed that after a threshold is reached, photoinhibition and damage to the photosynthetic apparatus (i.e., photosynthesis suppression) were causally associated with the loss of symbionts (Verde and McCloskey, 2002). We did not measure photosynthesis rates, but the evident loss of zooxanthellae at strong ALAN levels suggests a similar mechanism. Similar patterns of variation can be found in other symbiotic organisms, such as the Mediterranean reef-forming coral *Cladocora caespitosa* (see Roveta et al., 2023 and references therein). In field and laboratory trials, these authors assessed the concurrent influence of light and heat waves on growth rates and zooxanthellae counts. As expected, while they detected some positive effects associated with light, these effects were reversed when light and/or heat conditions turned unfavourable (Roveta et al., 2023).

In a comparable study, Leutenegger et al. (2007) quantified zooxanthellae concentrations in the same anemone studied here (*Anemonia viridis*, formerly known as *A. sulcata*). These authors found that anemones exposed to light-driven bleaching events ended up with significantly lower densities of symbionts than non-bleached anemones. That seems to correspond closely with the results obtained with the four-week exposure of snakelocks anemones to high versus low ALAN intensities. Given that photo-oxidative stress causes bleaching (Jokiel, 1980; Jokiel and York, 1982; Lesser et al., 1990; Downs et al., 2002; Pey et al., 2016), the effects of reactive oxygen species being produced are exacerbated by light (Asada and Takahashi, 1987; Valenzeno and Pooler, 1987). It is therefore very likely that sea anemones, and other species with symbiont-associated algae, will experience at least partial bleaching when exposed to severe ALAN intensities, such as 50 lx.

4.2. The inverse changes in SOD concentrations

Interestingly, SOD concentrations followed an almost perfectly inverse trend to the one showed by zooxanthellae concentrations. Anemones exposed to a low ALAN intensity showed a decline in SOD concentration compared to controls, but the more severe ALAN intensity caused a sharp increase in SOD concentrations. This pattern is comparable to the 'hormetic' patterns of variation that have been thoroughly discussed by Godínez-Mendoza et al. (2023). These authors showed that plants exhibit similar patterns of response to different sources of stress, with a decline at low levels of stress and a much stronger response with an increase in stress levels. The decline observed in anemones exposed to 10 lx is comparable to the one reported by Lynn et al. (2024) when exposing non-symbiotic sea anemones from Atlantic Canada (*Metridium senile*) to a 30-lux white ALAN source. It is also comparable to the results reported by Main et al. (2010), who exposed another species (*Aiptasia pallida*) to a different type of stressor, water-borne Copper pollution. The latter authors suggested that Copper either inhibited the production of SODs or that the anemone diverted energy into various other pathways. Nii and Muscatine (1997) studied a congeneric symbiotic anemone (*Aiptasia pulchella*) and showed that in response to thermal stress, their zooxanthellae simply did not produce superoxide ions, which are usually rendered safe by SOD enzymes.

The response of the snakelocks anemones to the more severe ALAN (50 lx) was a sharp 350 % increase in SOD concentrations when compared to control levels. Since the anemones were showing signs of bleaching, we interpret this as a physiological response involving a decline in the number of zooxanthellae well below control levels, and in parallel, the aforementioned rise in SODs. Such response resembles closely the results documented by Dykens and Shick (1984), who exposed the aposymbiotic anemone *Anthopleura elegantissima* to light and reported an even higher (590 %) increase in SOD activity compared to symbiotic controls. Similarly, Leutenegger et al. (2007) reported an increase in SOD concentrations in snakelocks anemones (*A. viridis*) exposed to bleaching. These authors suggested that the over-production of hydrogen peroxide (a product of the reaction catalysed by SOD enzymes) may have contributed to the exocytosis of symbiotic zooxanthellae in these anemones. This seems plausible considering the concurrent loss of zooxanthellae and the large increase in SOD taking place in our trials. Nii and Muscatine (1997) showed that in response to sub-lethal stress, it is not only the zooxanthellae the ones producing superoxide ions, but also the tissues of the anemone, which can contribute to a sharp increase in these enzymes, as observed in our trials.

4.3. A limited metabolic response

The few studies reporting changes in anemone respiration rates, following exposure to different stressors, have gathered inconsistent results. Suggett et al. (2012) showed that respiration rates in Snakelocks anemones from Sicily increased in response to seawater acidification, while Jarrold et al. (2013) found no changes in anemones from the UK subjected to short-term acidification. Meanwhile, clonal anemones were found to use less rather than more oxygen when exposed to thermal stress (Ishii et al., 2019). Our trials found that anemones exposed to 50 lx showed a nonsignificant increase in oxygen consumption when compared to control animals. Since anemones show a high degree of plasticity when compared to other cnidarians (Urbarova et al., 2019), we can speculate that snakelocks anemones may have adjusted their respiration rates in accordance with the changes taking place in zooxanthellae and oxidative enzymes. It is also possible that the evidence available simply reflects local intra-specific conditioning to sites located over a wide range of geographic regions. Lastly, the limited number of replicates used for these tests may have also contributed to the lack of clearer differences among treatments, and that must be acknowledged. Follow-up studies on ALAN and respiration rates should attempt identifying dose-response relationships (Quintanilla-Ahumada et al., 2022) that could be applied in rapid assessments and monitoring.

4.4. *Implications*

The condition and performance of sea anemones, and their possible alteration by ALAN, have branching implications. First, ALAN nonlinear alterations of zooxanthellae densities and SOD enzyme concentrations may in the long-term reduce this species fitness and contribute to bleaching events already known to be caused by thermal stress. This finding is key since symbiotic anemones are already under the threat of other global stressors, including prominently bleaching due to global warming and changes in ocean pCO_2 (Pryor et al., 2021). As the severity and frequency of climate-driven warming events increases (Gibbons et al., 2025), as virtually every climate forecast suggests (Tommasi et al., 2017; Kennedy-Asser et al., 2021; Jacox et al., 2022), the effects of ALAN adding, triggering or possibly exacerbating warming-driven effects (including bleaching) is a serious concern for these and other microalgal-symbiotic species (Hobbs et al., 2013).

Second, sea anemones provide shelter, habitat, and various other benefits to a variety of species (Chadwick et al., 2008; Cantrell et al., 2015; Colombara et al., 2017; Lozano-Bilbao et al., 2023). Such services can be challenged by the ongoing expansion of ALAN (and its potential synergy with global warming bleaching events), as our results clearly add to an already growing body of research identifying harmful ALAN effects on rocky shore organisms (Underwood et al., 2017; Davies and Smyth, 2018; Manríquez et al., 2021b; Lynn et al., 2021b). This may be particularly the case in high-biodiversity regions of the world where anemones are key habitat providers, and/or where coastal ALAN is pronounced (Smyth et al., 2022). In practice, symbiotic sea anemones may then become suitable indicators of the impacts caused by ALAN and related stressors, so further research on these species' responses to ALAN is strongly encouraged. Equally important are the study of the light properties driving ALAN's worse effects (Quintanilla-Ahumada et al., 2024a, 2024b), and the examination of potential interactions and synergies (Crain et al., 2008; Manríquez et al., 2020; Pryor et al., 2021) between the global stressors pinpointed here (ALAN and ocean warming). Whereas bleaching events have been widely associated with temperature, until recently they had not been explicitly linked to ALAN. However, given the steady expansion of ALAN sources along most coastal habitats (Lynn and Quijón, 2022; Marangoni et al., 2022), the interaction and potential synergy between these stressors is becoming much more likely. Monitoring of key indicator species such as sea anemones, as suggested here, in parallel to experimental studies assessing each stressor individually and combined (see Crain et al., 2008) are well needed research approaches that warrant impactful results.

CRediT authorship contribution statement

K. Devon Lynn: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ana Queirós:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elizabeth Talbot:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Thomas Mesher:** Writing – review & editing, Resources, Methodology, Investigation. **Christine Pascoe:** Writing – review & editing, Resources, Methodology, Investigation. **Pedro A. Quijón:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Pedro Quijon reports financial support, equipment, drugs, or supplies, and travel were provided by Natural Sciences and Engineering Research Council of Canada. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank two anonymous reviewers and the Handling Editor for their valuable feedback on earlier versions of this manuscript. Funding for KDL research visit to PML was provided by the Natural Sciences and Engineering Research Council, Canada (NSERC) through a Michael Smith Foreign Study Supplement (KDL) and a Discovery Grant (PAQ). We also thank Dr. Rachel Coppock for her laboratory assistance.

Data availability

Data will be made available on request.

References

Anthony, K.R.N., 1997. Prey capture by the sea anemone *Metridium senile* (L.): effects of body size, flow regime, and upstream neighbours. Biol. Bull. 192, 73–86.

Asada, K., Takahashi, M., 1987. Production and scavenging of active oxygen in photosynthesis. In: Photoinhibition. Elsevier Science Publisher, Amsterdam, pp. 227–287.

Batham, E.J., Pantin, C.F.A., 1950. Inherent activity in the sea anemone, *Metridium senile*. J. Exp. Biol. 27, 290–301.

Bedgood, S.A., Levell, S.T., Bracken, M.E.S., 2023. Sea anemone microhabitats enhance the diversity and biomass of mobile invertebrates on temperate rocky shores. Mar. Ecol. Prog. Ser. 715, 57–68.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377.

Cantrell, C., Henry, R.P., Chadwick, N.E., 2015. Nitrogen transfer in a Caribbean mutualistic network. Mar. Biol. 162, 2327–2338.

Chadwick, N.E., Duris, Z., Horka, I., 2008. Biodiversity and behavior of shrimps and fishes symbiotic with sea anemones in the Gulf of Aqaba, northern Red Sea. In: The improbable gulf: history, biodiversity, and protection of the Gulf of Aqaba (Eilat). Magnes Press, Hebrew University, Jerusalem, pp. 209–223.

Colombara, A.M., Quinn, D., Chadwick, N.E., 2017. Habitat segregation and population structure of Caribbean Sea anemones and associated crustaceans on coral reefs at Akumal Bay, Mexico. Bull. Mar. Sci. 93 (4), 1025–1047.

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11 (12), 1304–1315.

Davies, T.W., Smyth, T., 2018. Why artificial light at night should be a focus for global change research in the 21st century. Glob. Chang. Biol. 24, 872–882.

Davies, T.W., Duffy, J.P., Bennie, J., Gaston, K.J., 2014. The nature, extent, and ecological implications of marine light pollution. Front. Ecol. Environ. 12, 347–355.

Davies, T.W., McKee, D., Fishwick, J., Tidau, S., Smyth, T., 2020. Biologically important artificial light at night on the seafloor. Sci. Rep. 10, 12545.

Downs, C.A., Fauth, J.E., Halas, J.C., Dustan, P., Bemiss, J., Woodley, C.M., 2002. Oxidative stress and seasonal coral bleaching. Free Radic. Biol. Med. 33 (4), 533–543.

Duarte, C., Quintanilla-Ahumada, D., Manríquez, P.H., Widdicombe, S., Pulgar, J., Silva-Rodríguez, E.A., Miranda, C., Manríquez, K., Quijón, P.A., 2019. Artificial light pollution at night (ALAN) disrupts the distribution and circadian rhythm of a sandy beach isopod. Environ. Pollut. 248, 565–573.

Duarte, C., Quintanilla-Ahumada, D., Anguita, C., Silva-Rodriguez, E.A., Manríquez, P. H., Widdicombe, S., Pulgar, J., Miranda, C., Jahnsen-Guzmán, N., Quijón, P.A., 2023. Field experimental evidence of sandy beach community changes in response to artificial light at night (ALAN). Sci. Total Environ. 872, 162086.

Dwyer, R.G., Bearhop, S., Campbell, H.A., Bryant, D.M., 2013. Shedding light on light: benefits of anthropogenic illumination to a nocturnally foraging shorebird. J. Anim. Ecol. 82, 478–485.

Dykens, J.A., Shick, J.M., 1984. Photobiology of the symbiotic sea anemone *Anthopleura elegantissima*: defenses against photodynamic effects, and seasonal photoacclimatization. Biol. Bull. 167, 683–697.

Gibbons, E.G., Tummon Flynn, P.T., Quijón, P.A., 2025. Even protected seaweeds must face a warming ocean: sea surface temperatures trigger tissue bleaching and breakdown in the unique giant Irish moss (*Chondrus crispus*). Mar. Environ. Res. 204, 106907.

Glon, H.E., Coasta, M., de Lecea, A.M., Goodwin, C., Cartwright, S., Diaz, A., Brickle, P., Brewin, P.E., 2020. First record of the plumose sea anemone, *Metridium senile* (Linnaeus, 1761), from the Falkland Islands. BioInvasions Rec. 9, 461–470.

Godínez-Mendoza, P.L., Rico-Chávez, A.K., Ferrusquía-Jimenez, N.I., Carbajal-Valenzuela, I.A., Villagómez-Aranda, A.L., Torres-Pacheco, I., Guevara-González, R. G., 2023. Plant hormesis: revising of the concepts of biostimulation, elicitation and their application in a sustainable agricultural production. Sci. Tot. Env. 894, 164883.

Hall, D.M., Pantin, C.F.A., 1937. The nerve net of the Actinozoa. J. Exp. Biol. 14, 71–78.

Hatcher, B.G., 1997. Coral reef ecosystems: how much greater is the whole than the sum of the parts? Coral Reefs 16 (Suppl. 1), S77–S91.

Hiddink, J.G., Burrows, M.T., Molinos, J.G., 2014. Temperature tracking by North Sea benthic invertebrates in response to climate change. Glob. Change Biol. 21, 117–129.

Hobbs, J.A., Frisch, A.J., Ford, B.M., Thums, M., Saenz-Agudelo, P., Furby, K.A., Berumen, M.L., 2013. Taxonomic, spatial, and temporal patterns of bleaching in anemones inhabited by anemonefishes. PloS One 8 (8), e70966.

Hu, Z., Hu, H., Huang, Y., 2018. Association between nighttime artificial light pollution and sea turtle nest density along Florida coast: a geospatial study using VIIRS remote sensing data. Environ. Pollut. 239, 30–42.

Ishii, Y., Maruyama, S., Takahashi, H., Aihara, Y., Yamaguchi, T., Yamaguchi, K., Shigenobu, S., Kawata, M., Ueno, N., Minagawa, J., 2019. Global shifts in gene expression profiles accompanied with environmental changes in Cnidarian-Dinoflagellate endosymbiosis. G3 9, 2337–2346.

Jacox, M.G., Alexander, M.A., Amaya, D., Becker, E., Bograd, S.J., Brodie, S., et al., 2022. Global seasonal forecasts of marine heatwaves. Nature 604, 486–490.

Jarrold, M.D., Calosi, P., Verberk, W.C.E.P., Rastrick, S.P.S., Atfield, A., Spicer, J.I., 2013. Physiological plasticity preserves the metabolic relationship of the intertidal non-calcifying anthozoan-*Symbiodinium* symbiosis under ocean acidification. J. Exp. Mar. Biol. Ecol. 449, 200–206.

Jokiel, P.L., 1980. Solar ultraviolet radiation in the sea. Nature 116, 111–112.

Jokiel, P.L., York, R.H., 1982. Solar ultraviolet photobiology of the reef coral *Pocillopora darnicornis* and symbiotic zooxanthellae. Bull. Mar. Sci. 32, 301–315.

Kennedy-Asser, A.T., Andrews, O., Mitchell, D.M., Warren, R.F., 2021. Evaluating heat extremes in the UK. Climate Projections (UKCP18). Environ. Res. Lett. 16, 014039.

Kinzie, R.A., Jokiel, P.L., York, R., 1984. Effects of light of altered spectral composition on coral zooxanthellae associations and on zooxanthellae *in vitro*. Mar. Biol. 78, 239–248.

Lesser, M.P., Stochaj, W.R., Tapley, D.W., Shick, J.M., 1990. Physiological mechanisms of bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs. 8, 225–232.

Leutenegger, A., Kredel, S., Gundel, S., D`Angelo, C., Salih, A., Wiedenmann, 2007. Analysis of fluorescent and non-fluorescent sea anemones from the Mediterranean Sea during a bleaching event. J. Exp. Mar. Biol. Ecol. 353, 221–234.

Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2, 191–198.

Lozano-Bilbao, E., Espinosa, J.M., Thorne-Bazarra, T., Hardisson, A., et al., 2023. Monitoring different sources of marine pollution in the Canarian intertidal zone using *Anemonia sulcata* as a bioindicator. Mar. Pollut. Bull. 195, 115538.

Ludvigsen, M., Berge, J., Geoffroy, M., Cohen, J.H., De La Torre, P.R., Nornes, S.M., Singh, H., Sørensen, A., Daase, M., Johnsen, G., 2018. Use of an autonomous surface vehicle reveals small-scale diel vertical migrations of zooplankton and susceptibility to light pollution under low solar irradiance. Sci. Adv. 4, 1–8.

Lynn, K.D., Quijón, P.A., 2022. Casting a light on the shoreline: the influence of light pollution on intertidal settings. Front. Ecol. Evol. 10, 980776.

Lynn, K.D., Quintanilla-Ahumada, D., Anguita, C., Widdicombe, S., Pulgar, J., Manríquez, P.H., Quijón, P.A., Duarte, C., 2021a. Artificial light at night alters the activity and feeding behaviour of sandy beach amphipods and pose a threat to their ecological role in Atlantic Canada. Sci. Total Environ. 780, 146568.

Lynn, K.D., Tummon Flynn, P., Manríquez, K., Manríquez, P.H., Pulgar, J., Duarte, C., Quijón, P.A., 2021b. Artificial light at night alters the settlement of acorn barnacles on a man-made habitat in Atlantic Canada. Mar. Poll. Bull. 163, 111928.

Lynn, K.D., Quintanilla-Ahumada, D., Duarte, C., Quijón, P.A., 2024. Artificial light at night alters the feeding activity and two molecular indicators in the plumose sea anemone *Metridium senile* (L.). Mar. Poll. Bull. 202, 116352.

Main, W.P.L., Ross, C., Bielmyer, G.K., 2010. Copper accumulation and oxidative stress in the sea anemone, *Aiptasia pallida*, after waterborne copper exposure. Comp. Biochem. Physiol. C 151, 216–221.

Manríquez, P.H., Jara, M.E., González, C.P., Díaz, M.I., Brokordt, K., Lattuca, M.E., Peck, M.A., Alter, K., Marras, S., Domenici, P., 2020. Combined effect of *p*CO2 and temperature levels on the thermal niche in the early benthic ontogeny of a keystone species. Sci. Total Environ. 719, 137239.

Manríquez, P.H., Jara, M.E., González, C.P., Seguel, M., Quijón, P.A., Widdicombe, S., Pulgar, J.M., Quintanilla-Ahumada, D., Anguita, C., Duarte, C., 2021a. Effects of artificial light at night and predator cues on foraging and predator avoidance in the keystone inshore mollusc Concholepas concholepas. Environ. Pollut. 280, 116895.

Manríquez, K., Quijón, P.A., Manriquez, P.H., Miranda, C., Pulgar, J., Quintanilla-Ahumada, D., Duarte, C., 2021b. Artificial light at night (ALAN) negatively affects the settlement success of two prominent intertidal barnacles in the southeast Pacific. Mar. Poll. Bull. 168, 112416.

Marangoni, L.F., Davies, T., Smyth, T., Rodríguez, A., Hamann, M., Duarte, C., Pendoley, K., Berge, J., Maggi, E., Levy, O., 2022. Impacts of artificial light at night in marine ecosystems - A review. Global Change Biol. 28, 5346–5367.

Miranda-Benabarre, C., Quijón, P.A., Lohrmann, K.B., Manríquez, P.H., Pulgar, J., Quintanilla-Ahumada, D., Davies, T.W., Widdicombe, S., Jahnsen-Guzmán, N., González, C., Duarte, C., 2024. Crustacean photoreceptor damage and recovery: applying a novel scanning electronic microscopy protocol in artificial light studies. Sci. Total Environ. 957, 177561.

Muller-Parker, G., Davy, S.K., 2001. Temperate and tropical algal-sea anemone symbioses. Inv. Biol. 120, 104–123.

Nii, C.M., Muscatine, L., 1997. Oxidative stress in the symbiotic sea anemone *Aiptasia pulchella* (Carlgren, 1943): contribution of the animal to superoxide ion production at elevated temperature. Biol. Bull. 192, 444–456.

North, W.J., 1957. Sensitivity to light in the sea anemone *Metridium senile* (L.). J. Gen. Physiol. 40, 715–733.

Pawlik, J.R., McMurray, S.E., 2020. The emerging ecological and biogeochemical importance of sponges on coral reefs. Ann. Rev. Mar. Sci. 12, 315–337.

Pey, A., Zamoum, T., Christen, R., Merle, P.L., Furla, P., 2016. Characterization of glutathione peroxidase diversity in the symbiotic sea anemone *A. viridis*. Biochimie 132, 94–101.

Pryor, S.H., Andrews, L., Kelaher, B.P., Taliafico, A., Scott, A., 2021. Ocean temperature, but not acidification, causes sea anemone bleaching under a near-future climate scenario. Coral Reefs 40, 355–364.

Pulgar, J., Zeballos, D., Vargas, J., Aldana, M., Manriquez, P.H., Manriquez, K., Quijón, P.A., Widdicombe, S., Anguita, C., Quintanilla-Ahumada, D., Duarte, C., 2019. Endogenous cycles, activity patterns and energy expenditure of an intertidal fish is modified by artificial light pollution at night (ALAN). Env. Pollut. 244, 361–366.

Pulgar, J., Manríquez, P.H., Widdicombe, S., García-Huidobro, R., Quijón, P.A., Carter, M., Aldana, M., Quintanilla-Ahumada, D., Duarte, C., 2023. Artificial Light at Night (ALAN) causes size-dependent effects on intertidal fish orientation. Mar. Poll. Bull. 193, 115190.

Queirós, A.M., Talbot, L., Pascoe, C., Staff, A., Widdicombe, S., 2022. Marlan: Plymouth marine laboratory's marine artificial light at night research facility. *Plymouth marine* laboratory. 9pp..

Quintanilla-Ahumada, D., Quijón, P.A., Manríquez, P.H., Pulgar, J., García-Huidobro, M. R., Miranda, C., Molina, A., Zuloaga, R., Duarte, C., 2022. Artificial light at night (ALAN) causes variable dose-responses in a sandy beach isopod. Environ. Sci. Pollut. Res. 29, 35977–35985.

Quintanilla-Ahumada, D., Quijón, P.A., Jahnsen-Guzmán, N., Lynn, K.D., Pulgar, J., Palma, J., Manríquez, P.H., Duarte, C., 2024a. Splitting light pollution: wavelength effects on the activity of two sandy beach species. Environ. Poll. 356, 124317.

Quintanilla-Ahumada, D., Quijón, P.A., Jahnsen-Guzmán, N., Zúñiga-Cueto, N., Miranda-Benabarre, C., Lynn, K.D., Pulgar, J., Palma, J., Manríquez, P.H., Duarte, C., 2024b. The impacts of artificial light at night (ALAN) spectral composition on key behavioral traits of a sandy beach isopod. Mar. Poll. Bull. 208, 116924.

Roveta, C., Coppari, M., Calcinai, B., Di Camillo, C.G., Marrocco, T., Pulido Mantas, T., Puce, S., Torsani, F., Valisano, L., Cerrano, C., 2023. What's the key for success? Translocation, growth and thermal stress mitigation in the Mediterranean coral *Cladocora caespitosa* (Linnaeus, 1767). Front. Mar. Sci. 10, 1199048.

Sanchez de Miguel, A., Bennie, J., Rosenfeld, E., Dzurjak, S., Gaston, K.J., 2021. First estimation of global trends in nocturnal power emissions reveals acceleration of light pollution. Remote Sens. (Basel) 13, 3311.

Savage, G., Porter, A., Simpson, S.D., 2022. Uptake of microplastics by the snakelocks anemone (*Anemonia viridis*) is commonplace across environmental conditions. STOTEN 836, 155144.

Shick, J.M., Dykens, J.A., 1984. Photobiology of the symbiotic sea anemone *Anthopleura elegantissima*: photosynthesis, respiration, and behaviour under intertidal conditions. Biol. Bull. 166, 608–619.

Shick, J.M., Lesser, M.P., Stochaj, W.J., 1991. Ultroviolet radiation and photooxidative stress in zooxanthellate Anthozoa: the sea anemone *Phyllodiscus semoni* and the octocoral *Clavularia* sp. Symbio 10, 145–173.

Shumway, S.E., 1978. Activity and respiration in the anemone, *Metridium senile* (L.) exposed to salinity fluctuations. J. Exp. Mar. Biol. Ecol. 33, 85–92.

Smyth, T.J., Wright, A.E., Edwards-Jones, A., McKee, D., Queirós, A., Rendon, O., Tidau, S., Davies, T.W., 2022. Disruption of marine habitats by artificial light at night from global coastal megacities. Elem. Sci. Anth. 10, 1.

Stanley, M.C., Beggs, J.R., Bassett, I.E., Burns, B.R., Dirks, K.N., Jones, D.N., Trowsdale, S.A., 2015. Emerging threats in urban ecosystems: a horizon scanning exercise. Front. Ecol. Environ. 13, 553–560.

Suggett, D.J., Hall-Spencer, J.M., Rodolfo-Metalpa, R., Boatman, T.G., Payton, R., Tye Pettay, D., Johnson, V.R., Warner, M.E., Lawson, T., 2012. Sea anemones may thrive in a high CO2 world. Global Change Biol. 18, 3015–3025.

Tezcan, O.D., Gozer, O., 2015. Severe toxic reaction caused by a common anemone and identification of the culprit organism. J. Travel Med. 22 (4), 269–271.

Tommasi, D., stock, C.A., Hobday, a.J., Methot, R., Kaplan, I.C., Eveson, J.P., Werner, F. E., 2017. Managing living marine resources in a dynamic environment: the role of seasonal to decadal climate forecasts. Prog. Oceanogr. 152, 15–49.

Underwood, C.N., Davies, T.W., Queiros, A.M., 2017. Artificial light at night alters trophic interactions of intertidal invertebrates. J. Anim. Ecol. 86, 781–789.

Urbarova, I., Forêt, S., Dahl, M., Emblem, Å., Milazzo, M., Hall-Spencer, J.M., Johansen, S.D., 2019. Ocean acidification at a coastal CO2 vent induces expression of stress-related transcripts and transposable elements in the sea anemone Anemonia viridis. PloS one 14, e0210358.

Valenzeno, D.P., Pooler, J.P., 1987. Photodynamic action. BioScience 37, 270–276.

Verde, E., McCloskey, L.R., 2002. A comparative analysis of the photobiology of zooxanthellae and zoochlorellae symbiotic with the temperate clonal anemone Anthopleura elegantissima (Brandt) II. Effect of light intensity. Mar. Biol. 141, 225–239.

Wahl, M., 1984. The fluffy sea anemone *Metridium senile* in periodically oxygen depleted surroundings. Mar. Biol. 81, 81–86.

Wood, C., 2013. Sea anemones and corals of Britain and Ireland, 2nd ed. Wild Nature Press, Plymouth, pp. 68–131.