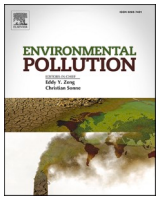
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Splitting light pollution: Wavelength effects on the activity of two sandy beach species☆

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ABSTRACT

Artificial Light at Night (ALAN) threatens to disrupt most natural habitats and species, including those in coastal settings, where a growing number of studies have identified ALAN impacts. A careful examination of the light properties behind those impacts is important to better understand and manage the effects of this stressor. This study focused on ALAN monochromatic wavelengths and examined which types of light spectra altered the natural activity of two prominent coastal species from the Pacific southeast: the talitroid amphipod *Orchestoidea tuberculata* and the oniscoid isopod *Tylos spinulosus*. We compared the natural daylight/night activity of these organisms with the one they exhibit when exposed to five different ALAN wavelengths: lights in the violet, blue, green, amber, and red spectra. Our working hypothesis was that ALAN alters these species' activity at night, but the magnitude of such impact differs depending on light wavelengths. Measurements of activity over 24 h cycles for five consecutive days and in three separate experiments confirmed a natural circadian activity pattern in both species, with strong activity at night (~90% of probability) and barely any activity during daylight. However, when exposed to ALAN, activity declined significantly in both species under all light wavelengths. Interestingly, amphipods exhibited moderate activity (~40% of probability) when exposed to red lights at night, whereas isopods shifted some of their activity to daylight hours in two of the experiments when exposed to blue or amber lights, suggesting a possible alteration in this species circadian rhythm. Altogether, our results were consistent with our working hypothesis, and suggest that ALAN reduces night activity, and some wavelengths have differential effects on each species. Differences between amphipods and isopods are likely related to their distinct adaptations to natural low-light habitat conditions, and therefore distinct sensitivity to ALAN.

1. Introduction

Natural light-dark cycles are used by organisms as cues in an array of physiological and behavioral processes (Torres et al., 2020; Sanders et al., 2021). However, the ongoing disruption of the nightscape by Artificial Light at Night (hereafter ALAN) threatens to alter some of those processes (Longcore and Rich, 2004; Gaston et al., 2021). Even though some authors still refer to ALAN as an emerging stressor, light pollution sources have been present and evolving for over a century (Holden, 1992), currently spreading along terrestrial and most coastal habitats (Lynn and Quijón, 2022; Marangoni et al., 2022). Studies documenting ALAN impacts have shown that this stressor can disrupt a wide range of life history traits, including among others species orientation (Lorne and Salmon, 2007), locomotor activity (Luarte et al., 2016; Lynn et al., 2021a), condition and decision making (Pulgar et al., 2019, 2023), foraging and predator-prey interactions (Dwyer et al., 2013; Underwood et al., 2017; Manríquez et al., 2019), reproduction (Fobert et al., 2019; Davies et al., 2023) and settlement (Lynn et al., 2021b;

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Manríquez et al., 2021). The evidence this far shows that ALAN impacts depend not only on the presence but also on the properties of the light (see Sanders et al., 2021). Therefore, a growing number of studies are calling for a closer examination of ALAN characteristics to envision the full scale of their potential impacts (van Langevelde et al., 2011; Gaston et al., 2013).

ALAN impacts have been documented on multiple coastal species (see reviews by Lynn and Quijón, 2022; Marangoni et al., 2022), yet the precise light properties behind the measured effects are not fully understood. Light sources with widely different properties have been used across ALAN studies, limiting our ability to identify general effects on e.g., taxonomically related species, or unrelated species living in similar habitats. One of these properties, light spectral composition, has been shown to exert a differential influence on biological processes such as activity rhythms, reproduction, hormone release, and gene expression (Brüning et al., 2016; Li et al., 2022; Botte et al., 2023). For example, blue lights have been shown to influence valve behavior and clock-associated gene expression in oysters (*Crassostrea gigas*) more so than red, green, or white lights (Botte et al., 2023). Conversely, arctic copepods have shown a greater sensitivity to red lights than to white, blue, or green lights (Båtnes et al., 2015), while the growth of cultured freshwater prawn has been observed to increase under green but not red lights (Wei et al., 2021).

The talitroid amphipod *Orchestoidea tuberculata* and the oniscoid isopod *Tylos spinulosus* are prominent sandy beach species in northern Chile, southeast Pacific (Jaramillo et al., 2003). Like other sandy beach peracarids elsewhere (e.g., Mezzetti and Scapini, 1995; Lynn et al., 2021a, 2023), adult stages of these species are active foragers during the night hours, remaining virtually inactive during daylight. This makes these species vulnerable to ALAN (see Luarte et al., 2016; Duarte et al., 2019), and suitable models for quantifying their response to different ALAN wavelengths. Hence, this study assessed various monochromatic light spectra that may potentially alter these species' locomotor (i.e., foraging) activity. Our working hypothesis was that ALAN reduces these species activity, with different wavelengths potentially eliciting distinct responses on these organisms. We tested this hypothesis using laboratory experiments that quantified the activity of amphipods and isopods in natural daylight/night conditions in comparison with the activity they exhibit when exposed to ALAN sources associated with five distinct wavelengths: violet, blue, green, amber, and red lights.

2. Material and methods

2.1. Collection and acclimation of amphipods and isopods

Adult specimens of *Orchestoidea tuberculata* and *Tylos spinulosus* (hereafter amphipods and isopods, respectively), were collected from their burrowing area at the upper intertidal zone of Las Conchitas sandy beach, northern Chile (29°15′19″ S, 71°26′47″ W). This location was chosen because it is distant from urban areas and networks of coastal lighting, providing natural dark conditions at night (see Duarte et al., 2019). In order to avoid possible seasonal biases in behavior or activity patterns, (Scapini et al., 1992; Jaramillo et al., 2003; Nardi et al., 2003), all the specimens used for the experiments were collected manually at night low tide conditions during the austral spring-summer season. Amphipods and isopods were separated per species and placed in plastic containers containing damp sand (~10% water content) and a few seaweed blades (the common *Durvillaea antarctica*), and then transported to the laboratory. Before the experimental trials begun (see below) both species were maintained in continuous darkness (0 lux), at 15 °C, and ~90% humidity for an acclimation period of 48 h. Acclimation under dark conditions follows the methodology used in prior ALAN experiments (see e.g., Duarte et al., 2019; Lynn et al., 2021a, 2021b) which has been shown not to influence the outcome of subsequent experiments. The temperature was maintained constant with an air conditioner system, while humidity was maintained by spraying filtered seawater from the field site daily. During acclimation, the specimens were provided with food *ad libitum* by placing a piece of seaweed collected from the same field site.

2.2. Actographs and activity trials

After acclimation adult isopods (20–25 mm body length) and amphipods (14–17 mm body length) were separately placed in 40 × 26 × 20 cm high acrylic tanks (20 specimens of either species per container) filled with 6 cm of clean moist sand previously collected from the field site. The use of 20 individuals per tank allowed for consistent measurements of locomotor activity using actographs, and followed the protocols successfully applied before in ALAN studies with these and other species (e.g., Duarte et al., 2019; Lynn et al., 2021a, 2021b). Clean sand was obtained by repeatedly sieving sediments until ensuring that there were no organisms or seaweed remains left. These sediments were deep enough to allow for natural burrowing under the surface, as directly observed in the trials and in prior studies with the same species (e.g., Duarte et al., 2019). Tanks with specimens were randomly allocated to one of the six independent light treatments described in detail below (control and five different ALAN sources), to conduct measurements in three separate experiments in the 2021 and 2024 seasons. Each tank with either amphipods or isopods was fitted on one side with an actograph (infrared recording systems built by Ingeniería y Servicios Paulo Leal EIRL; see Duarte et al., 2019), which allowed us to quantify organisms' locomotor activity. The actographs recorded the interruption of two infrared beams passing across the tank immediately above the surface of the sand. We worked with two beams to prevent potential data loss due to occasional failure of one of the beams (in cases where both beams worked properly, one was randomly chosen). Activity trials lasted five uninterrupted days, after which, using a predefined download interval period (1 min), data from the actographs were uploaded onto a computer. For the duration of the trials, all the tanks were kept at constant temperature (15 °C) and humidity levels (~90%; see above). Food included a small blade (~5 g) of seaweed (*D. antarctica*) placed over the surface of the sand every other day.

2.3. Natural day/night versus ALAN conditions

Each tank with either 20 amphipods or 20 isopods was maintained at identical conditions during the daylight hours, when they were exposed to a light intensity of ~6500 lux using white (cool; 5000 K) LED lamps. During the night hours, tanks were randomly allocated to six different light treatments, which were randomly arranged and fully independent from each other. In between experiments, the tanks associated with each treatment were randomly redistributed to avoid any potential biases associated with the position of the tanks. At each experiment, one of the tanks was maintained under a regular 12:12 light/dark photoperiod (i.e., at night those tanks remained in darkness; 0 lux) from dusk (20:00) to dawn (8:00). This treatment is hereafter referred to as natural day/night conditions or control. In separate tanks, we held organisms that at night were exposed to one of five distinct ALAN sources (from 20:00 to 8:00) using LEDs at a standard light intensity of 30 lux. Such intensity was well within the range of intensities measured at ground-level near the burrowing sites of amphipods and isopods (lights associated with e.g., public light posts from boardwalks or parking areas located nearby the upper intertidal; Duarte et al., 2019; Quintanilla-Ahumada et al., 2022). Light intensity was "moderate" and identical across ALAN treatments, but we acknowledge that our protocol assumed that light intensity had no effect on these species' sensitivity to different wavelengths (but see Alaasam et al., 2021 for an in-depth review on potential interactions in some circumstances). Organisms under ALAN treatments were (separately) exposed to one of five different monochromatic light wavelengths: violet (365 nm), blue (465 nm), green (520 nm), amber (588 nm), and red (720 nm) lights. Amphipods and isopods were exposed to only one of these light treatments (no specimen was used in more than

one experiment and treatment). In all instances (control and ALAN treatments) light intensity was measured with a PCE-L 100 luxmeter (minimum sensitivity of 0.00 l lux) on a daily basis.

2.4. Data analysis

The locomotor activity of amphipods and isopods exposed to different light treatments was analyzed separately per species (amphipods and isopods) and per experiment (1–3) using Generalized Additive Models (GAMs) available in the mgcv library in R (R Core Team, 2020). GAMs are useful for modelling non-linear data using non-parametric smoothers which are applied to predictor variables, to additively calculate the response upon the dependent variable (Wood, 2006). For each data set (i.e., species activity in response to a given light treatment over a 24 h period) we grouped the activity recorded by actographs in 1-min intervals, and then modeled the probability of activity (i.e., at least one activity record within a 1-min interval) using a binomial error distribution and logit-link functions. Predictor variables included in the models were treatment (i.e., darkness and light colors) and the hour of the day (0−23 h). Hour of the day was fitted non-linearly (to adjust the diel rhythm of these species) using smoothing splines functions available in the mgcv package. We fitted GAMs and calculated likelihood ratio tests using as a reference factor (i.e., intercept) the activity data of each light treatments to obtain pairwise contrasts (i.e., direct pairwise comparisons between each individual light treatment). In addition, a pseudo-R2 and a deviance explained were calculated for the models. Activity plots (fitted values) were made using the ggplot2 package (Wickham, 2009) for R.

3. Results

In all three experiments, variation in amphipods probability of locomotor activity was associated with light treatment and hour of the day ($GAM_{amphipods}$ adjusted-R2 = 0.504, 0.416, 0.433 and 52.5%, 46.2%, 46.4% of deviance explained for experiments 1, 2, and 3, respectively; fitted smoothing splines; $p < 0.001$ for each experiment). Pairwise contrasts between different ALAN wavelengths against controls were all significant (Table 1). The locomotor activity of amphipods (Fig. 1) recorded under natural day-night conditions (control) began at dusk, with a sharp increase starting between 20:00 and 21:30 h, reaching a peak of locomotor activity between midnight and 5:00 h (mean probability of locomotor activity of 0.89 and 95% confidence interval = 0.85–0.90; Fig. 1) across the three experiments. This was followed by a sharp decline in activity until ~10:00 h, followed by minimal probability of locomotor activity (<1%) during the daylight (~11:00–20:00 h; mean probability of locomotor activity of 0.005 and 95% confidence interval = 0.002–0.011; Fig. 1). Instead, amphipods exposed to amber, blue, green, and violet lights exhibited significantly lower levels of activity during the night hours (always under ~0.25 probability of locomotor activity; $p \leq 0.033$ in all individual comparisons against the controls; Table 1). However, among ALAN treatments, the activity of amphipods exposed to red lights showed a less drastic reduction (~0.50 probability of locomotor activity) compared with other wavelengths across the three experiments (Fig. 1) (see Table 2).

Like amphipods, variation in isopods probability of activity was significantly associated with light treatment and hour of the day ($GAM_{isopods}$ adjusted-R2 = 0.362, 0.390, 0.387 and deviance explained = 38.1%, 40.7%, 41.7% for experiments 1,2, and 3, respectively; fitted smoothing splines; $p < 0.001$ for the three experiments). Pairwise contrasts between different ALAN wavelengths and controls were all significant (Table 2). The locomotor activity of isopods (Fig. 2) under natural day-night conditions (control) was greatest during the night hours across all three experiments. Activity started at dusk (~between 19:00–20:00 h) and rose to a peak between ~4:00 and 6:00 h (mean probability of locomotor activity of 0.88 and 95% confidence interval = 0.85–0.91) in the experiment 1, while for the experiments two and three a more uniform locomotor activity were registered at night hours (~between 0:00–5:00 h; mean probability of locomotor activity of 0.82 and 95% confidence interval = 0.78–0.85). Then, the locomotor activity declined again to near zero during light hours (<1%; Fig. 2). The activity of isopods exposed to ALAN was drastically reduced by all light wavelengths (up to ~10% probability; $p < 0.03$ in all comparisons against the control; Table 2). However, in the case of the isopods exposed to light in the blue spectrum (Experiment 1), activity shifted, peaking at ~14:30 h to a maximum of ~40% probability (Fig. 2a). Likewise, isopods exposed to amber light exhibited an unusual activity peak at ~10:00 h in the third experiment (Fig. 2c).

4. Discussion

When ALAN impacts are detected, it is important to determine which properties of the light are behind the biological responses elicited. Our understanding of ALAN impacts on coastal organisms is still at an early stage (Lynn and Quijón, 2022; Marangoni et al., 2022). In fact, to the best of our knowledge this is the first one examining the influence of distinct ALAN wavelengths on sandy beach invertebrates. Our study was developed on the premises that a species is more vulnerable to a certain range of light wavelengths, and that such range is not necessarily the same when two or more species are compared, given the different evolutions and life histories that are at play (see Brown, 1996). In natural

Table 1
- Mean estimates and significance values for pairwise comparisons of the locomotor activity of amphipods (*Orchestoidea tuberculata*) in response to different light treatments.

Pairwise	Exp. 1		Exp. 2		Exp. 3	
Comparisons	Mdf = 57.55		Mdf = 55.71		Mdf = 55.54	
	Estimate	p	Estimate	p	Estimate	p
Control-Amber	−780.209	**<0.001**	14.190	**<0.001**	1.833	**<0.001**
Control-Blue	−14.830	**0.008**	14.770	**<0.001**	4.388	**0.025**
Control - Red	−3.312	**0.004**	−15.685	**0.019**	8.256	**<0.001**
Control - Green	−1.037	**0.033**	−1311.613	**<0.001**	7.655	**<0.001**
Control -Violet	−2.312	**<0.001**	13.834	**0.001**	6.422	**0.004**
Amber – Blue	756.2	**<0.001**	0.528	**0.004**	1.181	0.417
Amber – Red	2.892	**<0.001**	−33.033	**<0.001**	4.760	**0.001**
Amber – Green	776.0	**<0.001**	−1306.151	**<0.001**	4.165	**0.004**
Amber – Violet	776.0	**<0.001**	−0.2193	0.680	2.893	0.064
Blue – Red	9.883	0.071	−33.519	**<0.001**	0.255	0.224
Blue – Green	13.751	**0.014**	−1300.319	**<0.001**	−0.306	0.099
Blue – Violet	12.228	**0.027**	−0.395	0.135	−1.389	**<0.001**
Red – Green	2.786	**0.031**	−1292.126	**<0.001**	−0.628	**0.016**
Red – Violet	1.336	0.322	29.575	**<0.001**	−1.829	**0.001**
Green - Violet	−0.460	**0.005**	1.2396	0.163	−1.124	**0.031**

Table 2
- Mean estimates and significance values for pairwise comparisons of the locomotor activity of isopods (*Tylos spinulosus*) in response to different light treatments.

Pairwise	Exp. 1		Exp. 2		Exp. 3	
Comparisons	Mdf = 59.90		Mdf = 55.02		Mdf = 59.24	
	Estimate	p	Estimate	p	Estimate	p
Control-Amber	18.750	**<0.001**	2.376	**0.030**	−2.140	**0.028**
Control-Blue	19.477	**<0.001**	−11.521	**<0.001**	−12.809	**0.025**
Control - Red	18.711	**<0.001**	−2.731	**<0.001**	−3.513	**<0.001**
Control - Green	17.466	**<0.001**	−9.434	**0.002**	−3.010	**0.007**
Control -Violet	18.285	**<0.001**	−32.415	**0.019**	−3.938	**<0.001**
Amber – Blue	0.693	**<0.001**	−15.328	**<0.001**	−16.964	**0.001**
Amber – Red	−0.008	0.923	−2.086	0.070	−3.506	**<0.001**
Amber – Green	−1.271	**<0.001**	−13.458	**<0.001**	−0.731	0.561
Amber – Violet	−0.476	**<0.001**	−35.407	**0.013**	−1.665	0.189
Blue – Red	−0.736	**<0.001**	11.1728	**<0.001**	−315.123	**<0.001**
Blue – Green	−1.937	**<0.001**	−0.0842	0.811	15.971	**<0.001**
Blue – Violet	−1.157	**<0.001**	−18.758	0.148	15.056	**0.001**
Red – Green	−1.238	**<0.001**	−6.834	**0.024**	326.33	**<0.001**
Red – Violet	−0.443	**<0.001**	−29.759	**0.033**	325.43	**<0.001**
Green - Violet	0.765	**<0.001**	−18.945	0.144	−0.214	0.676

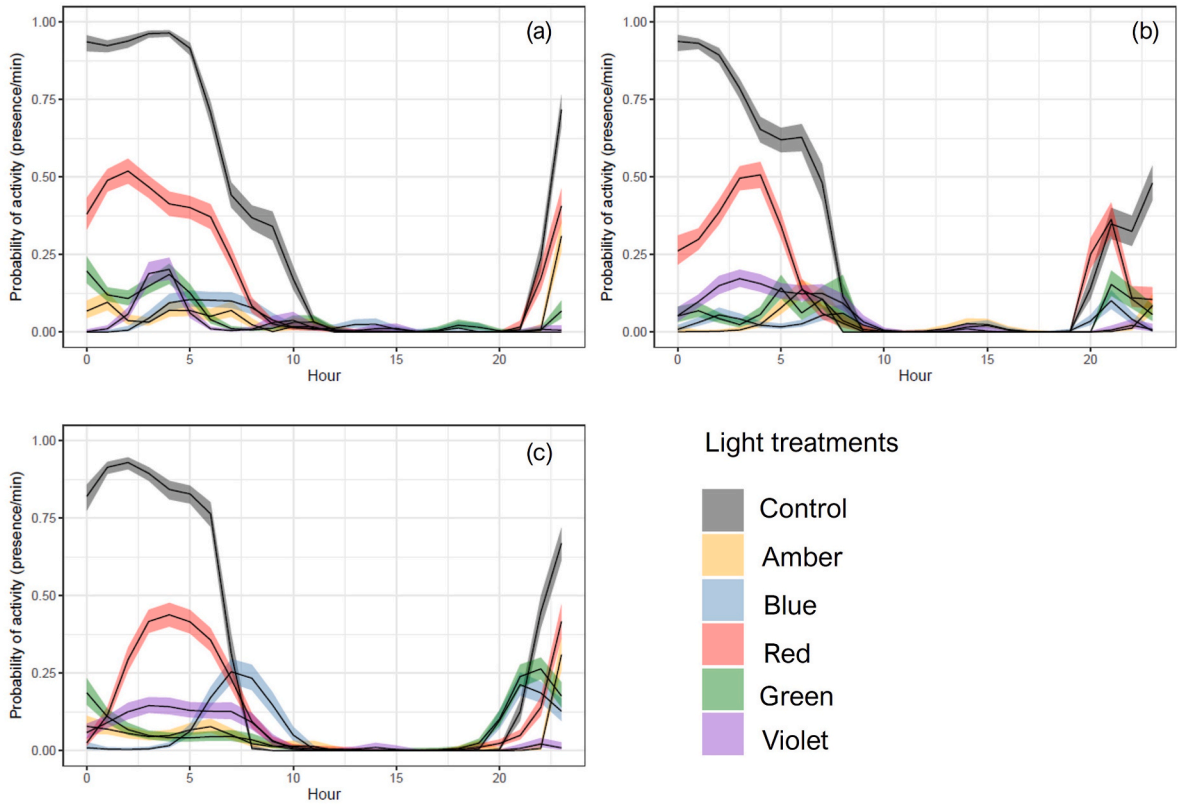


Fig. 1. Mean (±95% C.I.) probability of amphipod (*Orchestoidea tuberculata*) locomotor activity throughout a 24 h day/night cycle in response to natural daylight/night conditions (control; gray line) and five different ALAN sources (light colors) over the course of five consecutive days. Plotted curves correspond to fitted GAM values. Experiments 1, 2, and 3 are presented in (a), (b) and (c), respectively. On each experiment, 20 individuals per species and per tank were exposed to each treatment separately. A 12:12 photoperiod was used, with daylight conditions applied between 8:00 and 20:00 h. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

daylight/night conditions representative of the spring-summer season in Northern Chile, both species exhibited the known circadian activity of many adult peracarids (e.g., Bregazzi and Naylor, 1972; Forward et al., 2007; Ramus and Forward, 2012; Lynn et al., 2023): a lack of surface activity during daylight and strong activity during the night hours. In contrast, when exposed to ALAN these species' surface activity levels declined significantly, a result that aligns with the main predictions of our hypothesis. However, there were also interesting variations between species: while amphipods showed a moderate response to red lights, isopods responded also moderately to blue and amber lights at least in one of the experiments conducted, and in both cases, there was a shift in activity towards daylight conditions. These differences add an interesting element to the known repertoire of responses to ALAN by these and other coastal species.

4.1. *Amphipods' response to ALAN*

The normal circadian pattern of sandy beach amphipods has been related to avoidance of daylight physical stressors (high temperature and potential desiccation; Morrit, 1987; Brown and McLachlan, 2006)

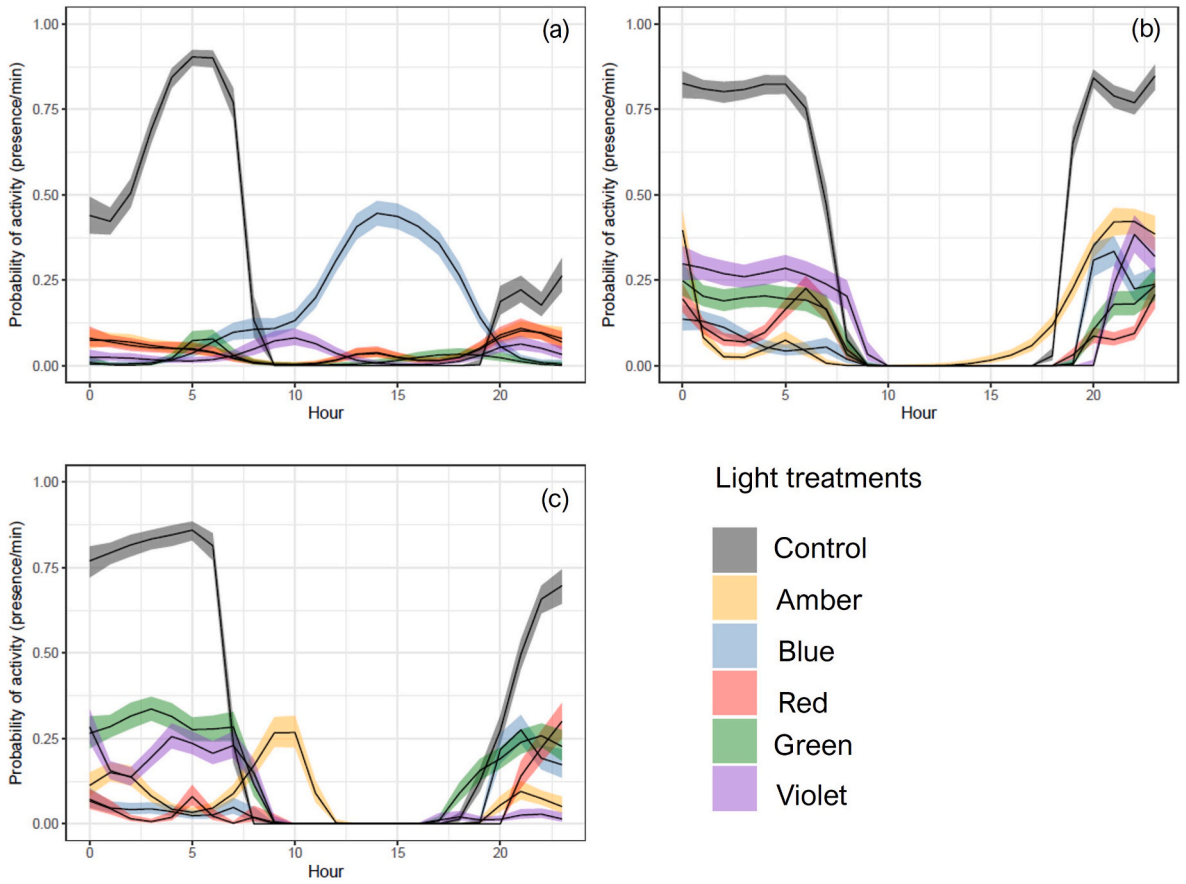


Fig. 2. Mean (±95% C.I.) probability of isopod (*Tylos spinulosus*) locomotor activity throughout a 24 h day/night cycle in response to natural daylight/night conditions (control; gray line) and five different ALAN sources (light colors) over the course of five consecutive days. Plotted curves correspond to fitted GAM values. Experiments 1, 2, and 3 are presented in (a), (b) and (c), respectively. On each experiment, 20 individuals per species and per tank were exposed to each treatment separately. A 12:12 photoperiod was used, with daylight conditions applied between 8:00 and 20:00 h. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and predation by visual consumers such as shorebirds (Dugan et al., 2003). Such patterns were confirmed here by actograph records and repeated observations in the field: during daylight, amphipods remained buried in the sand, whereas at night (i.e., after ~21:00 h) they emerged and exhibited a strong locomotor activity (~90% of probability). Such nocturnal activity has often been associated with the consumption of stranded seaweeds (Kennedy et al., 2000; Lastra et al., 2008; Quintanilla-Ahumada et al., 2023), and reflects a life history that is firmly adapted to naturally low light conditions at night (Scapini et al., 1989). The addition of ALAN sources changed that dynamics and, in fact, exposure to all light wavelengths restricted amphipod activity to levels significantly lower than in the controls. ALAN in the spectra of amber, blue, violet, and green lights supressed most amphipod surface activity, limiting their movement to peaks at or below ~20% (<10% at most times) or to a moderate level (40–50%) in the case of red lights.

The significant decline in amphipod night activity under ALAN exposure suggests that these organisms readily perceive a range of short to medium light wavelengths (~380–575 nm; although amber lights peak as high as 588 nm) and respond to it by interrupting their natural emergence from the sand. Those results align with the notion that crustaceans in general have a peak of sensitivity around 500 nm, making them more vulnerable (i.e., suppressing their activity) when exposed to lights in or around the green spectrum (Marshall and Cronin, 2011; Horvath, 2014). Studies focused specifically on talitroid amphipods (e.g., Mezzetti and Scapini, 1995) have reported similar visual sensitivity ranges, but with peaks closer to the blue spectrum (450–480 nm). Consistent with these findings, Ugolini et al. (1996) reported that talitroid amphipods may lose their ability to use the sun as a cue for seaward orientation when wavelengths shorter than 450 nm are eliminated from the light spectrum. This suggests again a high sensitivity to these and shorter light wavelengths, as observed in our trials.

An interesting variation from the general pattern of reduced activity under ALAN exposure was detected when the amphipods were exposed to red lights (720 nm). Although these organisms exhibited the same type of decline in activity, when exposed to red lights such decline was less severe, peaking consistently at a "moderate" ~40–50% probability level during night hours (between 2:30 and 4:30 h). Studies conducted at night with other types of amphipods, such as *Chaetogammarus olivia*, have found much stronger responses to red lights (full avoidance; Grintsov et al., 2022). Amphipod moderate peaks of activity under red lights did not deviate from the normal circadian pattern reported for this (Luarte et al., 2016) and other sandy beach amphipods (e.g., *Americorchestia longicornis* in Canadian sandy beaches; Lynn et al., 2021a). Ultimately, lights at the red spectrum are closer to the upper limit of the wavelength scale, and therefore, are less likely to be fully perceived by the amphipods. The measurement of a moderate (rather than a full) level of activity in these organisms suggests that red lights, unlike all other lights, were peripherally, perhaps indirectly, detected by the amphipods, as it has been shown to sporadically occur in other crustaceans such as mysids (see Lindström and Meyer-Rochow, 1987). While a further examination of the mechanisms used by amphipod eyes to partially detect red lights is clearly needed, the main conclusion we gathered is that the five ALAN wavelengths measured here did significantly, but not necessarily equally, limit amphipod locomotor activity.

4.2. Isopods' response to ALAN

The activity recorded for isopods exposed to natural daylight/night conditions resembled the activity recorded for amphipods: a natural circadian pattern with strong night activity (up to ~90%) and limited to no activity during daylight hours. Such natural cycle has been documented before from a nearby location (El Apolillado sandy beach; Jaramillo et al., 2003; Duarte et al., 2019), and as stated earlier, has been also observed in the field and in the laboratory. Exposure to ALAN elicited a response visually similar to the one recorded in amphipods, but with a couple of key differences. Although our statistical analyses did not directly compare between amphipod and isopod activity levels, a common (similar) suppression of locomotor activity was observed in both species. In fact, all types of ALAN prevented strong locomotor activity comparable to the ones exhibited by isopods in natural conditions over the full 24 h cycle. Such results were not surprising considering that the activity of these isopods has been shown to be halted even by natural full moon light conditions (Jaramillo et al., 2003). In addition, this and a few other crustaceans have been described before as highly sensitive to a range of wavelengths around green lights (500–565 nm; Briggs, 1961). Interestingly, we found evidence of a change with respect to the patterns measured in amphipods: isopods exposed to blue lights (465 nm) did exhibit a shift in their activity levels during one of the experiments, where a moderate peak (40%) was observed during mid-afternoon (~15:00 h). A similar (less prominent) 25% peak of activity was also observed at mid-morning (10:00 h) in a second experiment, when the isopods were exposed to amber lights (588 nm). Both instances seem maladaptive, as activity during daylight hours entails elevated risks of potential predation or exposure to desiccation, if not stranded seaweeds are readily available to provide a refuge (Dugan et al., 2003; MacMillan et al., 2016).

To the best of our knowledge, the distinct sensitivity of sandy beach isopods to blue lights (and amber lights) has not been documented before. However, at least some terrestrial isopods (Danielson, 1976) and some deep-sea marine isopods (Frank et al., 2012) have been in fact found to react and respond to lights in the blue spectrum. Still, the much stronger sensitivity to other lights in the lower end of the spectrum (e.g., violet light; 380–450 nm), which caused a more drastic reduction in activity, remains an intriguing result that is worth exploring in further studies. The instances of an apparent isopod's deviation from its natural circadian rhythm are interesting. Arguably, such a change may signal a more severe type of ALAN effect than the one detected in amphipods. This argument aligns with the results reported by Miranda (2020), who examined eye structural damage due to artificial light in the same two species examined here. According to that author, even though short-term ALAN exposure can elicit a response in both species, isopods seem comparatively more sensitive. In addition, the damage caused by ALAN exposure in the surface of the eye ommatidia is considerably more severe and recovers at a slower pace in isopods than in amphipods (Miranda, 2020). Whether isopods can quickly recover from the shift in activity reported here remains unknown, as no recovery experiment was attempted to see if such a disruption in the circadian rhythm was temporary or permanent (see Lynn et al., 2021a for an example). Regardless, ALAN consistently limited the isopods' locomotor activity, and in two cases (blue and amber lights) there were instances in which the circadian pattern of activity described for this species (Jaramillo et al., 2003; Duarte et al., 2019) shifted to daylight hours.

4.3. Implications

The strong response of amphipods and isopods to most light wavelengths, adds to the growing body of evidence showing that this stressor can disrupt intertidal organisms' activity and behavior (Gaston et al., 2013; Foster et al., 2018; Lynn and Quijón, 2022; Marangoni et al., 2022). In addition, the differential responses to two discrete light spectra (red and blue-amber lights in amphipods and isopods, respectively), suggests that ALAN doesn't necessarily trigger similar responses across different species. The response of amphipods to red lights was less pronounced than their response to all other light types (although still significantly different from controls). Such result suggests that this type of light may be less harmful than the other forms of ALAN, but in nature, that type of light may also favour those amphipods' visual predators that have the ability to detect prey under red lights (e.g., Dwyer et al., 2013). The same cannot be said about blue and amber lights and isopods, as the response of these organisms to both wavelengths entailed a change in their circadian rhythm. Such change would heighten the risk of mortality by e.g., desiccation (MacMillan et al., 2016) or shorebird predation (Dugan et al., 2003), so to stay in the side of caution, lights in the blue and amber spectrum should be avoided.

When active, particularly during the spring-summer season to which these results are directly applicable, sandy beach amphipods and isopods are highly mobile (Scapini et al., 1997). Therefore, it can be surmised that an increasingly regular exposure to most ALAN wavelengths may cause local-scale declines in the activity and the abundance of both species. In response to ALAN some peracarid species often migrate down towards the low intertidal (Duarte et al., 2023) or aggregate in areas with coverage from natural light (e.g., seaweed wrack; Poore and Gallagher, 2013; Fanini et al., 2016; MacMillan et al., 2016; Quintanilla-Ahumada et al., 2023). It is therefore conceivable that local-scale displacements can turn into larger-scale changes if ALAN sources become permanent features nearby sandy beaches. The type of lights assessed here (monochromatic) are unusual in nature, so their effects on coastal crustaceans or more broadly on wildlife associated to any other habitat, are not yet fully understood. Likewise, studies comparing photosensitivity to natural or artificial lights among different amphipod species or among different isopod species are limited, and do not yet grant general conclusions about the responses of each type of organism. Nonetheless, if ALAN sources continue to expand, their impacts on activity are more likely to occur in sites located close to urban areas, where ALAN sources often concentrate along boardwalks, ports, marinas, roads, or parking areas (Gaston et al., 2013; Orlando et al., 2020; Smyth et al., 2022). As stated earlier, amphipods and isopods are important trophic links between primary producers (algal wrack) and top consumers (Bower, 1964; Dugan et al., 2003; Bird et al., 2004). It follows that their displacement due to ALAN sources may locally alter some of these trophic interactions (see Underwood et al., 2017, Manríquez et al., 2019; Moyse et al., 2023 for relevant comparisons) and deter services such as the natural beach grooming that these species provide (Schlacher et al., 2014; Hyndes et al., 2022).

As shown here, the management of ALAN sources and their potential impacts should no longer focus solely on the presence or number of ALAN sources (Orlando et al., 2020) or whether they are transient or persistent in nature (see Gaston and Holt, 2018). Management should also consider ALAN properties, including their light wavelengths. Although the use of LED lighting continues and would likely continue to grow in cover area and intensity (Kyba et al., 2017), this type of technology is perceived as flexible and therefore readily manageable. However, our results show that all light wavelengths examined here had a significant (negative) influence on the amphipod and isopod activity, when compared to natural day/night conditions. The few variations detected, however, suggest further (targeted) studies. Such research should aim at exploring collateral benefits and impacts of e.g., red lights for amphipods, or variations in ALAN intensity or frequency that may prove to be less harmful for these and other key sandy beach species.

CRediT authorship contribution statement

Diego Quintanilla-Ahumada: Writing – review & editing, Formal analysis, Data curation. **Pedro A. Quijón:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Nicole Jahnsen-Guzmán:** Writing – review & editing, Formal analysis. **K. Devon Lynn:** Writing – review &

editing, Formal analysis. **José Pulgar:** Writing – review & editing, Formal analysis. **Javier Palma:** Writing – review & editing, Formal analysis. **Patricio H. Manríquez:** Writing – review & editing, Formal analysis. **Cristian Duarte:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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