Light pollution alters the skeletal morphology of coral juveniles and impairs their light capture capacity

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Abstract

Urbanization and infrastructure development have changed the night-time light regime of many coastal marine habitats. Consequently, Artificial Light at Night (ALAN) is becoming a global ecological concern, particularly in nearshore coral reef ecosystems. However, the effects of ALAN on coral architecture and their optical properties are unexplored. Here, we conducted a long-term *ex situ* experiment (30 months from settlement) on juvenile *Stylophora pistillata* corals grown under ALAN conditions using light-emitting diodes (LEDs) and fluorescent lamps, mimicking light-polluted habitats. We found that corals exposed to ALAN exhibited altered skeletal morphology that subsequently resulted in reduced light capture capacity, while also gaining better structural and optical modifications to increased light levels than their ambient-light counterparts. Additionally, light-polluted corals developed a more porous skeleton compared to the control corals. We suggest that ALAN induces light stress in corals, resulting in a decrease in the solar energy available for photosynthesis during daytime illumination.

1. Introduction

Natural light cycles, including sunlight and moonlight, play a crucial role in regulating various physiological, biological, and behavioral processes in reef-building corals (Iluz and Dubinsky, 2015; Kaniewska et al., 2015). The increase in urbanization along coastal areas is exposing marine environments to excessive anthropogenic light sources (Gaston et al., 2015; Rosenberg et al., 2019; Tamir et al., 2017). The potential damage caused by these artificial lights to various ecosystems is commonly termed 'ecological light pollution' (Longcore and Rich, 2004). The negative impact of artificial light at night (ALAN) on coastal and marine environments has only recently been recognized as a novel environmental stressor (Davies and Smyth, 2018; Tidau et al., 2021). Research on the effects of widespread ALAN exposure on marine fauna is limited compared with studies on terrestrial organisms (Davies et al., 2014; Falcón et al., 2020; Hölker et al., 2010). For tropical reef-building corals, artificial lighting could constitute a major perturbation to nocturnal light regimes, as it disrupts the natural photoperiod cycle of light and darkness (Lynn and Quijón, 2022; Marangoni et al., 2022). Consequently, ALAN affects crucial processes synchronized with the diel light-dark cycle of corals, including metabolism and photophysiology (Ayalon et al., 2021a, 2019; Rosenberg et al., 2019; Tamir et al., 2020) as well as gametogenesis and spawning synchronicity (Ayalon et al., 2021b). Recently, light pollution has been shown to induce photoinhibition and oxidative stress in symbiotic corals (Levy et al., 2020) and might thus play an important role in modulating the ecophysiology of corals in urban environments.

Solar radiation plays a key role in controlling the physiology and morphology of corals due to the mutualistic symbiosis between the coral host and their photosynthetic dinoflagellate algae (family: Symbiodiniaceae) (Roth, 2014). Coral have thus adapted to optimize their light capture mechanisms to enhance the symbiotic relationship in response to varying light quantities (i.e., intensity) and qualities (i.e., spectrum) (Hoogenboom et al., 2008; Iluz and

Dubinsky, 2015; Kahng et al., 2019). For example, corals are well adapted to the harsh irradiance conditions experienced in shallow-water coral reefs (Wangpraseurt et al., 2014) through a range of structural and physiological adaptations, including the modulation of skeletal architecture and host tissue thickness (Kramer et al., 2022b; Wangpraseurt et al., 2012), as well as the synthesis of photoprotective animal host proteins that modulate light capture and photosynthesis (Lyndby et al., 2016; Salih et al., 2000). Typically, corals exposed to high-light conditions have a greater ability to cope with excess light, whereas corals residing in low-light environments exhibit highly efficient photosynthetic performance (Einbinder et al., 2016; Kramer et al., 2022c; Martinez et al., 2020).

Similar to corals, plant morphology, growth, and development are influenced by light-driven factors, including day length, light intensity, and light quality (Cope and Bugbee, 2013; Lee et al., 2007). For instance, some plant species have shown changes in leaf size and morphology upon exposure to ALAN (Wang et al., 2015; Zheng and Van Labeke, 2017). However, although extensive research has demonstrated the effects of light pollution on plant morphology, the impact of these effects on calcifying organisms, apart from corals, remains relatively unexplored. Nevertheless, a study conducted by Rocha et al. (2014) demonstrated how different spectral distributions of light can influence coral skeletal architecture at macro- and micro-scales. That study has shown that corals grown under different light spectra during the day (photoperiod of 12-hr light: 12-hr dark), emitting the same photosynthetically active radiation (PAR), exhibited significant morphological variability (i.e., corallite diameter, septal length, etc.) in two symbiotic scleractinian coral species. Despite this finding, the full extent of the effect of nocturnal light pollution on the morphological traits and ecophysiological responses of corals remains largely unknown.

Here, we investigated whether light pollution could lead to changes in coral skeletal morphology and optical properties, thereby affecting their ability to effectively capture light.

We conducted a comparative study of *Stylophora pistillata* coral juveniles that grew under three light conditions (control and two different artificial light treatments) over a period of 30 months starting from settlement. The altered night-time light regime over the long term led to significant changes in skeletal morphology, algal physiology, and skeletal reflectance, indicating a host-level response to light-induced stress. Since photosynthesis is a fundamental process that enables the growth and survival of reef corals, any decline in this process could disrupt the entire coral reef ecosystem. We thus discuss the potential undesirable decline in photosynthetic performance by ALAN exposure in coral reefs.

2. Materials and Methods

2.1 Study species and collection

Since the shallow waters are in close proximity to the shore, corals at these depths are significantly more exposed to artificial illumination than deeper ones. *Stylophora pistillata* corals are interesting to consider with respect to ALAN, as this species dominates the shallow waters of the Gulf of Eilat/Aqaba (GoE/A), the Red Sea (29.50°N, 34.92°E), from juveniles to adults (Kramer et al., 2020, 2019; Loya, 1976). It is worth noting that on a global scale, the northern coast of the GoE/A has been identified as a heavily light-polluted area, with Eilat's reef night sky brightness being on average 470% brighter than the natural night sky (Ayalon et al., 2021b; Tamir et al., 2017), thus making it a fundamental location for studying the effects of ALAN on coral species.

The study by Tamir et al. (2020) provided the *S. pistillata* coral juveniles used in this study. Briefly, planulae were collected in front of the Interuniversity Institute for Marine Sciences in Eilat (IUI) at shallow-water depths (< 5 m) to avoid phenotypic variations caused by different light or flow environments. The planulae have settled in three separate open-circuit seawater tables (i.e., no water exchanged between them; Fig. 1): a control (ambient conditions

126 at night – moonlight only) and two light pollution treatments with distinct spectra in the visible
127 light wavelengths, which simulated the most common city lighting methods (LED and
128 fluorescent lamps; Tamir et al. (2017)). The lamps were turned on and off daily using a
129 photocell sensor, illuminating the same nighttime irradiance levels as those found in nearshore
130 artificial lighting systems in Eilat (1×10−6 μmol photons m^{-2} s^{-1}; Tamir et al., 2017). For
131 further details on the experimental setup (e.g., light parameters and spectrum), please see
132 Methods S1 and Fig. S1. The coral juveniles that survived post-settlement mortality were
133 maintained and monitored under controlled conditions at the IUI from June 2017 to December
134 2019.
135
136 *2.2 Cell density and chlorophyll-a extraction of microalgae symbionts*
137 After two and a half years of growth, ten intact juvenile colonies were randomly
138 sampled from each treatment to determine cell density and chlorophyll-*a* content. Their tissue
139 was removed using an airbrush at high pressure with 0.2 nm filtered seawater. Subsequently,
140 the skeletons were bleached in a 6% sodium hypochlorite solution for 24 h, thoroughly rinsed
141 with deionized running water to remove the remaining organic matter, and then left to dry at
142 room temperature for 24 h. The microalgal fraction was extracted from the host tissue by
143 homogenization and centrifugation (5,000 rpm for 5 min). Samples were then immediately
144 frozen at -80°C for later analysis. Cell counts were assessed using a hemocytometer on five
145 replicate micrographs (scaled to 0.1 mm^3), then normalized to the coral surface area to measure
146 algal density (cells/cm^2). Chlorophyll-*a* was extracted from the remaining algae using 100%
147 cold acetone for 15 h at 4°C, quantified using spectrophotometry (Ultrospec 2100 pro,
148 Amersham Pharmacia Biotech, USA), and calculated following Jeffrey and Humphrey (1975).
149 Chlorophyll-*a* was normalized to both the surface area (μg/cm^2) and algal cells (pg/cell).
150

151 *2.3 Morphological analyses*

152 To accurately capture the influence of different light conditions on the diversity of coral
153 skeletal features, morphometric quantitative information was extracted using high-resolution
154 computed tomography (Nikon XT H 225ST μCT, Nikon Metrology Inc., USA). The coral
155 skeletons were scanned with a voxel size of 10-15 μm (depending on specimen size), 0.25 mm
156 stainless steel filter, voltage of 65 kV, amperage of 123 μA, and exposure time of 1.15 s. Scans
157 from each specimen were saved in TIFF image format for 3D volume rendering and
158 quantitative analysis using Dragonfly software (© 2023 Object Research System (ORS) Inc.).
159 The volume and surface area of each coral juvenile were determined, and nine skeletal
160 morphological traits were measured from intact corallites and the coenosteum region: calyx
161 diameter (CD), theca (corallite height) height (TH), septal length (SL), septal width (SW),
162 columella height (CH), coenosteal spine length (SPL), coenosteal spine width (SPW), corallite
163 spacing (CS), and coenosteal spine spacing (SS). These traits were chosen because they were
164 shown to exhibit significant variations in different light environments, highlighting their
165 importance in understanding complex skeletal architecture and its implications (Kramer et al.,
166 2022b; Rocha et al., 2014). In addition, the apparent porosity was assessed as the percentage
167 ratio of the pore volume to the total volume occupied by the coral skeleton.

168

169 *2.4 Coral optical measurements*

170 To characterize the skeletal optical properties, we measured the diffuse spectral
171 reflectance (R) and scalar irradiance $E_0(\lambda)$ of coral juveniles. The samples were placed in a
172 black acrylic chamber filled with water and illuminated with homogeneous diffuse light
173 provided by a semi-sphere coated with barium oxide (BaO) and a LED lamp (CRI-MAX TM
174 PAR 30, Yuji Lighting). R was measured using a flat-cut fiber-optic reflectance probe
175 (diameter = 0.23 cm, Ocean Insight) connected to a miniature spectrometer (Flame, Ocean

Insight; n = 5 scans per measurement, boxcar width = 2 nm, resolution = 0.2 nm) (Enríquez et al., 2005; Vásquez-Elizondo et al., 2017). The probe was placed 5 mm away from the skeletal surface at a 45° angle relative to the surface. Three random surface regions per colony (n = 8 colonies) were chosen for the measurements, and the experimental outcomes were normalized against a 99% diffuse reflectance standard (Spectralon, Labsphere).

Scalar irradiance was measured using a fiber-optic scalar irradiance microprobe with a spherical tip diameter of 80 µm mounted on a micromanipulator (Pyro-Science GmbH, Germany) (Kramer et al., 2022c; Wangpraseurt et al., 2012). To avoid bias measurements resulting from nearby branch junction light scattering and optical variability between corallites and coenosteum, $E_0(\lambda)$ spectra were measured in three randomly selected areas on the coenosteum and three corallites near the coral branch tips. $E_0(\lambda)$ was measured for five coral juveniles per treatment. After each measurement, reference measurements of the incident downwelling irradiance $E_d(\lambda)$ were taken over a black non-reflective surface. The spectral irradiance $E_0(\lambda)$ was then normalized to the incident downwelling irradiance $E_d(\lambda)$.

2.6 Statistical analyses

Statistical analyses were performed using the R software (R Development Team, 2023). Since in most cases, the data did not conform to parametric test assumptions, variations between treatments (fixed effect) for each morphological trait were tested using a mixed-effects permutational analysis (MEPA; 999 permutations), and models included the coral's colony ID as a random effect. These analyses were performed using the {lme4}(Bates et al., 2015) and {predictmeans}(Luo et al., 2022) packages. When significant differences were found, the standardized effect sizes and 95% confidence intervals (CI; 5000 bootstrap samplings) of the treatments were estimated by calculating Hedges' *g* (*Hg*) using the package {dabestr}(Ho et al., 2019). CIs that did not overlap with zero were considered significant effects. A principal

coordinates analysis (PCoA) based on a Euclidean distance matrix of standardized data was created using the {vegan} package to visualize the pattern of morphological variation between depths in a multivariate trait space (hereafter, 'morphospace'). Finally, permutational multivariate analysis of variance (PERMANOVA; 999 permutations) was performed to determine the overall effect of depth on morphological patterns.

3. Results

3.1 Skeletal porosity, symbiont cell density, and chlorophyll-a content

The coral skeletal porosity (%) differed significantly among the three treatments, ranging from 6.18% to 22.61% (MEPA, $p < 0.001$**;** Fig. 2a). The porosity increased by over two-thirds for corals grown under the LED treatment (16.04 ± 1.45%; mean ± SE) compared to the control (9.15 ± 0.53%) and fluorescent (11.54 ± 0.84%) groups. Likewise, corals in the fluorescent treatment exhibited a smaller but significant porosity increase compared with the control group (*Hg* = 1.19 [$CI_{95\%}$ 0.162; 2.25]). Juvenile corals grown under fluorescent light exhibited the highest areal chlorophyll-*a* content (μg chl cm^{-2}; Fig. 2b), whereas no significant difference was observed between the control and LED treatment groups (*Hg* = 0.169 [$CI_{95\%}$ -0.731; 1.16]). Similarly, algal symbiont density (cells cm^{-2}; Fig. 2c) was the highest in the fluorescent group, however, a marked four-fold reduction was observed in LED-grown corals compared to the fluorescent group (*Hg* = −3.90 [$CI_{95\%}$ -5.22; -2.75]), exhibiting the lowest concentration levels among treatments (1.81×10^5 cells cm^{-2}). The cellular chlorophyll-*a* content (pg $cell^{-1}$; Fig. 2d) was significantly influenced by LED lighting, with a three-fold increase (MEPA, $p < 0.001$), while the control and fluorescent treatments showed similar concentrations (*Hg* = 0.33 [$CI_{95\%}$ -0.52; 1.24]).

3.2 Morphometrics

Thirty months post-settlement, juvenile *S. pistillata* colonies exhibited three distinct morphotypes among the three illumination methods (PERMANOVA, $p < 0.001$; Figs. 3, 4). The first two PCOA axes explained 66.89% of the total variation in the morphospace among the light treatments (Fig. 4). The first axis explained 45.32% of the variance with over half of the contribution deriving from calyx diameter (CD), theca height (TH), and septal length (SL). Substantial differences were observed in all traits among the three treatments, except for corallite spacing (CS) which was statistically non-significant (MEPA, $p = 0.469$, Fig. 3f). Generally, both or one of the ALAN conditions led to larger morphological trait sizes compared to their control counterparts. For example, the calyx diameter (CD) was 9% wider in LED-grown corals than in corals grown under moonlight and fluorescent light (MEPA, $p < 0.001$; Fig. 3b). In certain instances, both LED and fluorescent treatments exhibited similar trends; for example, the light-polluted conditions led to corallites that were substantially deeper (i.e., 21% increase in theca height (TH)) than their control counterparts (MEPA, $p < 0.001$; Fig 3c).

3.3 Skeletal optical properties

The light field parameters (R and E_0) were significantly different among the treatments. The coral specimens subjected to light pollution displayed significantly diminished skeletal reflectance (R) compared to the control group (70.20 ± 0.44%; mean ± SE; at $\lambda = 675$ nm), with percentages of 61.30 ± 0.44% and 66.80 ± 0.8% for LED and fluorescent-treated corals, respectively (Fig. 5a; MEPA, $p < 0.01$). Similarly, LED had a stronger effect on the percentage of the incident downwelling irradiance (E_0; at $\lambda = 675$ nm) measured at the corallite surface, exhibiting nearly 50% lower E_0 than the control counterparts (Fig. 5b; 201.86 ± 2.08% vs. 247.06 ± 2.05%; Hg = -2.33 [CI95% -2.68; -1.96]), whereas the fluorescent-grown corals exhibited a smaller yet significant reduction in the spectral irradiance (238.06 ± 2.55%; Hg = -0.41 [CI95% -0.71; -0.12]). Likewise, E_0 measurements over the coenosteum revealed lower

values for the light-polluted corals (MEPA, $p < 0.01$; Fig. 5c), exhibiting a 46% and 11% E_0 reduction in the LED and fluorescent treatments, respectively.

4. Discussion

Light plays a critical role in the development and survival of scleractinian corals, as it provides energy through photosymbiotic algae residing within the coral's tissue (Roth, 2014). Therefore, maintaining a delicate balance between light quality and quantity is essential for corals to thrive and sustain healthy coral reef ecosystems. Yet, our understanding of light pollution and its impact on marine environments is still in its early stages. Since corals at the northern GoE/A are increasingly and constantly confronted with exposure to ALAN, it is expected that ALAN plays a significant role in shaping the essential aspects of coral light harvesting. One of the key aspects is the complex skeletal architecture of corals, which creates a variety of light microhabitats (Enríquez et al., 2017). As a result, corals are expected to exhibit a morphological structure that adequately supports the amount of light reaching their photosymbionts.

Here, we show that long-term exposure to ALAN induces noticeable physiological, optical, and morphological changes in *S. pistillata* juveniles, revealing three distinct morphotypes (Figs. 1b, 4). We suggest that exposure to ALAN may have complex effects on symbiont physiology and coral skeletal growth and structure. Owing to the higher photon energy (i.e., receiving more photons from higher wavelength frequencies) than that of the ambient-light corals, the experimental corals exposed to artificial nocturnal light exhibited lower light capture demands for photosynthesis.

4.1 Morphometrics and optical properties

The skeletal morphology of light-polluted corals appears to resemble that of corals inhabiting “high-light” environments in comparison with the control group (Einbinder et al., 2016; Kramer et al., 2022b, 2022c; Malik et al., 2020; Tamir et al., 2020). Coral juveniles under ALAN exhibited skeletal characteristics and optical properties that make them better suited to handle higher levels of photon flux, presumably because of the additional light acquired at night.

We found that among the morphological traits, theca height (TH), calyx diameter (SPL), and septal length (SL; the vertical structures that divide the corallites) were the most influential traits that were affected by varying light spectra at night. Several previous studies have established that these skeletal characteristics play a key role in determining the amount of light that can reach the photosymbionts (Kramer et al., 2022b; Ow and Todd, 2010; Studivan et al., 2019; Swain et al., 2018). While all skeletal traits have a certain degree of influence on the coral's light environment, these traits are considered particularly relevant in shaping the surface complexity. We showed that the morphological traits of corals exposed to either one or both ALAN conditions generally exhibited larger trait sizes than those grown under the natural night sky regime (Fig. 3). Deeper and larger corallites, taller columella, longer septa, and longer coenosteal spines, for example, contribute to the complexity of the skeletal architecture and can affect the direction and intensity of light reaching the microalgae, thereby altering their light exposure (Kramer et al., 2022b). They create a more convoluted surface that allows for better self-shading in increased light environments, thus preventing photodamage to the photosymbionts due to excess light.

Additionally, optical measurements performed on the skeletons of corals exposed to light pollution revealed a significant reduction in both bulk light reflection and spectral irradiance near the skeletal surface compared to the control group (Fig. 5). In particular, LED had a more significant impact on the coral juveniles light field than the fluorescent lighting.

300 The data suggests a photo-acclimation to the altered light regime by reducing excess *in hospite*
301 light exposure of Symbiodiniaceae. This phenomenon has also been observed in a study
302 comparing shallow and mesophotic optical properties, revealing a reduced skeletal
303 backscattered light under high-light levels (Kramer et al., 2022c). Other factors that regulate
304 the availability of photons for photosynthesis, such as the spatial distribution of the symbiotic
305 algae in the tissue layer or the presence of coral fluorescent pigments (FPs) (Lyndby et al.,
306 2016), could also potentially be influenced by ALAN and consequently impact the coral's
307 internal light environment. However, investigating these aspects was beyond the scope of this
308 study, highlighting the need for further research in these areas.
309 Given these results, our findings support the notion that light-driven changes often
310 occur in parallel between the host's morphology, algal physiology, and optical properties
311 (Enríquez et al., 2017; Kramer et al., 2022c; Swain et al., 2018). We show that the optical traits
312 of the coral host skeleton complement the photosynthetic demands of coral photosymbionts,
313 that is, the lower algal cell densities are compensated by the reduced light available from the
314 skeleton, thereby preventing photodamage. Since photosynthesis and energy production in
315 corals are primarily carried out by the photosymbionts, the observed skeletal changes may also
316 be linked to the altered symbiont physiology caused by ALAN (Fig. 2), as previous research
317 has highlighted the crucial role of symbiotic algae in coral calcification and skeletal growth
318 (Goreau, 1959; Mass et al., 2007). Moreover, we can infer that the observed changes imply a
319 level of light-induced stress under altered nightlight conditions, as both the symbiont and the
320 host's traits appear to have reduced the potential for the oversaturation (i.e., photoinhibition)
321 of the photosystem complexes.
322
323 *4.2 Porosity*

The μCT analysis revealed that light-polluted corals were substantially more porous than their control counterparts (Fig. 2a). While Rocha et al. (2014) previously reported no significant changes in the skeletal porosity of *S. pistillata* that were only exposed to different daytime spectra, our results indicate that changes in the internal void space of coral skeletons depend not only on the combination of sunlight intensity and spectrum (Kramer et al., 2022b; Malik et al., 2020), but also on the night-time light spectrum. Interestingly, despite showing the fastest growth rate among the three treatments (Tamir et al., 2020), coral juveniles grown under the LED light exhibited similar porosity values to their slow-growing conspecifics found in low-light depths (Kramer et al., 2022b). This suggests that the growth rate of a given coral species may not be the sole determinant of its skeletal porosity, and implies that other factors such as water chemistry, temperature, and light, may play a crucial role in determining the porosity of coral skeletons (Fantazzini et al., 2015; Foster et al., 2016; Kramer et al., 2022b).

4.3 Insights on the effect of ALAN on coral growth

Only a limited number of studies have evaluated the effects of ALAN on the growth of marine organisms (Marangoni et al., 2022), let alone in reef-building corals. This study demonstrates that the spectral composition of the artificial light sources used for night-time illumination, which differs from that of night sky illumination (Tamir et al., 2017), may have a substantial adverse impact on coral skeletal growth, structure, and physical properties.

As expected, light-polluted corals exhibited either decreased symbiont cell density or reduced cellular chlorophyll-*a* (Fig. 2; Ayalon et al., 2019; Levy et al., 2020; Rosenberg et al., 2019). Specifically, LED-grown juvenile corals exhibited a paler surface color resembling lightly bleached corals, which was consistent with their reduced photosynthetic activity, as shown by Tamir et al. (2020). However, surprisingly, that study has also shown that despite lower photosynthetic rates during the day and negligible photosynthesis at night (light intensity

= 0.8 μmol photons m^{-2} s^{-1}, which is significantly lower than the photosynthetic compensation point), corals illuminated by LED lighting exhibited enhanced calcification rates at night and produced greater colony structures, as shown in Fig. 1b. This may be explained by the higher blue peak (i.e., greater photon energy) and broader spectrum prevalent under LED lighting, inducing light-enhanced calcification (LEC). As seawater in the open ocean attenuates blue light the least, many marine organisms are sensitive to this spectral region (Marshall et al., 2015). Specifically, corals possess an array of sensitive photoreceptors that mainly absorb in the blue region of the light spectrum (Gorbunov and Falkowski, 2002; Levy et al., 2007). As demonstrated by previous studies, blue light can enhance calcification rates in hermatypic corals despite reduced photosynthesis, suggesting that the effect of light on LEC is not solely due to photosynthetic energy, but may involve direct signaling through the host's receptors (Cohen et al., 2016; Eyal et al., 2019). Therefore, cumulative exposure to sunlight and LED at night may increase total energy production and ultimately promote coral growth. As such, our results provide evidence of increased skeletal growth despite the lower photosynthetic activity, supporting the assumption that blue-light absorbing photoreceptors activate other physiological processes (e.g., proton [H^+] pumps, $Ca2^+$-ATPase pumps, etc.) to further induce coral calcification at night.

A study on the effects of exposure to ALAN on coral reef fish larvae during the recruitment stage found that while ALAN-exposed fish grew faster, they also experienced changes in behavior, higher susceptibility to predation, and significantly higher mortality rates (O'Connor et al., 2019). Similarly, as previous studies proposed, faster coral growth rates are not a reliable indicator for coral health since it does not necessarily confer advantages or optimize the fitness of corals, but rather there is a trade-off between energy allocation for coral growth and fecundity (Darling et al., 2012; Edinger et al., 2000; Harrison and Wallace, 1990; Kramer et al., 2022a; Loya et al., 2004). For example, Loya et al. (2004) found that although

coral growth is accelerated under chronic eutrophication, it also renders corals more susceptible to lower reproductive output. As previously mentioned, corals exposed to photopollution at night exhibit lower fecundity (Ayalon et al., 2021b), which subsequently reduces the supply of planulae and further hinders successful settlement (Tamir et al., 2020). Taken together with previous research, we suggest that ALAN may favor faster coral growth at the cost of reduced reproductive investment (Ayalon et al., 2021b; Loya et al., 2004; Tamir et al., 2020).

4.4 Additional potential detrimental effects of light pollution in corals

In addition to light pollution, coral reef ecosystems are already subjected to unprecedented degradation, resulting mainly from warming oceans (Leggat et al., 2019) as well as a growing threat from the uptake of anthropogenic carbon dioxide (Jiang et al., 2019). Coral juveniles subjected to elevated temperatures and ocean acidification, for example, have been shown to impair their skeletal structures (Foster et al., 2016). Thus, the interaction of these stressors with light pollution may further weaken skeletal structures, making them more vulnerable to damage from physical disturbances, predation, or harmful boring organisms.

We further suggest that light pollution may render corals more susceptible to thermal stress. For example, in the already symbiont-depleted tissue of LED-grown corals, one factor that can contribute to this process is the enhanced light flux promoted by the reflection of the incident light from the coral skeleton, which can further stimulate the loss of endosymbiotic algae and exacerbate the bleaching process, leading to an optical feedback loop (Wangpraseurt et al., 2017).

It is important to note that because of its higher energy efficiency and longer lifespan, many coastal regions have transitioned towards LED lighting to replace older lighting systems. LED lighting is anticipated to contribute 97% of the global lighting market by 2025 (Smyth et al., 2021; Zissis and Bertoldi, 2018). However, although our results show that LED lighting

has more pronounced effects on coral skeletal characteristics and photosymbiont physiology, the significance of fluorescent lighting should not be deemed less important. In areas where fluorescent lighting is still in use along urbanized near-shore coral reefs, it can still have moderate negative effects on coral biology. Given the expected increase in ocean warming and the global transition towards LED lighting in coastal urban regions in the coming decades, future research should explore the potential synergetic effects of ALAN and global climate change stressors.

5. Conclusions

We demonstrated that ongoing exposure to nocturnal artificial illumination can alter the skeletal architecture and optical properties of shallow-water juvenile corals, which in turn affects their light microenvironment. However, it is important to note that the effects of ALAN on photosymbiotic corals are complex and depend on various factors, such as the intensity, spectrum, and duration of night-light exposure, as well as on the respective coral species and their developmental stage. Thus, to gain a comprehensive understanding of the detrimental impacts of light pollution from coastal cities on benthic ecosystems, we advocate for conducting long-term studies to investigate the impacts of ALAN exposure from juveniles to adulthood. Given the significant role of light in various marine coastal fauna, preserving the natural underwater light regime should be a priority for coral reef conservation, making it an essential factor to consider in local coral reef management.

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Author contributions

N.K. and Y.L. conceived and designed the study; N.K., R.T., and C.T.G.M. executed the experiment; N.K. performed data analyses and generated figures; Y.L. and D.W. supervised the study; N.K. wrote the original manuscript with contributions and final approval from all authors.

Competing interests

The authors declare no competing interests.

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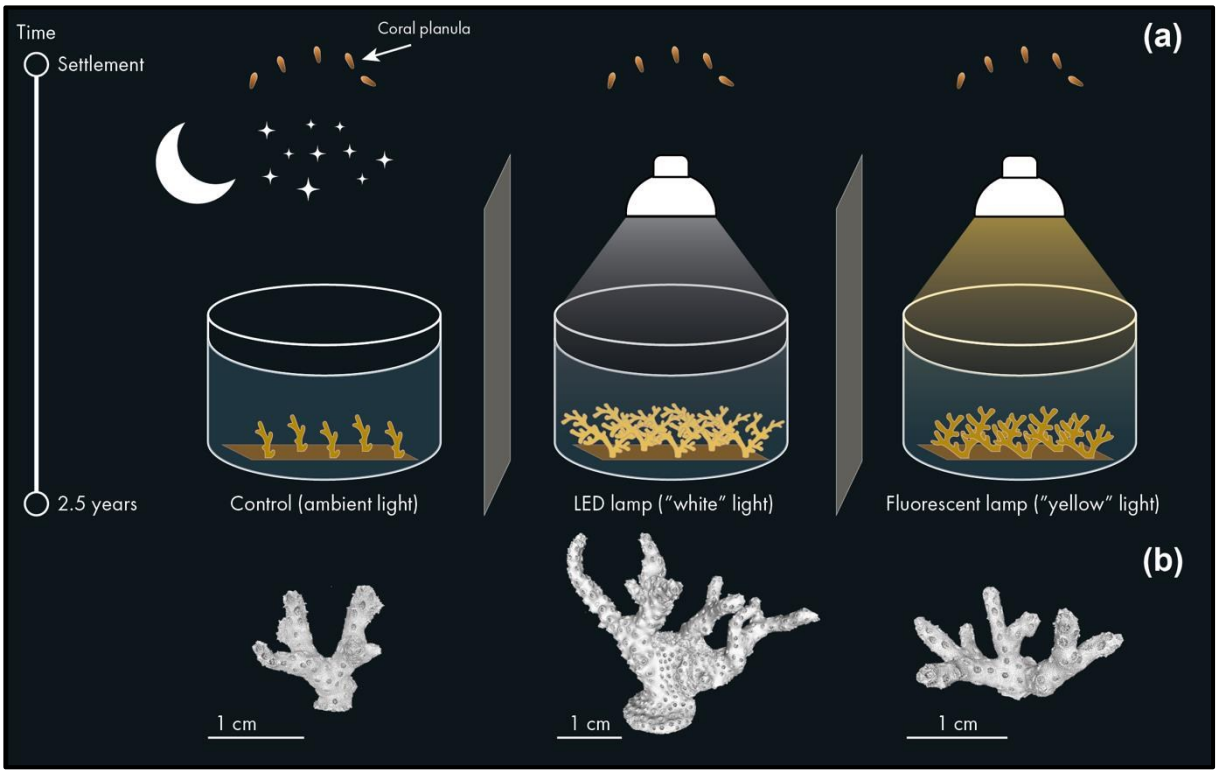

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684 **Figure 1.** Schematic illustration of the experimental design. **(a)** *Stylophora pistillata* coral
685 planulae were collected from the shallow reef and allowed to settle and grow for 2.5 years in
686 three separate seawater tables. One table was kept under natural conditions, while the other two
687 were subjected to artificial light at night (LED and fluorescent), replicating common city
688 lighting methods. **(b)** 3D colonies rendered from µCT X-ray scans.

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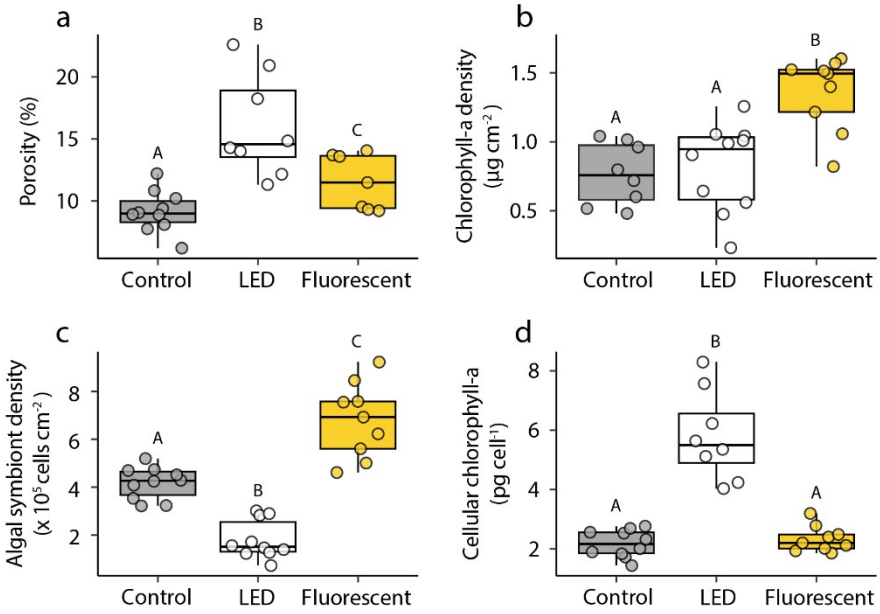

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700 **Figure 2.** Boxplots showing **(a)** skeletal porosity, **(b)** Chlorophyll-*a* density, **(c)** algal symbiont
701 density, and **(d)** cellular chlorophyll-*a* of the experimental corals 30 months post-settlement in
702 the three light treatments – control (ambient; *gray*), fluorescent lamp (*yellow*), and LED lamp
703 (*white*). Horizontal lines depict the median, box height depicts the interquartile range, whiskers
704 depict ±1.5× interquartile range. Capital letters indicate significance among treatments.

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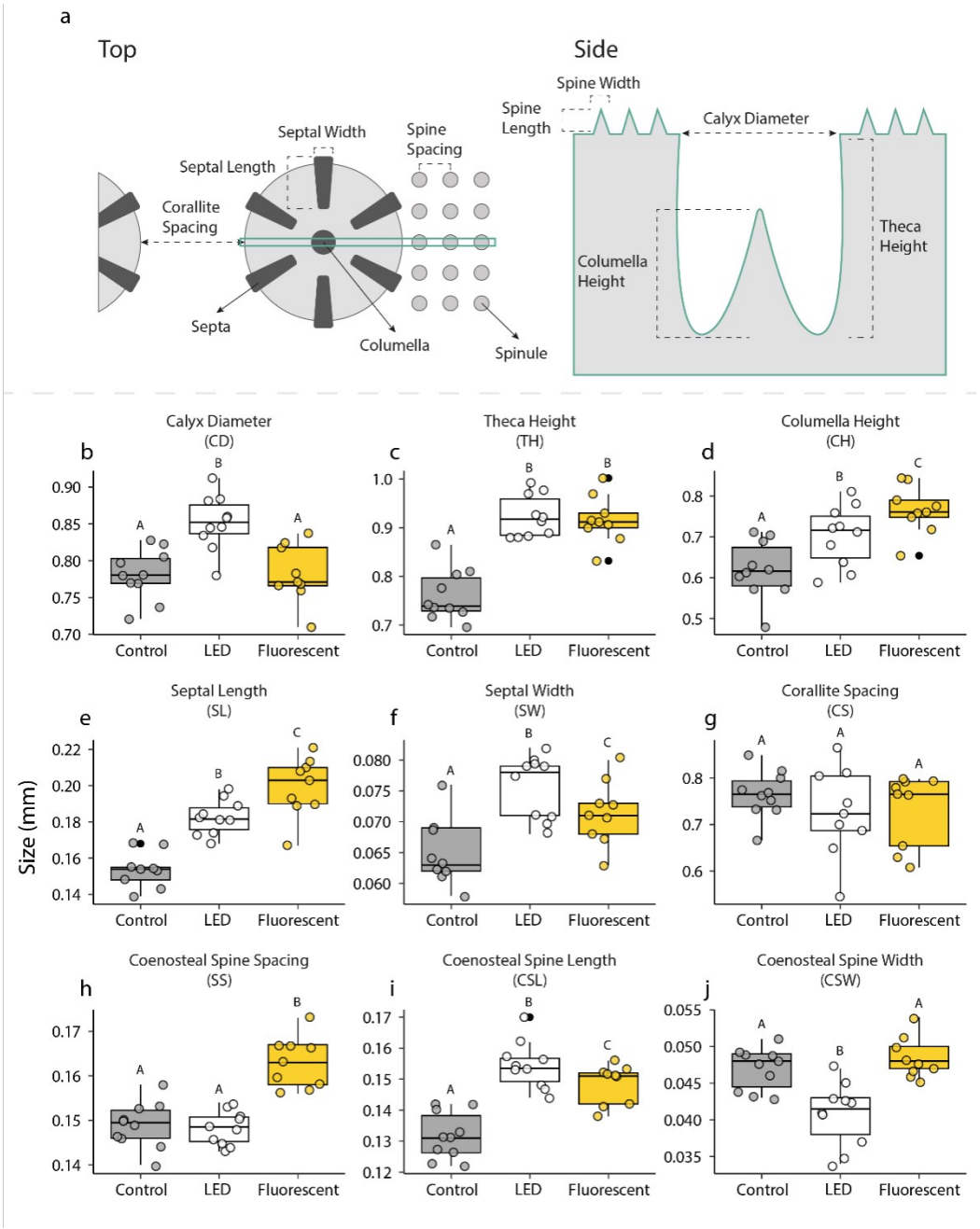
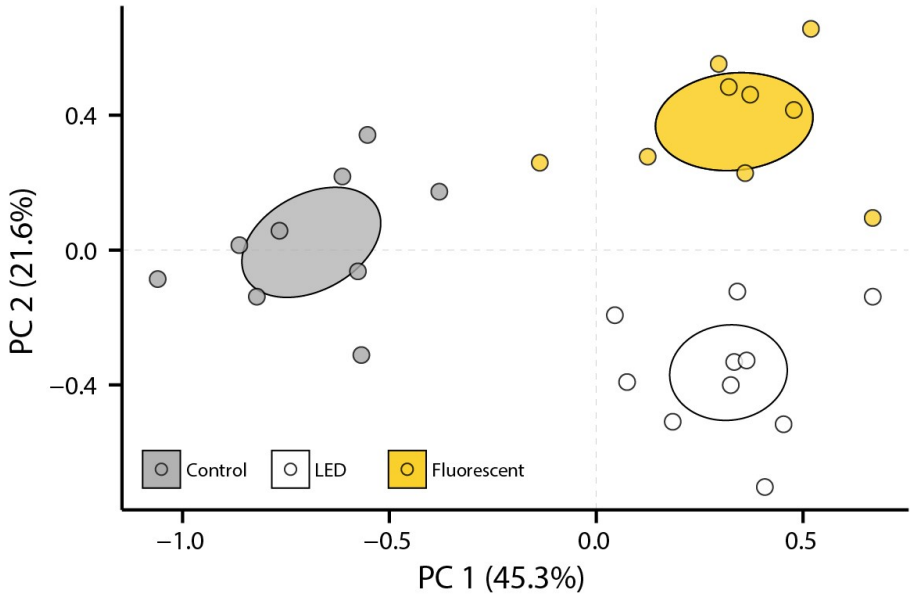


717 **Figure 3. (a)** A 2D illustration of the top and side views of a corallite, along with its
718 surrounding coenosteum (modified after Kramer et al. (2022b)). **(b-j)** Morphometric results of
719 the experimental corals' skeletal traits 30 months post-settlement for the three light treatments
720 – control (ambient; *gray*), fluorescent lamp (*yellow*), and LED lamp (*white*). Horizontal lines
721 depict the median, box height depicts the interquartile range, whiskers depict ±1.5×
722 interquartile range, and black dots represent outliers. Capital letters indicate significance
723 among treatments.



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725 **Figure 4.** Principal coordinate analysis (PCoA) of the morphological traits of juvenile *S.*
726 *pistillata* corals based on Euclidean space. Each circle represents a particular colony and is
727 colored by light treatment. Ellipses are standard error.

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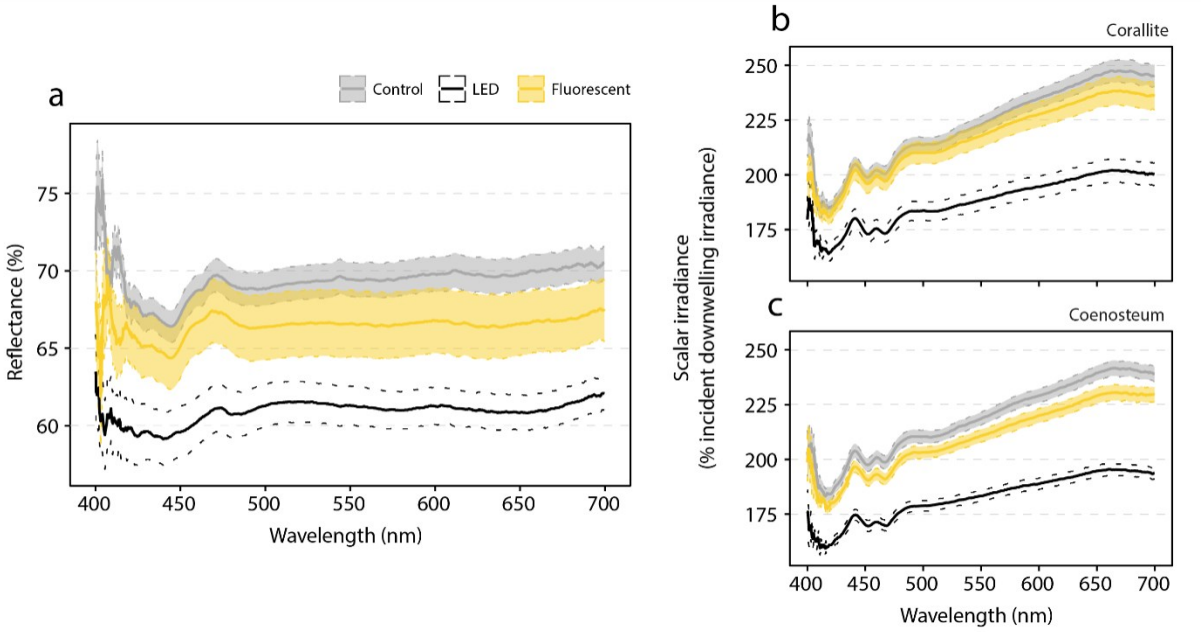

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742 **Figure 5.** Apparent optical properties at 400–700 nm. **(a)** Normalized spectral reflectance of
743 light over the coral skeleton (%). **(b-c)** Scalar photon irradiance (% incident downwelling
744 irradiance) at the skeleton surface of the **(b)** corallites and **(c)** the coenosteum. Solid lines are
745 means, and dashed lines are standard errors.