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Effects of artificial light at night on the early benthic stages of the prominent sea urchin *Loxechinus albus*

Patricio H. Manríquez [a,b,*], Diego Quintanilla-Ahumada [c,d], Claudio P. González [a,b], Paolo Domenici [e], Jorge Bravo [f], Andrés Camaño [g], José Pulgar [c,h], Pedro A. Quijon [d], Cristian Duarte [c,h]

[a] Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile
[b] Laboratorio de Ecología y Conducta de la Ontogenia Temprana (LECOT), Coquimbo, Chile
[c] Departamento de Ecología y Biodiversidad, Facultad de Ciencias de la Vida, Universidad Andrés Bello, Santiago, Chile
[d] Coastal Ecology Laboratory, Department of Biology, University of Prince Edward Island, Charlottetown, PE, Canada
[e] Consiglio Nazionale delle Ricerche-Istituto di Biofisica, (CNR-IBF), Pisa, Italy
[f] Sustainability & Environmental Consulting (BSEC), Copiapó, Chile
[g] Sistemas Socio-Ecológicos (SISEC), Santiago, Chile
[h] Centro de Investigaciones Marinas de Quintay (CIMARQ), Quintay, Chile

A B S T R A C T

Artificial light at night (ALAN) is a growing anthropogenic stressor, yet its effects on marine invertebrates, particularly during early benthic stages, remain understudied. The edible sea urchin *Loxechinus albus*, an important herbivore along the Pacific coast of South America, shows behavioural traits such as covering that suggest sensitivity to environmental factors, including light. Therefore, this study examined the potential influence of ALAN on small juvenile sea urchins, hypothesizing effects on their behaviour and physiology. In the field, an exploratory survey revealed aboral surface covering behaviour that suggest a natural avoidance of light by the sea urchins. In the laboratory, covering behaviour was quantified, measuring also their preference for contrasting dark and lit (ALAN) conditions in a Y-maze. Additional trials measured food consumption, horizontal speed, self-righting, metabolic and growth rates in individual exposed to dark and ALAN. Laboratory observations identified covering behaviours that were heightened under ALAN exposure. These behaviours were consistent with a strong preference for dark areas in Y-maze tests, where food consumption was also consistently higher than under ALAN. Speed and self-righting times were higher under ALAN and dark, respectively. Meanwhile, metabolic rates and growth rates were lower under ALAN, indicating possible long-term physiological effects. Altogether, ALAN exposure disrupted key behavioural and physiological traits leading juveniles to prioritize survival behaviours like avoiding light and speeding up locomotion and self-righting over foraging and growth. These findings suggest that ALAN could alter interactions and energy allocation in *L. albus*, with potential implications for kelp forest ecosystems and the fisheries of this species.

1. Introduction

Artificial light at night (ALAN) is a growing anthropogenic disturbance caused by the alteration of natural nocturnal light conditions through human-made sources, with its prevalence rapidly increasing worldwide (Davies and Smyth, 2017; Gaston et al., 2021). Among the environments most vulnerable to ALAN, coastal areas are particularly affected due to increasing human activities such as urban development, tourism, industrial activities, and infrastructure lighting (Ferretti et al., 2025). In these habitats, the effects of ALAN include disruptions to circadian rhythms (Duarte et al., 2019; Pulgar et al., 2019; Quintanilla-Ahumada et al., 2024a), settlement (Lynn et al., 2021; Manríquez et al., 2021a, 2021b), oxygen consumption (Manríquez et al., 2019a), foraging behaviour and locomotion (Pulgar et al., 2023; Quintanilla-Ahumada et al., 2022, 2024a), trophic and non-trophic interactions (Underwood et al., 2017; Manríquez et al., 2021a, 2021b), and community structure (Duarte et al., 2023), among other impacts (Marangoni et al., 2022; Lynn and Quijón, 2022).

Echinoderms are vital components of marine ecosystems worldwide, often serving as ecosystem engineers or keystone species (Lessios et al., 2001; Hereu et al., 2008; Steneck, 2013). Among them, sea urchins play a critical role in structuring benthic communities through grazing, which can shape the composition and abundance of many algal populations (Hughes, 1994; Harrold and Pearse, 1987). Their ecological impact is so profound that changes in sea urchin populations can trigger cascading effects throughout ecosystems, influencing biodiversity, trophic interactions, and habitat availability (Sala et al., 1998). Despite their importance, there is rather limited research on the effects of ALAN

* Corresponding author at: Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Coquimbo, Chile.

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on sea urchins, even though there is clear evidence suggesting that they are susceptible to light. Sea urchins often cover themselves with algal fragments, small rocks, or shells, a behaviour that has been linked to protection from mechanical injuries associated with abrasion and dislodgement, and, to a lesser extent from UV radiation (Dumont et al., 2007). Aboral surface covering may have also evolved as a behavioural response acting as a light screen (Millott, 1956). If natural light is an important in sea urchin behaviour, we argue that artificial nighttime light is likely to affect their behaviour and life history story traits.

The few studies examining the effects of ALAN on sea urchins have provided conclusions that are not necessarily consistent. For example, ALAN did not affect the feeding rates of two sea urchins, *Arbacia lixula* and *Paracentrotus lividus*, under laboratory conditions (Bauer et al., 2022). However, ALAN did induce a shift from diurnal to nocturnal feeding in the latter species. Also under laboratory conditions, prolonged exposure to ALAN in the sea urchin *Heliocidaris crassispina* resulted on slow behavioural responses, such as reduced food consumption, delayed self-righting, and decreased surface covering (Xu et al., 2003). That latter study also detected growth inhibition and increased gonad sensitivity to light exposure. Additionally, a semi-controlled field study conducted in a rocky shore near a promenade that was lit at night reported a potential influence of ALAN on the locomotor behaviour of the sea urchin *P. lividus* (Sanna et al., 2024). Individuals of this species tended to move away from light sources, while their movements and distribution in the dark were uniformly distributed in all directions. Similarly, a previous study on this species found that light-stimulated locomotion speed is higher than that observed during spontaneous activity, as a result of negative phototaxis (Domenici et al., 2003). These previous studies suggest that ALAN may alter the behavioural and physiological traits of sea urchins, potentially disrupting their interactions and ecological roles. These previous studies suggest that ALAN may alter behavioural and physiological traits of sea urchins, potentially disrupting their interactions and ecological roles. However, none of them simultaneously assessed behavioural, physiological, and performance-based responses under controlled conditions.

The sea urchin *Loxechinus albus* (Molina, 1782), locally known as the Chilean red sea urchin, is an ecologically and commercially important benthic herbivore found along the Pacific coast of South America, from Isla Lobos de Afuera in Perú (~6° S) to the southern end of South America in Tierra del Fuego (~56° S) (Vásquez, 2001; Molinet et al., 2012). In shallow-water coastal ecosystems of Chile, this species is a target for local fishers (Vásquez et al., 1984; Guisado and Castilla, 1987; Castilla, 1990; Vásquez and Donoso, 2013) and represents one of the largest sea urchin fisheries in the world (Andrew et al., 2002). Across its wide latitudinal range and large depth distribution (from the intertidal zone to 100 m depth) (Molinet et al., 2012), *L. albus* is most often found in low rocky intertidal and shallow subtidal habitats. In these habitats, populations of this species are mainly found in areas with difficult access to shellfish gatherers, but variable exposure to natural light conditions. Given the exposure of these habitats to a growing number of ALAN sources, our study aimed to assess the influence of this stressor on prominent behavioural and life history traits of this species.

This study encompasses the first systematic, multi-dimensional assessment of ALAN effects on *L. albus*, combining field observations and controlled laboratory experiments to evaluate key behavioural (covering, spatial preference, locomotion) and physiological (metabolism, growth) fitness-related traits. Aiming at the strength of a multiple-response approach (see e.g., Auguste et al., 2023), and compared to previous studies on other sea urchin species, this work integrates multiple response dimensions, thus providing a comprehensive understanding of ALAN's ecological impacts on a keystone marine species. A priori, our working hypothesis was that ALAN exposure has an influence (plausibly negative) on behavioural and physiological traits of *L. albus*. We expected ALAN to affect covering behaviour, as benthic juvenile stages of this species may use this strategy to shield themselves from artificial light and visual predators. Based on evidence from other rocky shore species, we also expected ALAN to affect habitat choice and inhibit feeding activity. We also anticipated that ALAN would impact the sea urchin's speed and, since overturned individuals become more vulnerable to visual predators, its self-righting behaviour. All these hypothesized changes could lead sea urchins to incur increased metabolic costs while searching for food in darker areas, with potential consequences for their fitness (e.g., growth rates).

2. Materials and methods

2.1. Aboral surface covering in nature

A field survey was conducted to explore the ubiquity and magnitude of sea urchin aboral surface covering behaviour in natural populations of *L. albus*, as a potential behavioural display to prevent light exposure. These exploratory measurements were conducted in Caldera, northern Chile (27°04′S; 70°51′W) during diurnal ebb tides of August 2022, and assessed the prevalence and extent of this behavioural trait across three habitats from the low rocky intertidal to the very shallow subtidal with distinct exposure to natural daylight conditions. The field site was unaffected by direct artificial light at night sources, ensuring that any sea urchin covering behaviour was influenced only by natural light variations. Our reasoning was that variation in natural light exposure across habitats may provide valuable cues regarding the ecological significance of aboral surface covering behaviour with respect to light exposure at night. The site selected for the covering behaviour survey is situated ca. 5 km southwest of the urban centre of Caldera, in the Atacama Region. Although relatively close to town, this site remains a semi-isolated area with minimal urban development and no industrial activity. Due to the region's hyper-arid climate, urban runoff is extremely limited and occurs only during rare precipitation events, such as those associated with El Niño or the winter in the South American Altiplano. There are no rivers, active streams, or drainage systems discharging directly into this site. Furthermore, the site is characterized by very low levels of ALAN. There is no street lighting, housing, or illuminated infrastructure near the shoreline, and the nearest light sources (Caldera) are distant and partially blocked by local topography. As a result, the coastal organisms at this site experience minimal to no ALAN, making it a suitable location for ecological studies requiring low anthropogenic interference, particularly those examining behavioural responses to natural vs. artificial light regimes.

The three habitats examined in this field site included flat rocks, where sea urchins are widely exposed to light, rocks nearby holdfasts of the brown algae *Lessonia berteroana*, where the urchins are partially exposed to light, and shadowed habitats beneath the canopy of algae (Fig. 1), where sea urchins are least exposed to natural light sources. In each habitat, 50 haphazardly selected sea urchins were collected to record the presence of aboral surface covering, using photographs taken from above. From the digital photographs collected, the percentage of the aboral surface covered by various materials (e.g., algal fragments, shells, pebbles, or other debris) was measured to assess the extent of their accumulation. The surface area covered by materials was expressed as a percentage of the total aboral surface area and further categorized by its nature (i.e., organic or inorganic).

2.2. Laboratory acclimation and experimental setting

Small juveniles of *Loxechinus albus* (hereafter sea urchins) ranging between 1.0 and 1.6 cm in diameter were obtained in December 2019 from a research hatchery at the Universidad Católica del Norte, Coquimbo, Chile (29°57′ S; 71°21′ W). At the time the experiments were conducted, these sea urchins had been raised for ca. 14 months in running seawater and fed with biofilms and fresh fronds of the green macroalga *Ulva* sp. and the brown macroalga *Lessonia* sp. During that period, the sea urchins were not exposed to predators and were maintained under a natural day/night light regime. The sea urchins were then

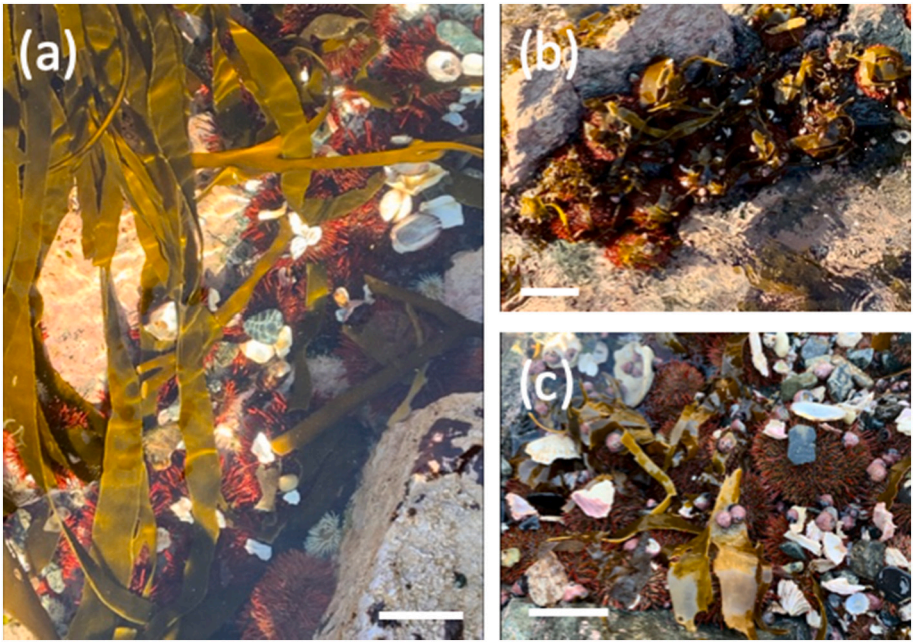


Fig. 1. Photographs of the sea urchin *Loxechinus albus* displaying aboral surface covering behaviour in three microhabitats with contrasting light exposure in the low intertidal and shallow subtidal zones: (a) shaded habitats beneath the canopies of the brown algae *Lessonia berteroana*, (b) habitats near the holdfasts of these algae but still exposed to light, and (c) fully light-exposed habitats on flat rocks. In each photograph, the white scale bars represent 5 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

transferred to the laboratory, where all the experiments described below were conducted following an acclimation period of 1 month. Here, the sea urchins were maintained in three 20 L Plexiglas aquaria with running seawater (1 μm filtered; hereafter FSW), aerated and semi-immersed in a water table at 16 °C. During this period the sea urchins were fed with fresh fragments of *Ulva* sp., and maintained under a light regime that was representative of the austral summer months (14:10 h, light: darkness), with light provided by cool-white LED lams (5.000 K) placed on top of the aquaria.

2.3. Aboral surface covering behaviour in the laboratory

After acclimation, sea urchin covering behaviour was quantified under two contrasting light conditions. This behavioural trait was measured using small black 0.15 L Plexiglas chambers, which were semi-immersed in a temperature-controlled (16 °C) water bath (the same temperature was used in all the experimental trials described below). Each chamber was equipped with an air stone to ensure strong aeration and fitted with a silicone pipe providing a continuous 1 μm filter seawater (hereafter FSW) supply. A small hole, located 1 cm from the top edge of each chamber, served as a seawater outlet, ensuring constant water flow and proper water exchange during the experiment.

The aboral surface covering behaviour was measured on 12 sea urchins assigned to two experimental conditions: natural dark conditions at night (hereafter dark; 0 lx), and lit conditions at night (hereafter ALAN). For the latter treatment, the same LED sources described above were set to a standard 30 lx intensity and maintained above the experimental chambers. Light intensities were measured in the air just above (ca. 2 cm) the water surface using an L-100 PCE Lux Meter. The light intensity used in this experiment (and in others, see below) was within the natural range measured during nighttime hours in rocky intertidal habitats exposed to ALAN (20 to 50 lx) in Chilean coastal habitats exposed to ALAN (Duarte et al., 2019: Pulgar et al., 2019) including the promenade area in Caldera (Manríquez, unpublished data). In each chamber, 30 square fragments of fresh brown algae (*Lessonia berteroana*; ca. 0.5 × 0.5 cm in size) were placed at the bottom alongside each sea urchin. The experiment was conducted during at night between 9:30 PM and 09:30 AM. At the end of that period, each sea urchin was carefully removed and photographed from above, to subsequently estimate the proportion of the sea urchin aboral surface covered by algae. These estimates were then expressed as a percentage and were used for a quantitative comparison of aboral surface covering levels under contrasting light conditions (dark vs. ALAN).

2.4. Y-maze spatial preference experiments

One week after acclimation, the directional responses (spatial preference) of sea urchins were evaluated in a two-choice test using Plexiglas® Y-mazes. The left and right arms of each Y-maze were 0.60 m long, 0.18 m wide and 0.10 m deep. Three Y-mazes (black lateral walls, black lid and white floor) were run simultaneously with both arms of each maze receiving FSW at a constant rate of 1.0 L h^{-1}. The seawater flowing into the arms dropped ca. 1 cm onto the surface of the water. These trials included four distinct experiments (1–4). In experiment 1, the left arm of the Y-maze was exposed to ALAN while the right side was maintained in darkness. In experiment 2, the position of ALAN and dark treatments was reversed, illuminating the right arm of the Y-maze. In experiment 3, both arms were kept in darkness, while in experiment 4, both arms were exposed to ALAN.

Light conditions were created by illuminating the corresponding arm of the Y-maze using a white LED light (30 lx) placed immediately above the arm (ALAN). Dark conditions were created by covering the corresponding arm of the Y-maze with black Plexiglas. As described above, light intensities were measured in the air just above the water surface of each arm (ca. 2 cm) and at the starting zone (center) located 50 cm away from the FSW inlets using a L-100 PCE Lux Meter. To stimulate sea urchin movement, a small fragment (ca. 100 g) of *Ulva* sp. Was placed near the seawater inlets in each arm of the Y-maze at the beginning of each trial. To standardize hunger levels, sea urchins were priorly starved for 24 h. The sea urchins were placed in an acclimation zone for 1 h, and then carefully placed carefully in the Y-maze starting zone (“no selection” area). Each trial lasted 15 h, after which the final position of the sea urchin in the Y-maze was recorded (9:00 AM). That position was categorized as ALAN (arm), dark (arm) or starting (no selection) zone. The Y-

mazes were semi-immersed in a second temperature-controlled water bath to maintain a constant temperature.

2.5. Food consumption experiments

Using the same four experimental trials described above (1–4), the amount alga (*Ulva* sp.) consumed by the sea urchins in each arm of the Y-maze was quantified. To estimate consumption rates, the standard amounts of algal fragments made available to the sea urchins on each arm were weighed at the beginning and then at the end (after 12 h) of each trial across all the experiments and the corresponding light treatments applied (dark and/or ALAN conditions).

2.6. Horizontal speed and self-righting

In laboratory conditions, sea urchins tend to move toward the inner edges of the rearing containers. Using this behaviour as a baseline, two weeks after acclimation, the horizontal speed of the sea urchins was measured in a randomly selected group of 20 sea urchins assigned to contrasting light conditions (dark vs. ALAN). This trait was assessed in a 70 mL flat-bottom plastic jar (4 × 14 cm; height × diameter) filled with FSW. To avoid confounding effects caused by light entering from the sides of the jars, they were covered with black plastic. The sea urchins were starved for 24 h prior to the experiments, placed in the jars for 5 min of acclimation, and then carefully placed at the center of the jars for 5 min. The time taken by each sea urchin to move from the center of the arena to a circular line drawn 6 cm from the jar wall was then measured. In sea urchin horizontal locomotion, speed may change with urchin size not necessarily proportionally (Domenici et al., 2003). Therefore, individuals of similar diameters were used, and the comparison between treatments used urchin diameter as a covariate. Speed was expressed as cm/min, and to avoid daily timing issues, all measurements were conducted during night hours, between 9:30 PM and midnight.

One week after acclimation, sea urchin self-righting times were measured under the contrasting light conditions described above (dark vs. ALAN), using a randomly selected group of 12 sea urchins. Each sea urchin was placed in a small 0.15 L black Plexiglas chamber, which was semi-immersed in a temperature-controlled water bath. The sea urchins were allowed to acclimatize for 10 min in the chamber before being placed upside down. Self-righting time was defined as the time (s) needed by each sea urchin to completely return to its normal upright position (Manríquez et al., 2019b). To avoid disrupting this behaviour, measurements in darkness were conducted with an infrared camera positioned above the chambers. Time (*sec*) was measured using a digital stopwatch and all measurements were conducted during nighttime hours, between 9:30 PM and midnight.

2.7. Metabolic rates and growth rates

Two weeks after acclimation, sea urchin oxygen consumption rates (used here as proxies of metabolic rates) were measured in a randomly selected group of 8 sea urchins assigned to each light treatment (dark vs. ALAN). All measurements were conducted during daylight hours, between 2:30 and 4:30 PM. Two experimental runs were conducted, each run consisting of 4 illuminated and 4 dark 60 mL glass respirometry chambers. The illuminated chambers were lit with a white LED, identical to those used in previous experiments, placed 3 cm above each chamber. The average (±SD) light levels in the artificially lit and dark chambers were 35.8 lx (±2.9; $N = 4$) and 0 lx, respectively. Dark chambers were identical except for being completely covered with sticky-back vinyl tape, leaving a small opening over the oxygen sensor spot (SP-PSt3-NAU, PreSens). The chambers were placed horizontally and semi-immersed in a black Plexiglas® container connected to a refrigerated and heating water bath circulator (Lab Companion RW-2025G) set to 16 °C. In this setup, the oxygen sensor spots (fixed on the inner sides of the chambers) remained 0.5 cm above the water level. To avoid stress during oxygen measurements, the chambers were left undisturbed while the fiber optic probe was applied to the sensor spots. Oxygen consumption rates were measured using a Fibox 3 PreSens fiber optic oxygen meter. Calibration was done with a Na_2SO_3 solution (0 % saturation) and air-bubbled seawater (100 % saturation). The sea urchins were starved in tanks with 1.0 μm filtered running seawater (FSW) for 24 h prior to the measurements. During this period, they were exposed to a standard light intensity of ca. 30 lx (SD = 6.5; $N = 6$), provided by daylight fluorescent tubes. Metabolic measurements lasted for at least 5 h, with the first 10 min being excluded to remove potential manipulation effects. Care was taken to ensure oxygen levels did not fall below 70 % of air saturation. Background respiration was determined in parallel by measuring oxygen consumption in chambers without sea urchins (seawater only), and then subtracting that from experimental oxygen consumption rates. While oxygen consumption by microorganisms potentially associated with the urchin's surface was not directly accounted for in this protocol, such consumption rates were considered negligible (<1 %) in comparison to the sea urchin's consumption rates and, therefore, were not expected to bias comparisons among treatments.

With regards to sea urchin growth rates, one week after acclimation these rates were measured in two randomly selected groups of 7 individuals each, assigned to the contrasting light conditions mentioned above (dark vs. ALAN) over a period of 14 d. In both measurements, the urchins were weighed between 15 and 18 h after the last feeding to ensure they had an empty stomach, thereby providing consistent (unbiased) growth rate measurements Each sea urchin was placed in a black Plexiglas square container filled with running FSW. The continuous flow of filtered seawater (FSW) was achieved through a thin silicone hose entering each container through a small opening 1 cm below the upper edge. A similar opening was on the opposite wall of the container, also 1 cm below the upper edge. In the dark treatment, each container was closed with a black Plexiglas lid, while in the ALAN treatment, the containers were maintained without lids. Each container was equipped with an air-stone placed near the bottom, receiving air through a silicone hose that entered each container through a small opening in the lids or freely, depending on the light treatment. Each group of containers was kept semi-immersed in different water baths (16 °C) and exposed to their corresponding light treatment. Potential biases associated with laboratory lighting were prevented by using blackout cloths. Timers were used to switch the light on and off during nighttime between 9:00 PM and 9:00 AM, and to switch a 6000 lx LED lamp (cool white; 5000 K) on and off during daytime (9:00 AM to 9:00 PM). During these trials, each sea urchin was offered a single fragment of fresh green algae (*Ulva* sp.; ca. 0.2 g) which was replaced every second day. We selected this algal species because it is the primary food item consumed and efficiently assimilated by juvenile sea urchins in the field (Vásquez, 2001; González et al., 2008). Growth was expressed as the Specific Growth Rate (SGR), calculated according to Hopkins (1992) as the percentage change in grams per day (g d^{-1}), considering the initial and final natural logarithms of the wet weight of each sea urchin.

2.8. Statistical analyses

The final position of the sea urchins in the Y-maze spatial preference experiments (1–4; $n = 12$ per experiment) under contrasting light regimes (dark and/or ALAN vs. no selection) were analyzed separately using the Fisher's exact probability test (see Manríquez et al., 2019a). Sea urchin consumption rates in the same Y-maze experiments (1–4; n = 12 per experiment) were also analyzed separately. In this case, given the lack of independence between groups (i.e., food consumption in one Y-maze arm was dependent on the consumption in the other arm or the selection area), we employed the aligned rank transform (ART; Wobbrock et al., 2011) available in the *ARTool* library in R, which allowed ANOVAs to be performed on ranked data.

The dark-ALAN comparison of sea urchin aboral surface covering,

Table 1
Mean (± SE) size and percentage of *Loxechinus albus* recorded in three microhabitats of the low rocky intertidal zone, holding material against their aboral surface (covering). The percentage of the total aboral surface area of these sea urchins covered by material, as well as the percentage of this area corresponding to organic (algal fragments) or inorganic material (e.g., shell fragments and pebbles) and the organic to inorganic ratio are also reported.

Microhabitat	Diameter (cm)	Covering (%)	Total surface (%)	Algal fragments (%)	Shell fragments and pebbles (%)	Algal / inorganic (ratio)
Beneath canopies	7.35 (0.30)	46	43.1 (4.5)	72.5 (5.6)	27.5 (5.6)	3.19 (0.63)
Near canopies	6.07 (0.20)	76	51.1 (3.5)	71.2 (5.4)	28.8 (5.4)	4.13 (1.07)
Open areas	7.11 (0.19)	38	27.3 (3.1)	24.8 (7.6)	75.2 (7.6)	0.93 (0.60)

horizontal speed, self-righting times, metabolic rates, and growth rates were conducted using separate *t*-tests (one-way ANOVAs comparing two groups). For the analysis of sea urchin horizontal speed, we used a univariate analysis of covariance (ANCOVA) to compare treatments, using sea urchin diameter as a covariate. Normality of residuals for all the analyses was checked with the Shapiro-Wilk test, and homogeneity of variances was assessed using Levene's tests. To meet normality requirements in the sea urchin aboral surface covered by algal fragments, data were arcsine-transformed. All data analyses were conducted using R software (R Core Team, 2020).

3. Results

3.1. Sea urchin surface covering in nature and in the laboratory

Regardless of the microhabitat analyzed, sea urchins with material covering their body surfaces were always found (Table 1, Fig. 1). The covering material was primarily fragments of *L. berteroana*, with smaller proportions of stones and shell fragments. The highest percentages of sea urchins with covered material were recorded on rocky substrates near the canopy of *L. berteroana* (ca. 76 %) and below the canopy of these macroalgae (ca. 46 %). In contrast, the lowest percentages were found on flat, open rocky substrates away from the macroalgae (ca. 38 %). In terms of aboral sea urchin surface covered by material, the highest percentages were recorded below the canopy (ca. 43 %) and near the canopy (ca. 50 %). The lowest values were recorded on open rocky substrates away from the macroalgae (ca. 27 %) (Table 1). The ratio of organic (algal) to inorganic (stones and shell fragments) material, in terms of the surface area covering the aboral surface of the sea urchin, was ca. 3 and 4 for individuals recorded beneath and near the canopies, respectively (Table 1). However, this ratio was ca. 1 for those recorded in open areas (Table 1).

Observations conducted in laboratory trials provided evidence of the active role of tube feet and spines in the displacement of algal fragments from the bottom of the containers to the aboral surface of the sea urchins. After 12 h, covering was recorded in all the sea urchins, regardless of light treatment. However, the aboral surface covered with algae was at least twice larger in sea urchins exposed to ALAN (84 %) than those in dark conditions (40 %) (Fig. 2; Table 2).

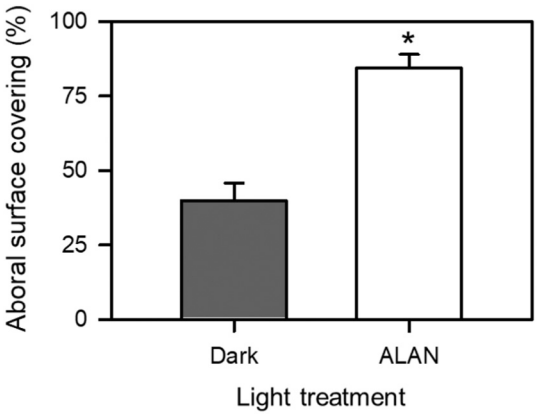


Fig. 2. Mean (+ SE) aboral surface covering measured in the sea urchin *Loxechinus albus*, when exposed to natural dark conditions (dark; filled bar), and ALAN (open bar). The sea urchins used fragments of the brown algae *Lessonia berteroana* for covering. An asterisk on top of the ALAN bar identifies a significant difference with the dark treatment. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Summary of the analyses conducted to evaluate covering prevalence in three microhabitats in nature and the influence of ALAN exposure on horizontal speed, self-righting times, oxygen consumption and growth rates of *Loxechinus albus*. The horizontal speed analysis was performed using ANCOVA with sea urchin diameter as covariate, while the other four variables measured in the laboratory were analyzed using one-way ANOVAs. *P*-values in bold indicate significant sources of variation. DF: degrees of freedom.

Response variable	Source of variation	DF	F-value	P
Covering in nature	Microhabitat type	1	27.21	**<0.001**
	Residual	18		
	Light treatment	1	9.68	**0.003**
Horizontal speed	Diameter	1	0.31	0.580
	Residuals	37		
Self-righting time	Light treatment	1	37.82	**<0.001**
	Residuals	38		
Oxygen consumption	Light treatment	1	37.31	**<0.001**
	Residuals	14		
Growth rate	Light treatment	1	36.25	**<0.001**
	Residuals	12		

3.2. Y-maze spatial preferences

Experiments 1 and 2 exposed alternate arms to dark and ALAN conditions, and in both cases, by the end of the trials a significantly higher number of sea urchins were found in the dark arm (Fig. 3a,b; $\chi^2 = 20.25$, DF = 2, $p < 0.001$; and $\chi^2 = 14.25$, DF = 2, $p = 0.001$, for Experiments 1 and 2, respectively). When both arms of the Y-maze were kept dark (Experiment 3), the distribution of sea urchins among the three final positions was not significantly different ($\chi^2 = 5.25$, DF = 2, $p > 0.05$; Fig. 3c). In contrast, when both arms were exposed to ALAN (Experiment 4), most sea urchins remained in the starting position (i.e., no selection) (Fig. 3d; $\chi^2 = 27.75$, DF = 2, $p < 0.001$; Fig. 3d).

3.3. Algal consumption rates

With regards to algal consumptions rates, sea urchins in the dark arm consumed nearly 14 and 5 times more algae than those in the ALAN arm, in Experiments 1 and 2, respectively ($F_{1,22} = 47.53$; $p < 0.001$ and $F_{1,22} = 14.24$; $p = 0.001$; Fig. 4a,b). By comparison, in experiments 3 and 4, when both arms of the Y-maze were kept either dark or lit (ALAN), no significant differences in consumption rates were detected between arms ($F_{1,22} = 0.07$; $p = 0.801$ and $F_{1,20} = 2.15$; $p = 0.158$, respectively; Fig. 4c, d).

3.4. Horizontal speed and self-righting

For the comparison of horizontal speed, the size (diameter) of the sea urchin was not different between treatments ($F_{1,38} = 0.192$; $p = 0.664$). The covariance analysis showed that sea urchins exposed to ALAN were

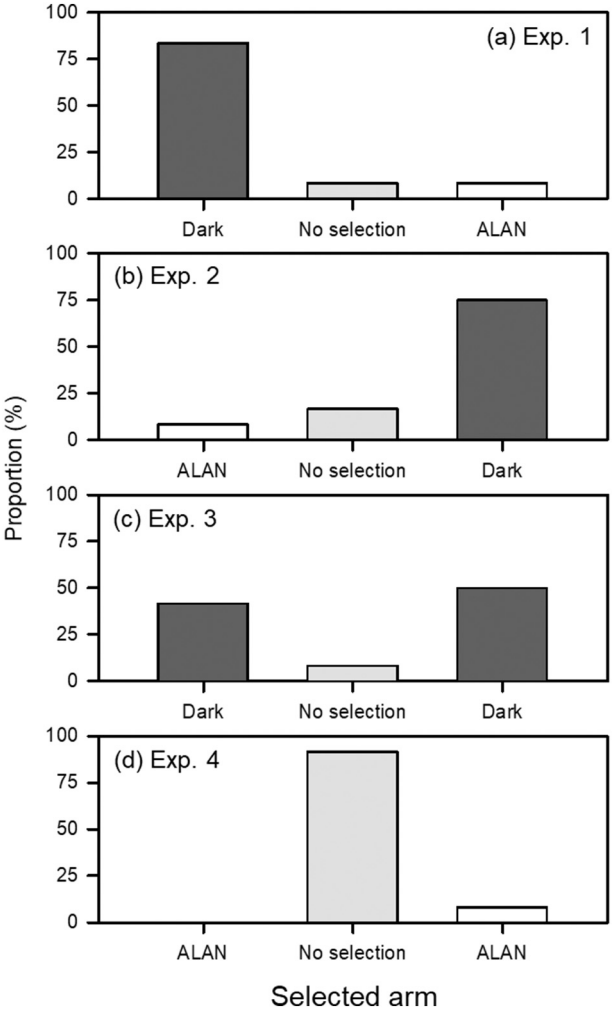


Fig. 3. Proportion (%) of sea urchins (*Loxechinus albus*) found in the arms of the Y-mazes and exposed to dark (dark filled bars), lit (ALAN, open bars) or at the initial area (no selection), in each of the four experiments conducted (a–d).

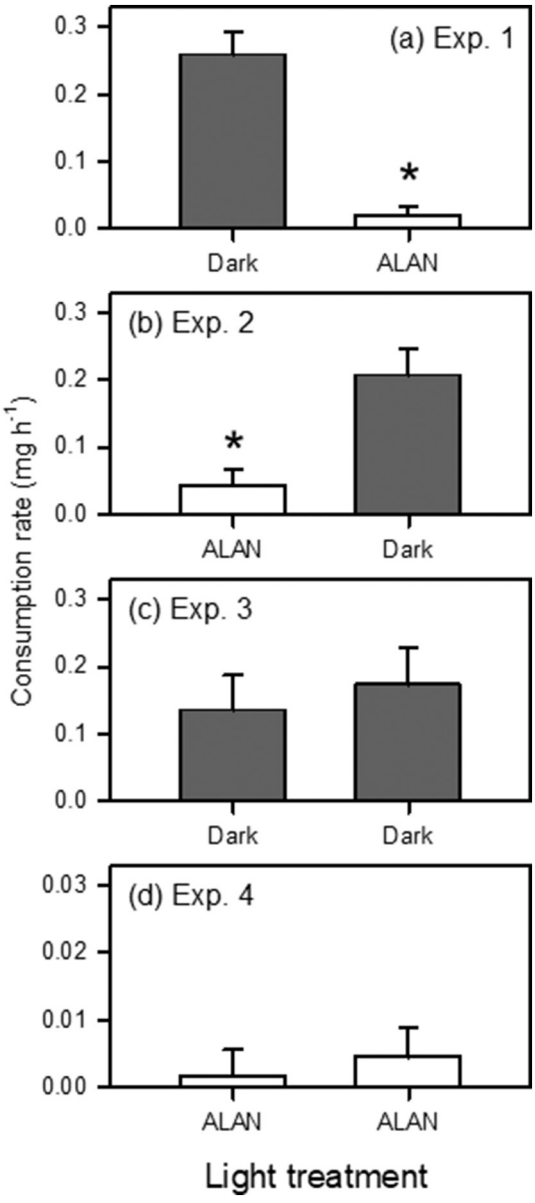


Fig. 4. Mean (+ SE) algal consumption rates by the sea urchin *Loxechinus albus*, at the arms of the Y-mazes exposed to natural dark conditions (dark; filled bars) or lit conditions (ALAN; open bars), in each of the four experiments conducted (a–d). An asterisk on top of the ALAN bar identifies a significant difference with the dark treatment.

nearly 43 % faster than those maintained in natural dark conditions ($F_{1,37} = 9.74$; $p = 0.003$; Table 2; Fig. 5a), a difference that cannot be attributed to sea urchin diameter ($F_{1,37} = 0.312$; $p = 0.580$). Sea urchins exposed to ALAN were nearly 40 % faster than those maintained in natural dark conditions ($F_{1,14} = 37.31$; $p < 0.001$; Table 2; Fig. 5a). Sea urchins exposed to ALAN also exhibited significantly shorter self-righting times than those maintained in dark conditions ($F_{1,38} = 37.83$; $p = 0.001$; Table 2; Fig. 5b).

3.5. Metabolic rates and growth rates

Sea urchins exposed to ALAN exhibited metabolic rates (i.e., oxygen consumption rates) that were 1.5 times higher than those measured on individuals kept in the dark ($F_{1,14} = 37.31$; $p < 0.001$; Table 2; Fig. 6a). Instead, sea urchins kept in darkness showed specific growth rates that were 2.5 times higher than those exposed to ALAN ($F_{1,11} = 36.25$; $p < 0.001$; Table 2; Fig. 6b).

4. Discussion

The bulk of the results gathered here, from a field site and from various experimental manipulations, provide strong support to our working hypothesis. While responses to ALAN are most often complex, both behavioural traits as well as physiological measures of sea urchin fitness indicate that ALAN exposure is consistently detrimental to *L. albus*. Given the key role played by this species in the rocky shore intertidal and shallow subtidal (Friedlander et al., 2020), behavioural and physiological responses to ALAN are likely to have branching effects on other species and resources.

In the field, *L. albus* individuals consistently covered their bodies with various materials, suggesting that this behaviour may protect them from daylight and other natural stressors, such as risk from visual predators. The highest percentages of covered sea urchins were measured near the *L. berteroana* canopy and in the rocky substrates beneath them (76 % and 46 %, respectively), while lower percentages were found on flat rocks (38 %). Likely, the proximity to macroalgae increases material availability, potentially encouraging covering behaviour. Instead, the lower proportion of sea urchins displaying covering beneath the algal canopy, may be related to the shading effect already provided by the canopy itself. A similar argument can be made for the individual aboral surface covering measured in sea urchins near

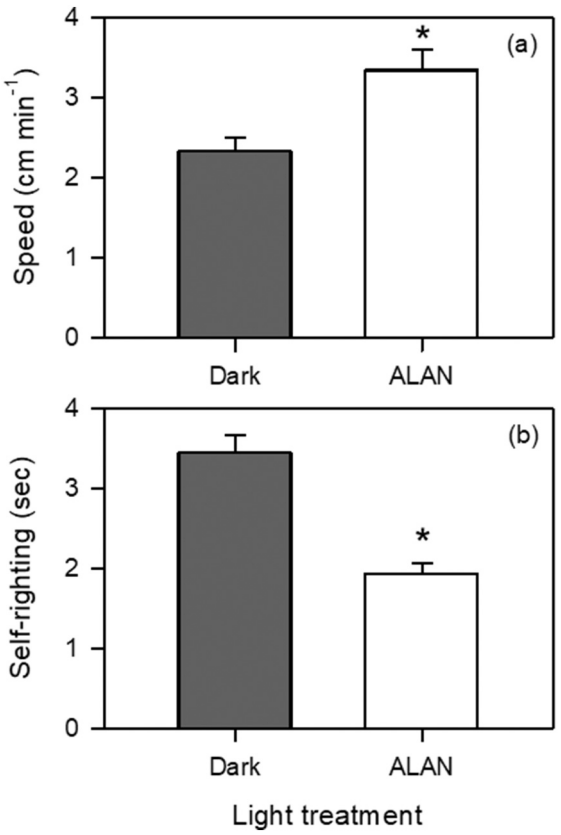


Fig. 5. Mean (+ SE) speed (a) and self-righting time (b) measured in the sea urchin *Loxechinus albus*, when exposed to natural dark conditions (dark; filled bar), and ALAN (open bar). An asterisk on top of the ALAN bar identifies a significant difference with the dark treatment.

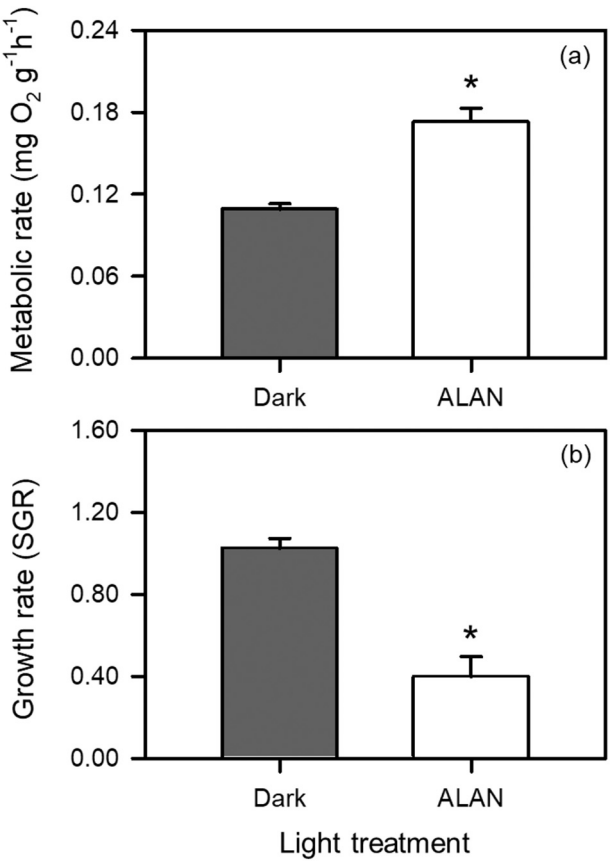


Fig. 6. Mean (+ SE) metabolic rates (a) and growth rates (Specific Growth Rate, % day^{-1}) (b) measured in the sea urchin *Loxechinus albus* when exposed to natural dark conditions (dark; filled bar) and ALAN (open bar). An asterisk on top of the ALAN bar identifies a significant difference with the dark treatment.

and beneath the canopy (50 % and 43 %, respectively) compared to individuals found in open rocky substrates (27 %). The relationship between the gradient of sunlight exposure, from open microhabitats to the more shaded conditions near or beneath the canopies, is not linear. This suggests, again, that in addition to light exposure, the availability of materials driven by debris accumulation nearby macroalgae, likely contributes to covering behaviour. While some of these algal fragments eventually move from the aboral to the oral surface to be consumed by the sea urchins, other algal fragments, shell and pebble fragments, remain on the aboral surface. Such cover helps against threats such as predation (Watts et al., 2013), harmful ultraviolet light (Adams, 2001; Sigg et al., 2007), strong light (Millott, 1956), dislodgment by waves or strong currents (Sharp and Gray, 1962), and as a lever in righting behaviour (Lawrence, 1976). The organic-to-inorganic ratio of covering material also indicates that microhabitat strongly influences the type of material sea urchins use for covering. Under and near canopy habitats, where algal cover is higher, urchins carry three to four times more organic (algal) material than inorganic fragments. In open areas, by contrast, they use roughly equal amounts of organic and inorganic material. This suggests that sea urchins adjust their covering behaviour based on local resource availability, favouring algal cover when it is plentiful but relying more on stones and shell fragments when algae are scarcer.

In daylight, *L. albus* likely seeks access to covering materials to face light exposure and alternate stressors. In fact, a laboratory study found that the presence of a predator modulated the effects of light (in that case ALAN) on prey feeding rates by the gastropod *Concholepas concholepas* (Manríquez et al., 2019a). Similar trade-offs likely operate and contribute to covering behaviours in the small sea urchins, particularly at night, when they are known to be most active (Smith et al., 2024). ALAN exposure is likely to stress the sea urchins, inducing behavioural responses such as covering behaviour to avoid light exposure. Future studies should experimentally evaluate how a gradient of ALAN exposure might affect surface covering and other behavioural traits of *L. albus*, to further clarify its ecological implications (see Quintanilla-Ahumada et al., 2022 for a study on ALAN dose-response in intertidal isopods). However, some insights can be gained already from our laboratory experiments (see below), where exposure to contrasting light conditions prompted an aboral surface covering two times higher on sea urchins exposed to ALAN compared to those kept on natural dark conditions. We recorded algal fragments being actively moved by tube feet and spines to the aboral surface, so this seems an adaptive behavioural response to deal with light exposure, rather than merely a passive accumulation of material. This behaviour likely mitigates the effects of light during both daytime and nighttime hours by providing a barrier that shields individuals from harmful UV radiation, minimizing physiological stress and the disruption to natural behaviours such as foraging and resting.

The results of the four Y-maze experiments revealed a strong sea urchin preference for dark over lit (ALAN) habitats, indicating negative phototaxis. When given a choice, a large majority of the sea urchins chose the dark arm, showing an aversion to areas exposed to ALAN. These results align with previous evidence on the displacement and preference of other two species inhabiting rocky intertidal habitat in Chile: the gastropod *C. concholepas* (Manríquez et al., 2019a) and the intertidal fish *Girella laevisifrons* (Pulgar et al., 2023). They are also consistent with the findings of a field study conducted in the Mediterranean Sea with the sea urchin *Paracentrotus lividus* (Sanna et al., 2024). These authors found a significant effect of ALAN on the locomotion of

this species, with individuals actively moving away from light sources, a behaviour not observed in dark conditions. Despite the wide range of light-induced behavioural responses described in sea urchins (see Sun et al., 2019), no obvious eye-like structure has been reported in these animals. However, the presence of photoreceptor cells (PRCs) in the tube feet of another sea urchin, *Strongylocentrotus purpuratus*, has been proposed as the functional equivalent of a large compound eye in sea urchins (Ullrich-Lüter et al., 2011). These sensory organs likely help species such as *L. albus* to actively avoid natural and artificial light stress during day and night hours.

Sea urchin light avoidance (negative phototaxis) may partially explain the lower algal consumption rates consistently recorded in the lit arm of the Y-maze. When given a choice between light treatments (dark vs. ALAN), the sea urchins consumed drastically (significantly) lower amounts of the algae available. These findings suggest that ALAN may directly inhibit foraging and potentially alter additional types of activity in this species (see below). These results also closely align with previous studies that have documented reduced feeding rates in sessile (Christoforou et al., 2023; Xu et al., 2003; Hassan et al., 2024; Lynn et al., 2024) and mobile marine invertebrates (Lynn et al., 2021; Manríquez et al., 2021a, 2021b; Quintanilla-Ahumada et al., 2024b), when exposed to artificial lighting. In the long-term (i.e., under persistent ALAN exposure), a reduction in feeding rates may limit *L. albus* growth rates (see below) or other life history traits, underscoring the potential long-term impact of artificial light on this species.

In rocky intertidal habitats during daytime hours, or immediately before, most individuals of *L. albus* seek shadowed microhabitats to avoid light exposure. The laboratory measurements of horizontal speed were consistent with those field observations. Under ALAN exposure, sea urchins moved significantly faster than those in the dark conditions, a result that we interpret as a quick light-avoidance response. In direct correspondence with the preference patterns recorded in the Y-maze, ALAN seemed to prompt the sea urchins to quickly move away from the lit area, minimizing the stress associated with ALAN exposure (possibly from the perception of a heightened visual predator risk). If ALAN sources become permanent features nearby rocky shore habitats, as the continued spread of this stressor suggests (Gaston et al., 2013), it is reasonable to expect disruption in natural movement patterns, ultimately affecting habitat use and foraging efficiency (the latter already made evident by reduced algal consumption rates).

Self-righting responses are critical for sea urchin and many other slow-moving invertebrates. The oral surface of these organisms is not covered with spines, so this area is the most (if not the only area) susceptible to predator attacks. In our study, ALAN exposure reduced self-righting times, in other words, caused a faster self-righting reaction in the sea urchins. We interpret such response as a behavioural mechanism to minimize stressful light exposure, and more importantly, to minimize vulnerability to predators. These results align with a prior study that found that juvenile *C. concholepas* stressed by elevated pCO_2 and the presence of a predatory crab exhibited significantly shorter self-righting times compared to those maintained under control conditions (Manríquez et al., 2013). However, a study exposing the same species to ALAN showed no such differences (Manríquez et al., 2019a). This suggests that stressors such as pCO_2, predator cues, and ALAN may influence self-righting behaviour in complex ways, underscoring the need for further research to understand how these stressors (and their combination) affect the behaviour of marine organisms. This evidence also suggests that the effects of ALAN on self-righting times may differ among species and the context in which measurements are made.

The consumption of oxygen, used here as a proxy of metabolic rates, was significantly higher (nearly 58 % more in average) in sea urchins exposed to ALAN than in those maintained in natural dark conditions at night. While various factors may be at play to explain these differences (Carey et al., 2016), the most plausible factor is the heightening of stress levels due to light exposure. This entails that ALAN may have imposed added physiological demands and increased metabolic costs on the sea urchins (e.g., Carey et al., 2016). Such costs take away energy that could be used for alternative activities such as habitat exploration, feeding, reproduction and growth. As expected, the higher metabolic costs imposed by ALAN, along with the lower consumption rates measured in ALAN-exposed habitats (see above), had direct consequences on the sea urchin growth rates. Sea urchins exposed to ALAN did grow significantly less (less than half) than those maintained in natural dark conditions. The magnitude of such decline is striking considering that species most often have physiological mechanisms to cope with the effects of stressors while trying to maintain growth rates (e.g., feeding compensation, enhanced absorption rates, etc.; Hill and Lawrence, 2006). The differences are also striking considering the rather inconsistent evidence available on the effects of ALAN on growth rates. While some studies have detected a significant effect on growth (e.g., Luarte et al., 2016; this study) others have found milder or non-significant impacts (Tidau et al., 2023; Lynn et al., 2021; Quintanilla-Ahumada et al., 2022). An example of the latter (Tidau et al., 2023) found that ALAN had no effect on the early ontogenetic growth of the mussel *Mytilus edulis* and the barnacle *Austrominius modestus*. Regardless, the bulk of the results gathered in our study points toward strong (consistent) negative effects of ALAN on metabolic and growth rates.

5. Conclusions

Overall, our findings provide novel evidence on how ALAN influences multiple behavioural and physiological traits in *L. albus*. To our knowledge, this is the first study to conduct a multi-dimensional assessment of ALAN in a sea urchin species, highlighting the need for integrative approaches in future research. We conclude that ALAN exposure induces stress responses in *L. albus*, including negative phototaxis, faster self-righting, increased horizontal speed, reduced feeding, heightened metabolic rates, and diminished growth. These findings align with field observations suggesting that covering behaviour is modulated by daylight exposure, indicating that both nocturnal and diurnal light conditions influence the species' behavioural and physiological adaptations. However, if ALAN sources become persistent features in these habitats, they may interfere with the natural circadian cycle, and may pose a threat to sensitive species like *L. albus*. Unlike the predictable and gradual changes in natural light, ALAN introduces abrupt and continuous illumination during nighttime hours, disrupting the internal biological clocks that regulate essential processes such as metabolism, and behaviour. In this context, the observed reduction in feeding and growth, despite increased activity and metabolic rates, suggests a potential energy allocation trade-off, whereby individuals exposed to ALAN divert energy from foraging and somatic growth toward stress-induced locomotor and avoidance behaviours. Existing evidence collectively supports the idea that ALAN can cause organisms to reallocate energy away from essential processes like feeding and growth and toward coping responses, underscoring the ecological implications of light pollution. For example, in the common toad (*Bufo bufo*), ALAN disrupted activity patterns and energy allocation during the breeding period, leading to decreased locomotor activity and potential impacts on reproductive success (Touzot et al., 2020). In the nesting songbird *Parus major*, ALAN exposure reduced body mass gain in nestlings without affecting oxidative status, suggesting that increased nocturnal activity elevates metabolic demands and diverts energy away from growth (Raap et al., 2016). In the amphibian *Anaxyrus americanus*, exposure to ALAN altered feeding behaviour and slowed larval development, further supporting the idea of energy reallocation from growth to stress-coping mechanisms in amphibians (Dananay and Benard, 2018). Similarly, in the marine gastropod *C. concholepas*, feeding rates under ALAN conditions were three to four times lower than under control (day-night) conditions. Individuals exposed to ALAN also showed a significantly higher tendency to hide in dark refuges compared to controls. Although ALAN may not increase predation risk in this species, heightened vigilance (i.e., refuge-seeking) reduces the time available for foraging,

which may ultimately compromise long-term fitness and productivity (Manríquez et al., 2021a, 2021b).

The influence of ALAN on *L. albus* behavioural and physiological traits may have broad ecological implications, particularly for individuals inhabiting coastal areas increasingly impacted by ALAN (Davies et al., 2020). Since *L. albus* is a key ecological player along a rather vast shoreline system (6–56° S), any ALAN-related changes in its behaviour and physiology are likely to have branching (still unknown) effects on macroalgae and the communities they support. Aboral surface covering is part of the broad behavioural repertoire of sea urchins, and although it is complex and multifaceted in nature, it seems to be consistently used by these species against light exposure. This behaviour, along with active (fast) ALAN avoidance, could be crucial for minimizing the negative impacts of light pollution on this and potentially on other organisms sharing similar sensory mechanisms. Future research should explore the role of photoreceptors in light-induced, examining how ALAN affects intertidal species in a field context.

Our results provide empirical support for the idea that *L. albus*, like other echinoderms, relies on light cues to regulate a suite of ecologically relevant behaviours. The heightened covering responses observed under ALAN exposure, combined with a strong preference for dark environments in the Y-maze tests, suggest that ALAN disrupts the normal light-guided behavioural repertoire of juvenile sea urchins. These findings are consistent with the notion that sea urchins possess a decentralised but functional visual system, mediated by photoreceptor cells in their tube feet, which enables them to detect changes in ambient light and respond adaptively (Yerramilli and Johnsen, 2010; Ullrich-Lüter et al., 2011). While these photoreceptors are typically associated with regulating behaviours under natural daylight conditions, such as shelter-seeking, predator avoidance, and diurnal movement patterns, we suggest they may also mediate responses to ALAN. In contrast, other marine invertebrates such as arthropods and molluscs possess more advanced visual systems (Cronin, 1986a; Cronin, 1986b), which support more complex visually guided behaviours including orientation, feeding, and mating (Cronin, 1986a; Cronin and Jinks, 2001). For example, in sandy beach crustaceans with compound eyes, ALAN exerts more severe and longer-lasting effects on the isopod *Tylos spinulosus* than on the amphipod *Orchestoidea tuberculata*, as the former is active under lower ambient light levels at night (Miranda-Benabarre et al., 2024). These findings were attributed to ALAN causing photoreceptor damage and differing recovery capacities between the two species: ALAN caused structural damage in the isopod's rhabdom, with no signs of recovery after 1 and 24 h (Miranda-Benabarre et al., 2024). This aligns with reports showing that ALAN disrupts the distribution and circadian rhythm of the sandy beach isopod *T. spinulosus* (Duarte et al., 2019). These results highlight the importance of baseline visual sensitivity in determining species-specific vulnerability to ALAN, regardless of whether species rely on complex visual systems or not. Therefore, we suggest that ALAN may override natural diel light cues perceived by these photoreceptors, leading to altered behavioural patterns such as increased locomotion, faster self-righting, and reduced foraging activity.

In practical terms, our findings emphasize the need for less biologically disruptive lighting systems (Gaston et al., 2012). We argue that the development of beachfront lighting ordinances is essential to protect organisms inhabiting coastal areas. Given that LED lighting can be highly directional, one potential solution is to direct light sources toward specific targets where human activities occur (e.g., coastal pedestrian paths, street lighting, ports, marine research laboratories and routes). In fact, minimizing upward and lateral light emissions has been proposed to reduce the threat posed by residential and commercial nocturnal lighting to petrels and shearwaters (Rodríguez et al., 2019). Such proposal builds on evidence showing that directing light via shielding to minimize upward radiation can significantly reduce the fatal attraction of petrels to security lights (Reed et al., 1985). Additional examples of directional lighting used to mitigate the environmental impacts of ALAN are well documented in the literature (Longcore et al., 2017). A similar approach could help prevent or minimize the illumination of coastal habitats occupied by sensitive species, including *L. albus*. Moreover, this study focused on the influence of one type of ALAN at a conservative light intensity (Quintanilla-Ahumada et al., 2022). However, future research should investigate how different light intensities and/or spectra may differentially affect behavioural and physiological responses in *L. albus* and other species (see e.g., Quintanilla-Ahumada et al., 2024). Environmental stressors often co-occur in natural settings (Crain et al., 2008), highlighting the need for future studies that consider how ALAN might interact with these factors (but see Manríquez et al., 2021a, 2021b). In this context, a recent study reported that ALAN alters the foraging behaviour of freshwater amphipods depending on the light spectrum and the presence of predation cues (Hassan et al., 2024). Although the evidence remains limited, there is a growing body of research examining the combined effects of ALAN and climate change-related stressors. For instance, ALAN has been shown to enhance seaweed growth and functioning; however, these effects appear to be species-specific and may be counteracted by warming, suggesting a potential antagonistic interaction between these global stressors (Caley et al., 2024). In another example, ALAN alone had minimal impact on reducing male juvenile development time in the Pacific field cricket *Teleogryllus oceanicus* (McNamara et al., 2025). Interestingly, the same study found that while ALAN combined with warming had little overall effect, ALAN did reduce female developmental duration at control temperatures, but not under elevated temperatures. Furthermore, since ALAN alters the physiology and biochemistry of symbiotic reef-building corals (Levy et al., 2020), and ocean acidification reduces carbonate availability, affecting calcification and potentially disrupting intracellular acid-base balance and photosynthesis through cellular stress (Kaniewska et al., 2012), both stressors acting together may exert synergistic effects on these organisms. Understanding such complex interactions is especially critical given that ALAN rarely acts in isolation but frequently co-occurs with other global change drivers such as ocean warming and acidification. These multiple, simultaneous pressures may interact in synergistic, antagonistic, or additive ways, potentially amplifying or buffering the individual effects of each stressor. As such, future research should prioritise assessing how ALAN interacts with climate-related stressors to influence key physiological and behavioural fitness-related traits in coastal organisms. This integrated perspective is essential for developing realistic and ecologically meaningful mitigation strategies, including targeted lighting policies that account not only for ALAN itself but also for the broader environmental context in which it occurs.

CRediT authorship contribution statement

Patricio H. Manríquez: Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **Diego Quintanilla-Ahumada:** Visualization, Formal analysis, Data curation, Writing – review & editing, Writing – original draft. **Claudio P. González:** Investigation, Writing – review & editing, Writing – original draft. **Paolo Domenici:** Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **Jorge Bravo:** Resources, Writing – review & editing, Writing – original draft. **Andrés Camaño:** Funding acquisition, Writing – review & editing, Writing – original draft. **José Pulgar:** Funding acquisition, Conceptualization, Writing – review & editing, Writing – original draft. **Pedro A. Quijon:** Visualization, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **Cristian Duarte:** Resources, Project administration, Funding acquisition, Conceptualization, Writing – review & editing, Writing – original draft.

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.

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Data availability

Data will be made available on request.

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