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Artificial light at night (ALAN) disrupts behavioural patterns of reef corals

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ABSTRACT

Increasing levels of Artificial Light At Night (ALAN) alter the natural diel cycles of organisms at global scale. ALAN constitutes a potential threat to the light-dependent functioning of symbiotic scleractinian corals, the habit-founders of warm, shallow water reefs. Here, we show that ALAN disrupts the natural diel tentacle expansion and contraction behaviour, a key mechanism for prey capture and nutrient acquisition in corals. We exposed four symbiotic scleractinian coral species to different ALAN treatments (0.4–2.5 μmol quanta m^{-2} s^{-1}). Exposure to ALAN levels of 1.2 μmol quanta m^{-2} s^{-1} and above altered the normal tentacle expansion response in diurnal species (*Stylophora pistillata* and *Duncanopsammia axifuga*). The tentacle expansion pattern of nocturnal species (*Montastraea cavernosa* and *Lobophyllia hemprichii*) was less affected, which may indicate a greater capacity to tolerate ALAN exposure. The results of this work suggest that ALAN has the potential to affect nutrient acquisition mechanisms of symbiotic corals which may in turn result in changes in the coral community structure in shallow water reefs in ALAN-exposed areas.

1. Introduction

Along with the increase in human population, coastal urban agglomerations are growing globally at unprecedented rates (Neumann et al., 2015; Sterzel et al., 2020) with more than ~40 % of the world's population residing within 100 km of coastal areas (Small and Nicholls, 2003). Along with urbanisation, the coastal infrastructure and the associated night lighting network is steadily expanding (Davies et al., 2014). Artificial light at night (ALAN) is increasing rapidly at the global scale, with irradiance and sky brightness measurements over different time scales providing rate increase estimations ~2 to ~6 % per annum (Hölker et al., 2010; Kyba et al., 2017), affecting 22 % of coastline and 35 % of marine protected areas (Davies et al., 2014; Davies et al., 2017). Amongst the ecosystems that are most affected by coastal urbanisation are coral reefs, many of which are located in shallow waters (~20–50 m depth) in close proximity to human activity (Rosenberg et al., 2022). Currently, ~13 % of the global population lives within a 100 km distance to coral reefs and population growth rates near coral reefs is higher than global averages (Sing Wong et al., 2022). Nowadays, nearly 15 % of the world's reefs are experiencing light pollution (Ayalon et al., 2021), with the most affected reefs being located in the Singapore Strait, the Gulf of Thailand, and the Persian/Arabian Gulf, where night skies tend to be ~30 % brighter than normal.

Light pollution has been identified as one of the most pervasive forms of environmental pollution (Gaston et al., 2013; Ayalon et al., 2021) because it possesses the capability to impact organisms hundreds of kilometres away from human settlements (Davies and Smyth, 2017). ALAN can disrupt daily cycles, masking natural light signals or providing misleading cues, leading to deleterious physiological and behavioural responses (Duarte et al., 2019; Rosenberg et al., 2019a; Ayalon et al., 2021; Marangoni et al., 2022; Quintanilla-Ahumada et al., 2022; Davies et al., 2023). Nowadays, many street lighting networks are transitioning from low-pressure sodium lamps to LEDs, a change that results in an increased emission of light in the environment (3–8 fold), as well as in a different quality of light (Schulte-Römer et al., 2019; Sánchez de Miguel et al., 2022). Specifically, the narrow-banded, long wavelength light of low-pressure sodium lamps is replaced by the broad, white spectrum of LED lamps with strong peaks in the blue spectral region (Sánchez de Miguel et al., 2022; Schulte-Römer et al., 2019). This is of concern to reef-building corals since they have evolved a light-driven diel rhythmicity that has remained invariant throughout geological time (Gorbunov and Falkowski, 2002). Moreover, corals are

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particularly sensitive to the prominent blue wave band of the LED spectra (Lesser et al., 2000; D'Angelo et al., 2008; Davies et al., 2014; Tamir et al., 2020). Natural cycles of light and darkness act as an exogenous factor that regulates key processes in corals, including timing (e.g., reproduction, mass spawning events; Jokiel et al. 1985; Tanner, 1996), growth (e.g., calcification; Sorek et al., 2014), metabolism (e.g., photosynthesis; Sorek et al., 2013) and behavioural patterns (e.g., feeding times and associated tentacle expansion, Hoadley et al., 2011). There is an increasing body of evidence, that ALAN can affect these processes. For instance, ALAN disrupts the natural cycle of day and night and acts as an exogenous signal, masking the endogenous circadian clock (Rosenberg et al., 2019b). Exposure to ALAN has been shown to trigger unsynchronized gamete release, decrease coral settlement success (Tamir et al., 2020; Ayalon et al., 2021) and has been associated with global disruption of coral broadcast spawning (Davies et al., 2023). ALAN can also affect coral physiology causing oxidative stress, photosynthetic impairment, loss of symbionts and reduced chlorophyll content (Ayalon et al., 2019; Levy et al., 2020).

Many reef-building corals exhibit daily cycles of tentacle expansion-contraction associated with prey capturing and nutrient acquisition (Levy et al., 2006). Corals with "nocturnal behaviour" expand their tentacles at night to capture prey (e.g., *Montastrea cavernosa*, Lasker, 1979; *Favia favus*, Levy et al., 2006) to sustain their requirements for growth and reproduction by feeding on zooplankton, bacteria and suspended matter (Goldberg, 2018). During the day, tentacles are contracted which reduces the coral's metabolic expenditure (Levy et al., 2006). Corals exhibiting "diurnal behaviour", expand their tentacles mostly during the day (e.g., *Goniopora lobata*, *Hydnophora exesa*, Levy et al., 2006). These corals often meet their energy requirements mainly through the translocation of C-rich photosynthates from their symbionts by maximising the sunlight exposure of their photosynthetic partners through the extension of their tentacles (Levy et al., 2006). A number of other species pursue mixed nutritional strategies and tend to expand their polyps and tentacles continuously (e.g., *Galaxea fascicularis*, Levy et al., 2006).

Exposure to monochromatic blue light (~400–520 nm) results in tissue contraction (Levy et al., 2003), suggesting that ALAN might actually influence the regulation of tentacle expansion and contraction with potential detrimental consequences for the feeding and nutrient acquisition process of both diurnal and nocturnal corals.

The mechanisms regulating tentacle expansion and contraction remain unknown, but it is assumed that the endogenous circadian clock, and exogenous cues such as light, nutritional stimuli (prey size and density) and flow speed (Levy et al., 2001; Palardy et al., 2005; Sorek et al., 2014) could be involved in the regulation. We exposed four coral species to a series of experiments under controlled laboratory conditions to study the effect of four different ALAN regimes on tentacle expansion behaviour. We used two diurnal (*Stylophora pistillata and Duncanopsammia axifuga)*, and two nocturnal (*Montastraea cavernosa* and *Lobophyllia hemprichii)* coral species. The range of ALAN intensities applied in the experiments (0.4 to 2.5 μmol quanta m^{-2} s^{-1}, ~5–35 lx) is realistic for ALAN levels in light polluted coral reefs (Ayalon et al., 2019). Given that tentacle expansion behaviour in corals can be either diurnal or nocturnal, our work was guided by three hypotheses: (i) The diel tentacle expansion behaviour will be disturbed by ALAN, (ii) diurnal coral species will expand their tentacles at night in response to ALAN exposure, (iii) nocturnal species will contract their tentacles at night when they are exposed to ALAN.

2. Methods and material

2.1. Coral culture

The experimental corals were cultured and propagated by fragmentation in the experimental coral mesocosm facility of the Coral Reef Laboratory at the University of Southampton (D'Angelo and Wiedenmann, 2012; D'Angelo et al., 2012). Corals were kept under nutrient-replete conditions (NO_3 ~ 12 μM, PO_4 ~ 3 μM) in 3 separate compartments of a 230 l flow through aquarium connected to the main coral mesocosm system (2500 l). Replicate coral samples were produced by fragmentation for each of the four experimental species. Coral fragments were attached to ceramic tiles using two-component epoxy resin (D-D Aquascape; D-D The Aquarium Solution Ltd., Ilford, UK) and allowed to regenerate for >4 weeks prior to the acclimation period at the start of the experiments. Corals were fed twice per week during the experimental night on non-measurement days with live rotifers and *Artemia* nauplia (Wijgerde, 2013). At the start of the experiments, the system was isolated from the room light by black-out curtains. Corals were acclimatised for 4 weeks to a reverse 12-h light/dark cycle prior to the start of the measurements to facilitate dark-hour data collection during daytime. The experimental "day" was set from 19:15 to 07:15 UTC and the experimental "night" was set from 07:15 to 19:15 UTC. White daylight was simulated with metal halide lamps (150 W ArcaAqualine 10,000, Aqua Medic, Germany), exposing the corals to a light intensity of ~130 μmol m^{-2} s^{-1} during the day hours. Turbulent flow was generated with Turbelle® nanostream® 6045 pumps (Tunze, Penzberg, Germany), operated at a flow rate of 4500 l/h. Temperatures (~27 °C) and salinity (~33 psu) were monitored regularly and kept constant during the experimental period.

2.2. Recording of tentacle expansion status

Corals were photographed underwater with a digital Olympus Tough F2.0 camera to record the polyp and tentacle expansion status. Semi-quantitative photographic analyses of tentacle expansion-contraction responses were scored on an arbitrary scale based on Lasker, 1979 (Table 1, Fig. 1), ranging from 0 to 4, where "1" represents corals who exhibit fully closed polyps, contracted oral tissue and no visible tentacles, to "4" representing corals exhibiting full polyp and tentacle expansion.

2.3. Tentacle expansion behaviour under control conditions (no ALAN)

The tentacle expansion responses were recorded on 24 days over a period of 120 days. The expansion status was assessed for all experimental corals at hourly intervals, starting 2.5 h before and ending 2.5 h after the simulated night period.

2.4. ALAN exposure experiments

ALAN was provided by full-spectrum white light LED strips (Supplementary Materials, AquaRay©, BioLumen, TMC London, UK). Experimental ALAN exposure duration at night was chosen based on Davies et al., 2017, while light levels range within the variability of coastal ALAN (Gaston et al., 2013; Ayalon et al., 2019). The different experiments featured ALAN intensities of 0.4, 1.2, 1.7 and 2.5 μmol quanta m^{-2} s^{-1} (~0 to 35 lx, Table S1). ALAN exposure started 3 h into the experimental night to allow the corals to adopt their regular tentacle

Table 1
Classification of polyp and tentacle extension behaviour.

Score	Visual appearance
1	**Full polyp and tentacle contraction** (all polyps closed, polyp tissue contracted, no tentacles visible)
2	**Weak partial tentacle expansion** (polyp tissue slightly expanded, some tentacles visible but not well extended)
3	**Strong partial tentacle expansion** (polyps open, polyp tissue expanded, most tentacles visible but only partially extended)
4	**Full tentacle expansion** (polyps fully expanded, tentacles fully extended)

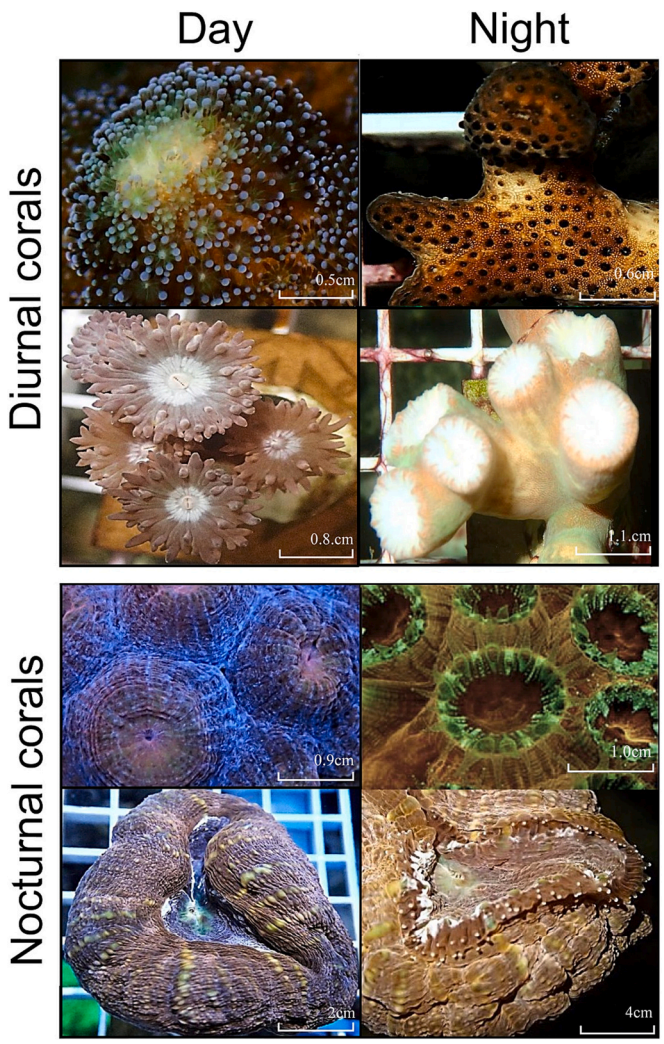

Fig. 1. Polyp and tentacle expansion behaviour in the diurnal (*S. pistillata*, 1st row, *D. axifuga*, 2nd row), and nocturnal (*M. cavernosa*, 3rd row, *L. hemprichii*, 4th row) model coral species used in the study during night and day. Each species is shown in their fully contracted and fully expanded state.

expansion status prior to the treatment. ALAN light intensity was ramped up and down over 15 min at the beginning and end of the treatment, to avoid sudden changes in light levels. The following ALAN regimes were applied:

2.5. Experiment 1 (single exposure to increasing ALAN intensities)

During a period of 12 weeks, experimental corals were exposed on 24 randomised days to a gradual ALAN intensity increase from 0 to 2.5 μmol quanta m^{-2} s^{-1} at 1.5 h intervals for 6 h. Exposure days were randomised to avoid habituation effects. Tentacle expansion was scored on ALAN exposure days ($n = 6$ observation days).

2.6. Experiment 2 (single exposure to fixed ALAN intensities)

To differentiate the effects of different ALAN intensities and to define a specific response threshold, corals were exposed on two randomised days per week over an experimental period of 4 weeks to ALAN of defined intensity for 6 h. The treatment days were separated by at least one non-treatment day in. Exposure levels were 0.4 μmol quanta m^{-2} s^{-1} in weeks 1–4, 1.2 μmol quanta m^{-2} s^{-1} in weeks 5–8, and 2.5 μmol quanta m^{-2} s^{-1} in weeks 9–12. Polyp and tentacle scores were recorded on every ALAN exposure day ($n = 8$ observation days per ALAN intensity).

2.7. Experiment 3 (continuous long-term exposure to 1.2 μmol quanta m^{-2} s^{-1} ALAN)

Over a period of 3 weeks, corals were exposed every night to ALAN with an intensity of 1.2 μmol quanta m^{-2} s^{-1}. The tentacle expansion response was recorded on four consecutive days per week ($n = 12$ observation days).

2.8. Statistical analysis

All statistical analyses were performed in R (version 4.0.3, R Core Developmental team). Generalized linear mixed effect analysis (GLMM) with a Gaussian error distribution were used to compare the effects of ALAN treatments on the polyp and tentacle expansion score data using the *lme4* package (Bates et al., 2015). The GLMMs enabled the identification of any independent or interaction effects between fixed terms: ALAN Treatment, Coral Species, and Experimental Time (Table S2-S7). Depending on the model, Time and the identity of coral colonies were incorporated into each GLMM as a random-effect term. This accounted for any random variation in response variables which could have resulted from the different experimental colonies. Raw data score values were used rather than percentage change. Visual inspection of residual plots (Q-Q plot) did not reveal any obvious deviation from homoscedasticity or normality. The car package (version 3.0–12) was used to carry out Type II Wald chi-square tests (analyses of deviance) on each GLMM. A P-value < 0.05 was considered statistically significant.

3. Results

3.1. Natural diel tentacle rhythmicity

We first determined the polyp and tentacle expansion-contraction activity in the absence of ALAN. We cultured two diurnal species (*Stylophora pistillata* and *Duncanopsammia axifuga*) and two nocturnal species (*Montastraea cavernosa* and *Lobophyllia hemprichii*) under laboratory conditions under a 12:12 h light/dark cycle to represent a standard equatorial light regime. The tentacle expansion behaviour was quantitatively assessed using an observer-based scoring system (Table 1). The scores of this system ranged from "1", representing contracted polyps with contracted oral tissue and no visible tentacles (Fig. 1), to "4", indicative of corals with maximal polyp and tentacle expansion (Fig. 1). Over 16 weeks, coral species showed either diurnal or nocturnal tentacle expansion behaviour: *S. pistillata* and *D. axifuga* expanded their polyps and tentacles consistently during the day and contracted them at night (diurnal species). On the contrary, *M. cavernosa* and *L. hemprichii* expanded their polyps and tentacles during the night and stayed mostly contracted during the day (nocturnal species). Diurnal species started to retract their tentacles at the simulated sunset (SS), reaching a fully closed state 2-3 h after sunset. After staying contracted throughout the night, tentacles started to expand already ~1 h before the simulated sunrise (SR) (Fig. 2). On the contrary, nocturnal species show a gradual increase in expansion throughout the night (Fig. 2).

3.2. ALAN effects on tentacle expansion behaviour

To investigate whether ALAN can disturb the diel rhythm of corals with diurnal or nocturnal tentacle expansion behaviour, we exposed our model corals every night to a gradual ALAN increase from 0.4 to 2.5 μmol quanta m^{-2} s^{-1} (~ from 5 to 35 lx) over a period of 6 h. Over 12 weeks, all coral species expanded their tentacles under this gradual increase in ALAN, regardless of whether corals exhibited diurnal or nocturnal behaviour. A generalized linear mixed model (GLMM) revealed that in diurnal species, ALAN exposure caused a shift from the baseline behaviour, in which polyps and tentacles are mostly completely

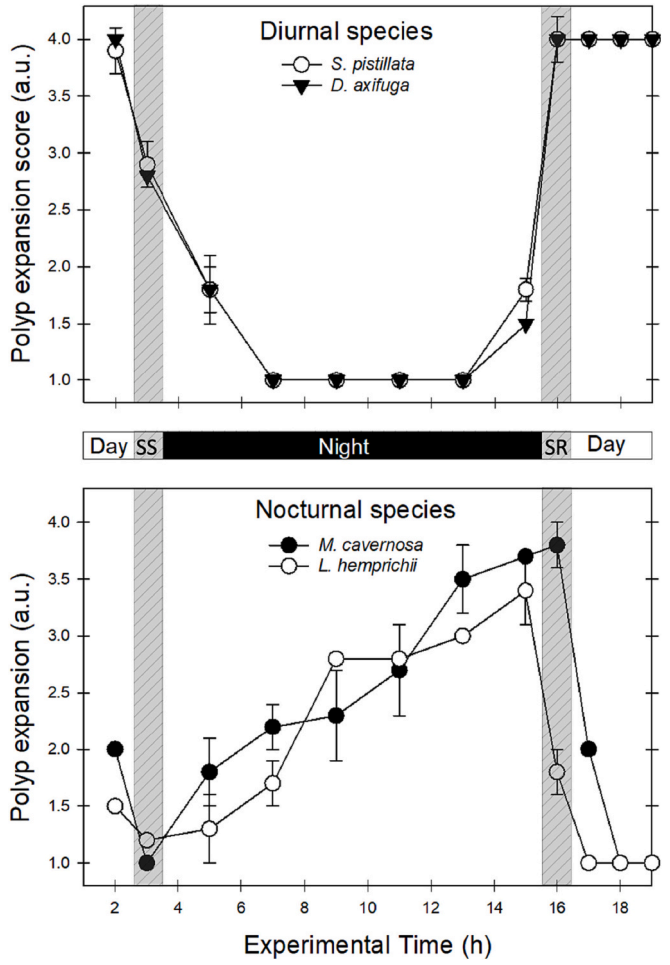

Fig. 2. Polyp and tentacle expansion behaviour of control corals in the absence of ALAN. Data points show the means of corresponding timepoints collected on 6 different measuring days ($n = 6$). Error bars denote means of ± SD. Upper panel: diurnal species (*S. pistillata*, *D. axifuga*). Lower panel: nocturnal species (*M. cavernosa*, *L. hemprichii*). Polyp expansion scores refer to Table 1. Grey shaded bars indicate the time points when the white daylight was switched off and on ("SS", experimental sunset; "SR", experimental sunrise).

contracted at night to a state of gradual tentacle expansion (Fig. 3a) ($\chi2(3) = 572.4$, $p < 0.0001$; Table S2). There was a significant interaction effect of ALAN exposure and coral species ($\chi2(4) = 94.4$, $p < 0.0001$). At ALAN intensities of ≤1.2 µmol quanta m^{-2} s^{-1} (10 lx), both diurnal species (*D. axifuga and S. pistilla*) did not show any significant tentacle expansion ($p > 0.05$). At the higher ALAN intensities (1.7 and 2.5 µmol quanta m^{-2} s^{-1}), *D. axifuga* expanded their polyps and tentacles completely, while to *S. pistillata* exhibited only partial tentacle expansion ($p < 0.05$). In contrast, nocturnal species expanded their tentacles regardless of the exposure to different ALAN intensities ($\chi2(3) = 422.8$, $p < 0.001$; Table S3), maintaining the same diel tentacle rhythmicity as the controls (Fig. 3b). Also, the slight, yet significant, differences between the species, similar to the control conditions, were retained under ALAN exposure ($\chi2(4) = 208.244$, $p < 0.001$). Specifically, *L. hemprichii* showed a higher expansion score at the end of the 6 h observational period compared to *M. cavernosa* ($p < 0.05$).

3.3. Effects of fixed ALAN intensities

To differentiate between the effects of ALAN intensity and the exposure time, three sets of experimental corals were treated independently every night with distinct ALAN intensities (0.4, 1.2 and 2.5 µmol quanta m^{-2} s^{-1}) over a period of 4 weeks. Both, diurnal and nocturnal coral species showed an increasing tentacle expansion trend over the 6-hour of ALAN exposure (diurnal: $\chi2(1) = 284.2$, $p < 0.0001$, Table S4; nocturnal: ($\chi2(1) = 69.3$, $p < 0.001$, Table S5; Fig. 4). In diurnal corals, there was a significant interaction effect of ALAN intensity and species ($\chi2(3) = 253.5$, $p < 0.0001$). At low-ALAN levels (~0.4 µmol quanta m^{-2} s^{-1}), diurnal corals showed no significant response to low-ALAN levels (Fig. 4a); however, at higher ALAN intensities (over 1.2 µmol quanta m^{-2} s^{-1}; Fig, 4bc) corals partially expanded their polyps and tentacles ($p < 0.05$; Fig. 4bc). At 1.2 µmol quanta m^{-2} s^{-1}, corals showed the largest increase in the mean tentacle expansion; with *D. axifuga* exhibiting a stronger tentacle response in comparison with *S. pistillata* ($p < 0.001$). As in the controls, both nocturnal species displayed a gradual increase in tentacle expansion over time at all ALAN intensities (Fig. 4d–f), reaching high expansion scores towards the end of the observational period ($\chi2(1) = 69.32$, $p < 0.001$).

3.4. Effects of constant ALAN exposure

Considering the clear change in tentacle expansion behaviour shown by the diurnal species under 1.2 µmol quanta m^{-2} s^{-1}, this condition was chosen to test the long-term effects of continuous ALAN exposure over a period of 3-weeks (Fig. 5). Over the course of the 6-hour ALAN treatment, diurnal corals showed significantly increased levels of polyp and tentacle expansion compared to untreated controls ($\chi2(1) = 13.37$; $p < 0.001$; Fig. 5a, Table S6), with maximal differences being reached at the end of the exposure period ($p < 0.05$). Nocturnal corals showed less polyp and tentacle expansion over the first 3 h of ALAN exposure compared to the controls, yet these differences were not significant ($\chi2$

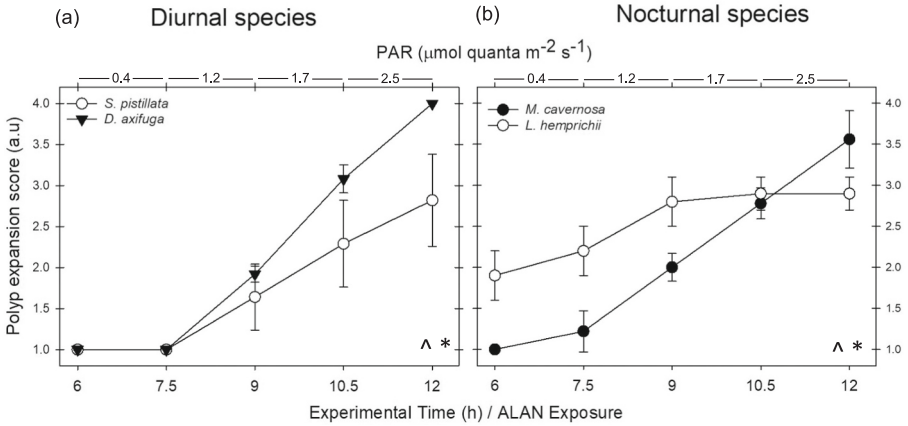

Fig. 3. Effects of exposure to increasing ALAN intensities (0 to 2.5 µmol quanta m^{-2} s^{-1}) on the polyp and tentacle expansion behaviour of diurnal and nocturnal corals during 6-hours of exposure during the night hours of isolated days. Data points show the means of corresponding timepoints collected on 8 different measuring days ($n = 8$). Error bars denote means of ± SD. **(a)** diurnal species (*S. pistillata, D. axifuga*). **(b)** Nocturnal species (*M. cavernosa, L. hemprichii*). Polyp expansion scores refer to Table 1. Symbols represent GLMM significance at the 0.05 probability level for the fixed effects "ALAN treatment" (^) and "coral species" (*).

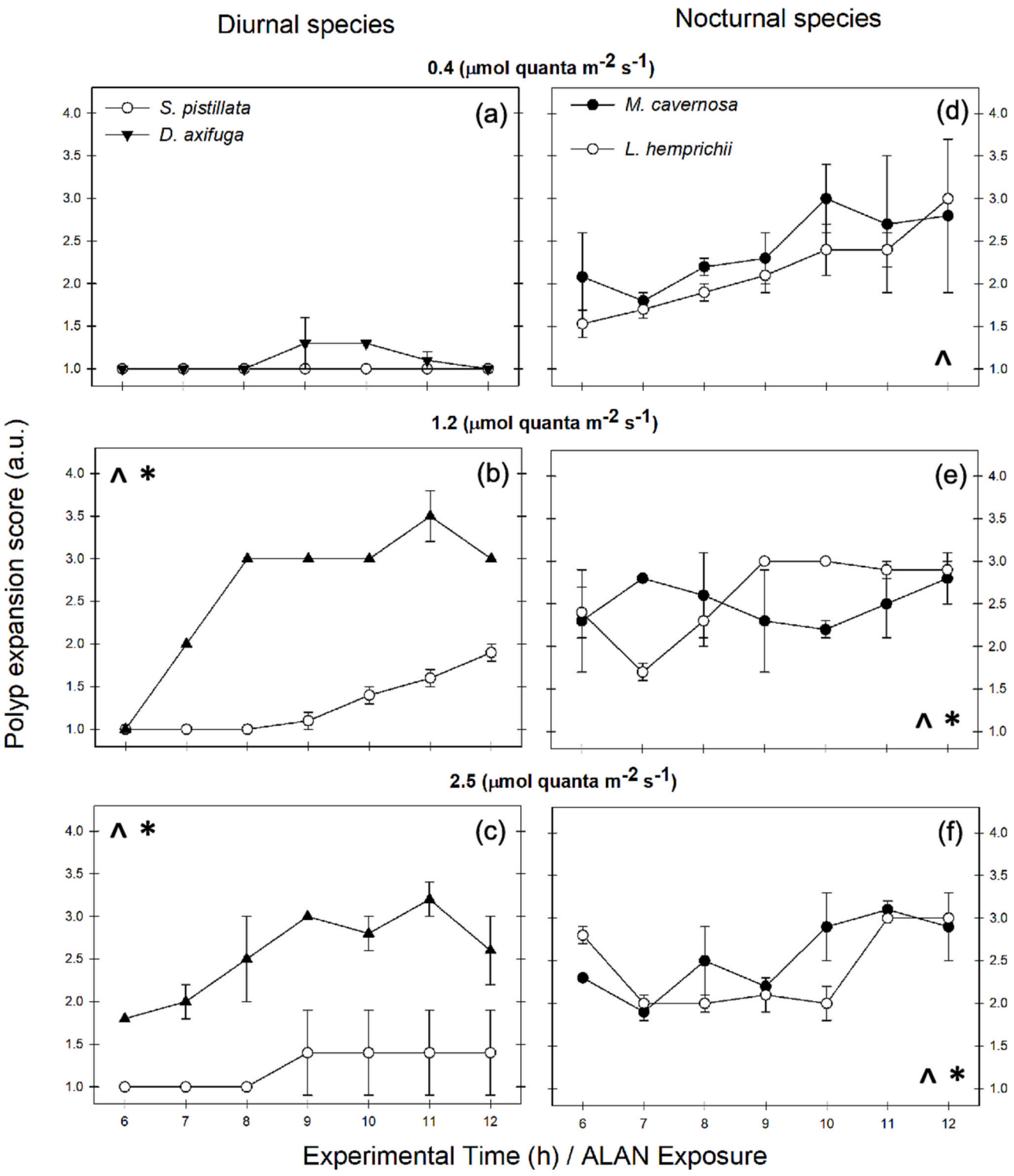

Fig. 4. The effect of exposure to fixed ALAN intensities (0.4, 1.2 and 2.5 μmol quanta m^{-2} s^{-1}) on the polyp and tentacle expansion behaviour of diurnal and nocturnal corals during 6-hours of exposure during the night hours of isolated days. Data points show the means of corresponding timepoints collected on 4 different measuring days ($n = 4$). Error bars denote means of ± SD. **(a–c)** diurnal species (*S. pistillata, D. axifuga*). **(d–f)** nocturnal species (*M. cavernosa, L. hemprichii*). Polyp expansion scores refer to Table 1. Symbols represent GLMM significance at the 0.05 probability level for ALAN treatments (^) and (*) coral species fixed effects.

(1) = 13.635; $p > 0.05$, Fig. 5b, Table S7). After this initial period, the expansion of the ALAN-exposed corals was comparable to the control corals ($\chi 2(1) = 37.864$; $p > 0.05$). There was no species-specific difference in the responses to ALAN within each coral group. The results of this 1.2 μmol quanta m^{-2} s^{-1} ALAN treatment suggest that the response of diurnal species was influenced by the length of daily exposure. In contrast, nocturnal species showed no significant response to the treatment under the present experimental conditions.

4. Discussion

Polyp and tentacle expansion and contraction are key processes for

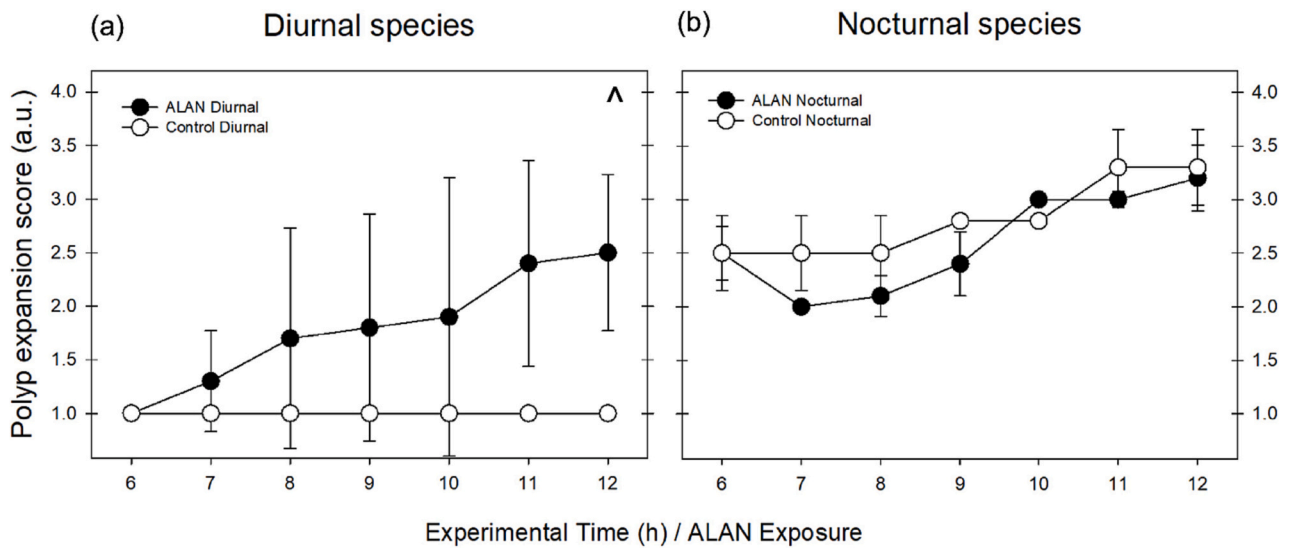

Fig. 5. Effects of continuously repeated exposure to 1.2 μmol quanta m^{-2} s^{-1} ALAN on the polyp and tentacle expansion behaviour of diurnal and nocturnal corals during 6-hours of exposure during the night hours over a 6-hour period for 3 weeks. Data points show the means of corresponding timepoints collected on 12 different measuring days (controls; $n = 12$) and 6 measuring days (ALAN treatment, n = 6). Error bars denote means of ± SD. **(a)** diurnal species (*S. pistillata*, *D. axifuga*). **(b)** nocturnal species (*M. cavernosa*, *L. hemprichii*). Polyp expansion scores refer to Table 1. (^) symbol represents GLMM significance at the 0.05 probability level for ALAN treatment fixed effects.

nutrient acquisition, tissue gas exchange and prey capture in symbiotic, reef-building corals (Levy et al., 2001; Levy et al., 2003; Levy et al., 2006). Disruptions in the diel tentacle activity can potentially affect the ability of corals to meet their energetic requirements and acquire sufficient nutrients to sustain growth and reproduction. Here, we demonstrate that ALAN acts as an exogenous cue that changes the natural day and night tentacle expansion behaviour in diurnal coral species. The tentacle response to ALAN shows species-specific patterns. Furthermore, our experiments indicate that ALAN exposure of ~1.2 μmol quanta m^{-1} s^{-1} (10 lx) represents a critical threshold controlling tentacle expansion behaviour. Establishing threshold values is important for strategic planning of urban development and mitigation of light pollution in proximity of coral reefs.

4.1. 24-h Coral tentacle rhythmicity: nocturnal and diurnal behaviour

The diurnal corals *S. pistillata* and *D. axifuga* expanded their tentacles during the day and contracted them at night, exhibiting a clear shift in tentacle activity around the experimental sunset and sunrise.

Previous research has suggested a link between the photosynthetic activity of the symbionts and the tentacle expansion state (Lasker, 1979; Levy et al., 2003; Levy et al., 2006). Corals exhibiting high photosynthetic activity expanded their tentacles during the day, promoting efficient light absorption by the symbionts (e.g. *Goniopora lobata*, Levy et al., 2003). Furthermore, the expansion of the tentacles during the day may aid the diffusion of excess oxygen away from the photosynthesizing coral tissues and reduce local hyperoxia by increasing the surface area of tissue gas exchange (Shick, 1990). The increased photosynthetic activity in diurnal corals suggests a greater reliance on photosynthates (i.e., C-rich compounds) being transferred from the symbiont to the host to meet the energetic requirements of the latter. Indeed, isotopic analysis has revealed lighter δ13C signatures in corals exhibiting diurnal tentacle expansion behaviour, indicating that the major source of carbon is supplied by the symbiotic algae (Levy et al., 2006).

On the contrary, the nocturnal corals *M. cavernosa* and *L. hemprichii* expanded their tentacles mostly at night, exhibiting a change in tentacle and polyp expansion around the times of the simulated sunset and sunrise. It has been proposed that nocturnal corals expand their tentacles to feed on plankton at night (Levy et al., 2006), which is more abundant during the dark hours (Brierley, 2014). Again, isotopic analysis conducted on the nocturnal species *Favia favia* and *Lobophyllia* sp. revealed heavier δ13C signatures supporting the notion that these corals have a greater reliance on feeding on particulate organic matter for nutrient acquisition (Levy et al., 2006). Tentacle contraction during the day may aid these nocturnal corals to reduce respiration and save energy during the day (Levy et al., 2006). Furthermore, in the nocturnal species *Favia favus* and *Plerogyra sinuosa*, lower symbiont densities in their tentacles have been associated with nocturnal tentacle expansion (Levy et al., 2003).

4.2. ALAN triggers tentacle expansion in diurnal corals

In our study, diurnal corals changed their normal tentacle expansion behaviour, exhibiting increased tentacle expansion along with increasing ALAN intensities in the range from 1.2 to 2.5 μmol quanta m^{-1} s^{-1}, with full polyp and tentacle expansion being reached at the highest ALAN level. When the diurnal corals were exposed to fixed ALAN levels of 0.4 μmol quanta m^{-1} s^{-1}, no significant change in tentacle expansion could be detected. In contrast, a clear change in tentacle expansion behaviour could be recorded at 1.2 μmol quanta m^{-1} s^{-1} and above. ALAN-driven disruption of behavioural and physiological processes have already been observed in other marine organisms (Duarte et al., 2019; Quintanilla-Ahumada et al., 2022). For example, the isopod *Tylos spinulosus* and the talitrid *Orchestoidea tuberculate* suffered a significant reduction in their locomotion activity when they were exposed to ALAN levels of ~4.5 μmol quanta m^{-1} s^{-1} (Luarte et al., 2016; Duarte et al., 2019). These species only emerge at night to feed, however, when they were exposed to ALAN, they remained most of the time buried in the sediments. After a few days of ALAN exposure, *Tylos spinulosus* started to emerge during daytime, a behaviour that has never been observed in the field. In symbiotic corals, biological processes synchronized by moonlight are most affected by ALAN (Tamir et al., 2020; Ayalon et al., 2021; Lin et al., 2021). Ayalon et al. (2021) demonstrated that ALAN interfered with the natural periodic solar and lunar illumination, de-synchronizing the gametogenesis cycle and gamete release, and disrupting the rhythmicity of the biological clock in two *Acropora* coral species, *A. millepora* and *A. digitifera*. Similarly, Rosenberg et al. (2019a) conducted transcriptomic analysis and found that ALAN (1.5 to 2 μmol quanta m^{-1} s^{-1}) de-synchronizes rhythmic processes of circadian genes and hormones in *Acropora eurystoma* and

altered gene expression patterns associated with symbiont photosynthesis, coral growth and cell proliferation.

Both, corals and their photosynthetic symbionts are highly photosensitive. They are able to detect light in the visible spectral range, specifically in the blue (425–450 nm) and red (600–700 nm) spectral region, including the very low levels of blue light irradiation provided by moonlight (Gorbunov and Falkowski, 2002; Levy et al., 2007). Symbiont photosynthesis is dependent on sunlight, and accordingly driven by natural day and night cycles. Symbionts photosynthesis has been suggested to stimulate tentacle expansion in diurnal corals (Levy et al., 2006). Since the photosynthetic machinery can theoretically function at irradiance levels slightly above those provided by moonlight (Raven and Cockell, 2006), it is possible that ALAN has triggered tentacle expansion in our experiments through low level photosynthesis by the symbionts. However, even if ALAN can be used by the coral symbionts for photosynthesis, the production of photosynthates will be low compared to regular daylight photosynthesis (Grubisic, 2018). Since tentacle expansion is an energy-demanding process (Pearse, 1974; Lasker, 1981; Levy et al., 2006), it is questionable whether the low energetic gain through ALAN-driven photosynthesis of the symbionts is sufficient to compensate for the energetic costs of night time tentacle expansion by the host. Indeed, oxygen uptake measurements revealed that coral species exhibiting diurnal behaviour, e.g., *Goniopora lobata*, increased their respiration rates by ~35 % when they extend their tentacles during the day (Levy et al., 2006). Therefore, the untimely expansion of tentacles at night by diurnal corals may result in a negative energy budget that could have negative effects on their productivity, especially if the corals are resource-limited.

Furthermore, coral symbionts require periods of darkness for the repair of their photosynthetic machinery (Hill et al., 2011). Indeed, the exposure of *Acropora eurystoma and Pocillopora damicornis* to ALAN levels of 0.15 μmol quanta m^{-1} s^{-1}, resulted in a decrease in photosynthetic capacity (i.e., photosynthetic efficiency and electronic transporter rate), low symbiont densities and high oxidative stress (Ayalon et al., 2019). This was also corroborated by Levy et al., 2020, who observed a significant decrease in symbiont photosynthetic rates, photosynthetic pigment content and elevated levels of oxidative stress after 8 weeks of ALAN exposure. The accumulation of reactive oxygen species (ROS) in the thylakoid membrane due to high light exposure is one of the first signals of photoinhibition, which can lead to coral bleaching (Suggett and Smith, 2019). Therefore, exposure to ALAN may cause impairments in symbiont physiology which in the long term could negatively affect the coral-dinoflagellate symbiosis.

4.3. ALAN effects on nocturnal corals

Our results suggest that the nocturnal species were not affected by the exposure to ALAN since they continued to gradually expand their tentacles over the course of the night. Previous research has observed tentacle contraction when nocturnal corals were exposed to light intensities of ~10–30 μmol quanta m^{-1} s^{-1} (Levy et al., 2003). Our experimental ALAN levels ranging from 0.4 to 2.5 μmol quanta m^{-1} s^{-1} were considerably lower to simulate environmentally relevant ALAN intensities over light-polluted areas (Ayalon et al., 2021), which may explain the less pronounced response of our nocturnal model corals. Nocturnal coral species have been shown to harbour lower symbiont densities in their tentacles compared to diurnal species (Levy et al., 2003). Considering that symbiont photosynthesis may be involved in modulating the tentacle expansion behaviour (Levy et al., 2003), the lower ALAN intensities in combination with lower symbiont numbers may result in response threshold levels not being reached under our experimental conditions. On the other hand, since symbiont photosynthesis is not the main driver for tentacle expansion in nocturnal corals, these species may use alternative regulation mechanisms, for instance on light-entrained circadian clock cycles relying on photoreceptors of the host (Levy et al., 2007; Schmal et al., 2020).

4.4. Implications for coral survival

ALAN is increasingly recognised as a stress factor for marine ecosystems with a high potential to change the community structure and function of coastal ecosystems (Davies et al., 2014; Tidau et al., 2021; Davies et al., 2023). Our findings demonstrate that ALAN can alter the diel tentacle expansion behaviour of diurnal corals. Diurnal corals showed a clear, untimely expansion towards the end of the experimental night. The increased expansion will raise the energy demand of the corals. This may result in a negative energy budget specifically for diurnal coral species with a greater reliance on symbiont photosynthesis to meet their energy demands, since low intensity ALAN may not promote photosynthesis to a level sufficient to compensate for the increased energy consumption. Furthermore, the untimely expansion of tentacles may result in corals not being able to access their preferred food in the optimal time window (Goldberg, 2018).

Nocturnal corals continued to increase their polyp and tentacle expansion over the course of the night despite ALAN exposure, showing no significant deviation from the behavioural pattern of the control corals. However, since ALAN can prevent the night-time migration of some species of zooplankton from deep to shallow water (Brierley, 2014; Berge et al., 2020; Marangoni et al., 2022), the timely expansion of tentacles may still result in an energy deficit as zooplankton prey becomes less abundant due to the ALAN impact. Over time, the energy drain potentially caused by ALAN, may add to other stressors experienced by corals in urbanized coastal environments such as nutrient enrichment and reduced water quality (D'Angelo and Wiedenmann, 2014). Under the overarching impact of global warming (Heron et al., 2016), ALAN could contribute together with other local stressors to the global decline of coral reefs, and hence, the declining provision of ecosystem services that affects the food and livelihood security of millions of people. To reduce stress to coral reefs, especially near coastal urbanized areas, ALAN levels should be kept well below the value of ~1.2 μmol quanta m^{-1} s^{-1} (~10 lx) at which corals showed already a significant deviation from their normal tentacle and polyp expansion pattern.

CRediT authorship contribution statement

Conceived and developed the study (JW and CDA with input from TD), Designed the aquarium experiments and the experimental set up (CDA, JW), Collected Data (JL), Analysed data (MLM), Discussed Data (All authors), Wrote manuscript (MLM, JW, CDA with input from all authors), Acquired funding (TD, JW, CDA).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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