



Artificial light at night alters the locomotor behavior of the Mediterranean sea urchin *Paracentrotus lividus*

Giorgia Sanna^a, Paolo Domenici^b, Elena Maggi^{a,*}

^a Dipartimento di Biologia, CoNISMa, Università di Pisa, via Derna No.1, Pisa 56126, Italy

^b IBF-CNR, Consiglio Nazionale delle Ricerche, Area di Ricerca San Cataldo, via G. Moruzzi No.1, Pisa 56124, Italy

ARTICLE INFO

Keywords:

ALAN
Light pollution
Sea urchin
Paracentrotus lividus
Behavior
Locomotion

ABSTRACT

Artificial light at night (ALAN) is a recognized source of anthropogenic disturbance, although its effects on biological systems have not been fully explored. Within marine ecosystems, coastal areas are the most impacted by ALAN. Here, we focused on the Mediterranean sea urchin *Paracentrotus lividus*, which has a crucial role in shaping benthic ecosystems. Our objective was to investigate if ALAN affects the nocturnal locomotor behavior of *P. lividus*. A semi-controlled field study was conducted along a rocky shore near a promenade lit at night. Results suggested a potential impact of ALAN on the locomotor behavior of sea urchins. Individuals of *P. lividus* tended to move away from the light sources while its directions in dark conditions were uniform. Their locomotor performance, in presence of ALAN, was characterized by shorter latency time, lower sinuosity and higher mean speed at increasing light intensity, with potential cascading effect at the ecosystem level.

1. Introduction

Artificial light at night (hereafter ALAN) is a recognized source of anthropogenic disturbance, caused by nocturnal alterations in the environmental light due to human-made light sources, and is rapidly increasing worldwide (Cinzano et al., 2001). To date, research on ALAN has shown that light pollution affects a variety of marine habitats (Davies and Smyth, 2017, Marangoni et al., 2022), and coastal ones in particular, due to high human presence (Small and Nicholls, 2003, Davies et al., 2014, Fobert et al., 2023). Here, ALAN impacts have been documented on spatial orientation (Bourgeois et al., 2009; Berry et al., 2013; Rivas et al., 2015; Dimitriadis et al., 2018), on foraging behavior and locomotion (Luarte et al., 2016), on circadian rhythms (Duarte et al., 2019; Pulgar et al., 2019) and on trophic and non-trophic interactions (Davies et al., 2015, Bolton et al., 2017, Underwood et al., 2017, Maggi and Benedetti-Cecchi, 2018, Maggi et al., 2019a, 2019b, Garratt et al., 2019, Manríquez et al., 2021). Furthermore, ALAN affects a great diversity of taxa, although the response of some marine organisms is still unknown (Marangoni et al., 2022).

Sea urchins are considered a key taxonomic group for the ecology and economy of coastal habitats, as they are often the predominant grazers shaping benthic ecosystems (Pearse, 2006, Boudouresque and Verlaque, 2013) and are also valued, in various regions of the globe, as

luxury seafood (Lawrence, 2013). Sea urchins tend to show nocturnal activity, and a variety of photic behaviors have been described (Holmes, 1912; Millot, 1955; Yoshida, 1956; Millott and Takahashi, 1963; Lawrence, 1976; Yoshida, 1956). Although the movements of sea urchins were found to be influenced by various biotic and abiotic factors, such as water flow (Benedetti-Cecchi and Cinelli, 1995; Cohen-Rengifo et al., 2018), food availability (Rodriguez and Ojeda, 1998; Tuya et al., 2004; Parnell et al., 2017), diel/lunar cycle (Crook et al., 2000; Tuya et al., 2004; Shulman, 2020), predation pressure (Rodriguez and Ojeda, 1998; Bernat Hereu, 2005; Pagès et al., 2021) and substrate characteristics (Laur et al., 1986; Domenici et al., 2003; Cho et al., 2014), few studies have considered the possible impact of light features (such as intensity and spectrum; Sun et al., 2019; Yang et al., 2021). Recently, Bauer et al. (2022) showed that the effects of ALAN on feeding behavior are highly species specific, and that long-term exposure to ALAN can cause alterations in the feeding rhythmicity, but not in the food consumption rates of *Paracentrotus lividus*.

The objective of this study was to investigate if ALAN affects the nocturnal locomotor behavior of the purple sea urchin *P. lividus* (Lamarck, 1816), the most important sea urchin in the Mediterranean sea for both ecologically and economically reasons (Benedetti-Cecchi and Cinelli, 1995; Barnes et al., 2002; Cirino et al., 2017). We hypothesized that the presence of ALAN may affect its locomotor behavior and,

* Corresponding author.

E-mail address: elena.maggi@unipi.it (E. Maggi).

<https://doi.org/10.1016/j.marpolbul.2024.116782>

Received 23 March 2024; Received in revised form 14 July 2024; Accepted 23 July 2024

Available online 2 August 2024

0025-326X/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

specifically, that in the presence of ALAN, sea urchin will crawl in a direction away from the light source while in the naturally dark environment, *P. lividus* will move with a uniform circular pattern (i.e., as a result of high directional variability among individuals) typical of food searching (Benhamou, 2004). In addition, we hypothesized that in artificially lit environments *P. lividus* will tend to move away from the light source with low sinuosity and its locomotor performance (speed, latency) will be highest in the highest light level.

To test these hypotheses, we took advantage of the presence of different ALAN conditions along a coastal urban area in Castiglioncello (Livorno, Italy), characterized by the presence of a restaurant and streetlamps along a promenade. The effects of ALAN on nocturnal locomotor behavior were examined in a semi-controlled field experiment, by means of infrared trail cameras that recorded the movement of sea urchins in small arenas located next to the collection sites.

2. Materials and methods

2.1. Study area

The study was conducted along a rocky shore in Castiglioncello, LI (43° 40' 08"N, 10° 40' 73"E), from April to September 2021 (Fig. 1). The area is mostly exposed to winds blowing from south to west, but the conformation of the coastline makes the site moderately exposed to sea storms. The area is characterized by the presence of a promenade along an urban coastal area, with streetlamps and a restaurant creating stretches of coast characterized by different artificial light intensities, from completely dark to brightly lit conditions. At 1–1.5 m depth, the rocky habitat is characterized by a benthic algal population varying throughout the seasons, mostly composed of algal turf and epilithon and, in smaller percentage, *Laurencia* spp., *Padina pavonica* and other sheet-like algae (e.g., *Dyctiota dichotoma*). The most frequently found animals are crabs, shrimps, gastropods, hermit crabs, actinia, mullets, starfish, holothurians and the two most common sea urchin species along the Italian coasts in shallow subtidal habitat: *Paracentrotus lividus* and *Arbacia lixula*. Given the spatial scale of the study, as well as observed communities, significant differences in biotic conditions for

sea urchins (such as in their resources or predators) were extremely unlikely.

In the study area, three sites differing in light intensity were chosen: a completely dark (0 lx) and two light conditions (1.5 and 18 lx). From west to east, the first site is far from the streetlamps and is completely dark at night (0 lx; "Dark"). The second site is in the proximity of a restaurant with two outdoor lights (separated by approximately 4 m) which provide bright night illumination (18 lx; "High"). The third and last site is in proximity of streetlamps (separated by 6–8 m) that create a low night illumination (1.5 lx; "Low"). Night light measurements were done in new moon nights, by means of a luxmeter (RS PRO, ILM 1332A) used out of the water to characterize the three sites. Night sky brightness of the Dark site was measured through a Sky Quality Meter (Unihedron), resulting 20.4625mag/arcsec². We used the LAN³ system to collect data on the red and blue bands of the spectrum at the two illuminated sites, as blue and red bands ratios to the clear band (which are linked to the percentage of blue and red to the total visible light; Aubé et al., 2013). Data from the Low (mean ± 1SE; Red/Clear: 0.3679 ± 0.0002, Blue/Clear: 0.2117 ± 0.0002) and the High site (mean ± 1SE; Red/Clear: 0.3492 ± 0.0016, Blue/Clear: 0.2476 ± 0.0002) resulted significantly different (one-way ANOVA, $p < 0.001$ and number of measurements at each site: $n = 27$ for both analyses; gad function in R package GAD).

2.2. Locomotor behavior

The experiment to observe potential differences in the locomotor behavior of *P. lividus* at varying ALAN intensities was performed in both sites.

At each site, about 1 h after the sunset and finishing no later than 1 h prior to the moon rise, we randomly collected sea urchin individuals with test diameter ranging from 31 mm to 69 mm. (mean ± 1SE; Dark: 43.26 ± 0.84, Low: 48.63 ± 0.75, High: 50.87 ± 0.90). A total of 57 individuals at "Dark" site, 69 at "Low" site and 69 at "High" site were tested between mid-July and late September 2021, during five nights characterized by absence of the moon (i.e., during new moon periods), clear sky and calm sea (specifically 12/07, 29/07, 11/08, 09/09 and 30/09). Given the density of sea urchins at all the sites, as well as the choice

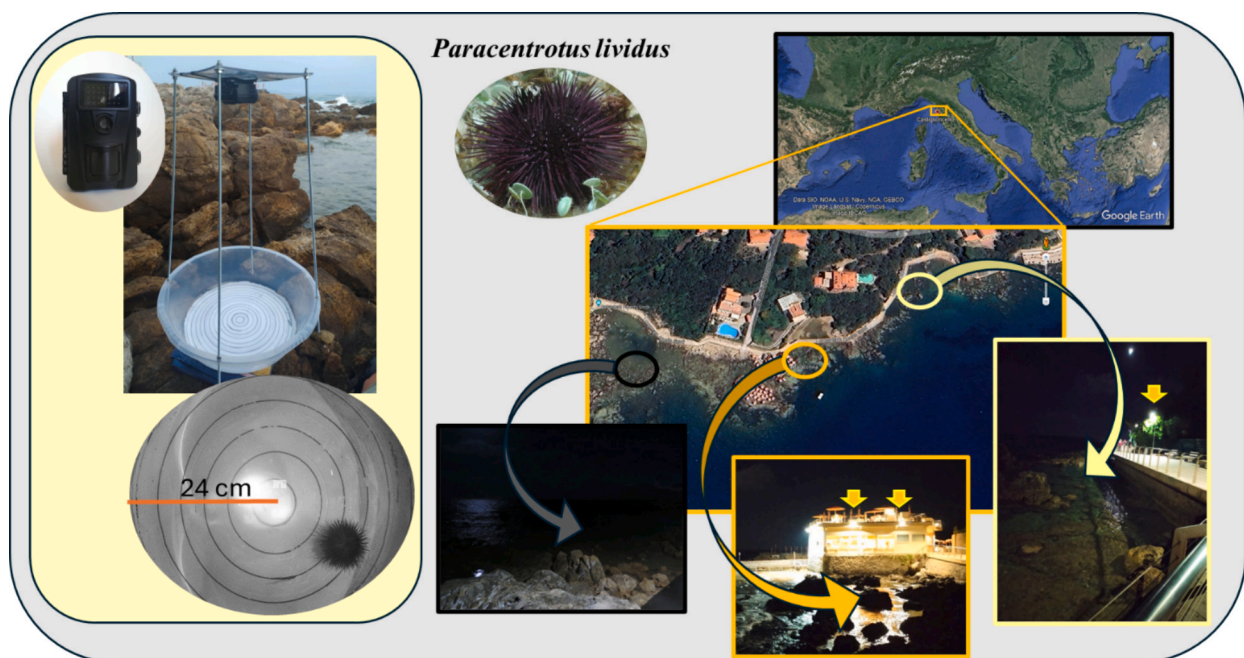


Fig. 1. The figure shows a map of the study area (Castiglioncello, Italy), with nighttime pictures of the three sites characterized by naturally dark conditions (Dark, left), by low (Low, 1.5 lx, right) and high intensity (High, 18 lx, middle) of artificial light at night. On the left, the transparent arena with the infrared camera mounted on the top (see the text for more details).

of different areas from which sea urchins were taken each time, we believe that the probability of having tested the same urchins is rather low.

Each individual was singularly placed in the middle of a transparent plastic arena filled with sea water. The arena was composed of a transparent circular plastic tank (48 cm diameter and 18 cm depth) above which an infrared camera was mounted. Recordings were done with time-lapse mode using infrared cameras (Coolife 28MP, 1520P/2.7 K HD digital trail camera), with a setting of 10 frames per minute. The camera was positioned 90 cm above the circular platform, so that it would not cast any shadows on the arena. The arena was placed on the rocks next to the sea urchin's collection point. At both lit sites, light sources were at a distance of 6–7 m from the collection point, and therefore from the arena. For each recording session, the direction of the light source of ALAN was marked in relation to the position of the camera, to calculate the direction of the light during the time-lapse video analysis.

Each sea urchin was given a maximum of 5-min period during which it was left free to move. The choice to use 5 min was dictated by the best trade-off between the range of speed of sea urchin movement (Domenici et al., 2003; Brundu et al., 2020) and the need to be able to test an adequate number of individuals on each night. Once it reached the edge of the arena (or after 5 min if it did not reach the edge in time), each sea urchin was collected, its size was measured using a caliper, after which it was released back in the field. To limit any stress, urchins were collected right before entering the arena.

2.2.1. Locomotor performance

The time-lapse videos were examined to assess the movement performance using the following variables: latency of locomotion (I), average speed (II), sinuosity (III) and direction (IV). The images and the x and y positions of the sea urchin were analyzed frame by frame with Kinovea 0.8.15 software (Joan Charmant & Contrib. ®).

- I) Latency of locomotion was measured as the time (s) between the beginning of the trial (i.e., when the individual was placed in the centre of the arena) and the first movement (defined as a distance of at least 2 cm from the centre of the arena). This variable measures the readiness to move after positioning (Brundu et al., 2020).
- II) Average speed (cm/s) was measured based on the cumulative distance between successive xy positions of the sea urchin, divided by time taken, excluding the latency time, till the individual reached the edge of the arena, or for a maximum of 5 min.
- III) Sinuosity was determined as $S = 2[p(((1-c)/(1-c)) + b^2)]^{-0.5}$ (Benhamou, 2004), where p is the step length, c is the mean cosine of turning angles, and b is the coefficient of variation of the step length. Therefore, a low sinuosity implies a relatively straight path.
- IV) Direction (0° to 360°) was determined as the angle formed by the line from the center of the arena to the north (0°) and the line linking the center of the arena with the final position of the individual. This was considered as a circular variable (Batschelet, 1981).

2.2.2. Statistical analyses

We carried out a mixed linear regression model for mean speed, sinuosity, and latency, to test the relationship between these variables and the "Site" factor. The analysis was set with "Site" (Dark, Low, and High) as a fixed factor. "Size" was included as a covariate in the fixed part of the model, to test for the possible influence of test diameter on linear variables. "Date" was included as a covariate in the random part of the model to consider the possible variation of different abiotic conditions among nights (function *lmer*, package *lme4*). The additional a posteriori contrast 'Low vs. High' for Site was performed through the *emmeans* function (package *emmeans*) (R-4.1.2 software version).

Locomotion direction was treated as a circular variable. Data were firstly checked for gaussian distribution (normal distribution in circular statistic) using the Watson's Test (Batschelet, 1981). Data were then analyzed for uniformity using the Rayleigh's test (site Dark and Low; Batschelet, 1981) or the newer version of the Hermans-Rasson's test when a gaussian distribution was not met (site High; Landler et al., 2019). The analyses were performed using Oriana software (Oriana v.4, Kovach Computing Services ®) and R software (function *HR_test* within package *circLME*; R Core Team, 2021). Finally, the effects of "Site" and "Date" were tested using Two-way ANOVA for circular data (Harrison and Kanji, 1988; Berens, 2009a, 2009b). These analyses were performed using CircStat Toolbox for Matlab (Berens, 2009).

3. Results

The analysis showed significant effects of different exposures to ALAN on locomotor behavior. Latency at Low site was significantly longer than at Dark site ($p < 0.001$), while mean speed was significantly lower at Low than Dark site ($p < 0.001$). Sinuosity resulted significantly higher at Low than at Dark site ($p < 0.01$). No significant differences were found between Dark and High site. Size did not significantly affect any of the linear variables ($p = 0.35$; 0.31 and 0.41 for latency, mean speed and sinuosity respectively). A posteriori contrasts for factor Site showed longer latency, lower mean speed and higher sinuosity at Low than at High light treatment conditions (Fig. 2, and Table 1).

Date did not significantly affect locomotion direction ($p = 0.11$), in contrast to Site ($p < 0.001$). Post-hoc comparisons showed that direction at each site was significantly different from the other sites ($p < 0.001$). Direction was uniform in Dark condition ($Z = 0.85$, $p > 0.05$), while significantly different from a uniform pattern at both "High" and "Low" site ($Z = 14.77$ and $T = 20.87$ respectively, $p < 0.001$ for both) (Table S2) and indicated a tendency to move away from the light source. For a negative phototactic behavior, we expect the angle between the light source and the locomotion direction to be near 180°. Specifically, the angle between the light source and the direction mode was 172° in site "Low", while in site "High", where two prevalent direction modes can be identified, the angles between each mode and the opposite light source were 168° and 171°. The mean direction was calculated only for the site with non-uniform, von Mises distribution (Table S2), i.e. "Low" (141.64°, with circular standard deviation 54.82°). The greatest mean vector length r of 0.63 was found in site Low, while r was 0.12 in site Dark and 0.46 in site High (Fig. 3 and Table 2 and Table S2).

4. Discussion

Using a semi-controlled approach, our study showed that the locomotor behavior of *P. lividus* significantly changed under different nocturnal artificial light conditions. As expected, in the naturally dark environment *P. lividus* individuals moved with a uniform pattern, while in artificially lit environments the direction of trajectories was non-uniform and nearly opposite to the direction(s) of the light source(s). As expected, in artificially lit environments locomotor performance increased with increasing light level; however, performance in naturally dark conditions was comparable to that observed under high artificial light intensity.

P. lividus is one of the most important organisms shaping benthic ecosystem in the Mediterranean Sea, due to its grazing activity on macroalgae and seagrasses community. The locomotor behavior of *P. lividus* is mainly related to its feeding activity, which takes place mainly at night as shown by various observations both in nature and during experimental procedures, (Boudouresque and Verlaque, 2013). Our data on mean speed are in line with an increase in activity at night; in fact, average values at our three sites ranged between 0.15 and 0.22 cm/s (corresponding to 9 cm/min and 13.2 cm/min), indicating high speed when compared to daytime data collected in previous studies, either in the field (5.4 ± 5.1 cm/min, Brundu et al., 2020) or under

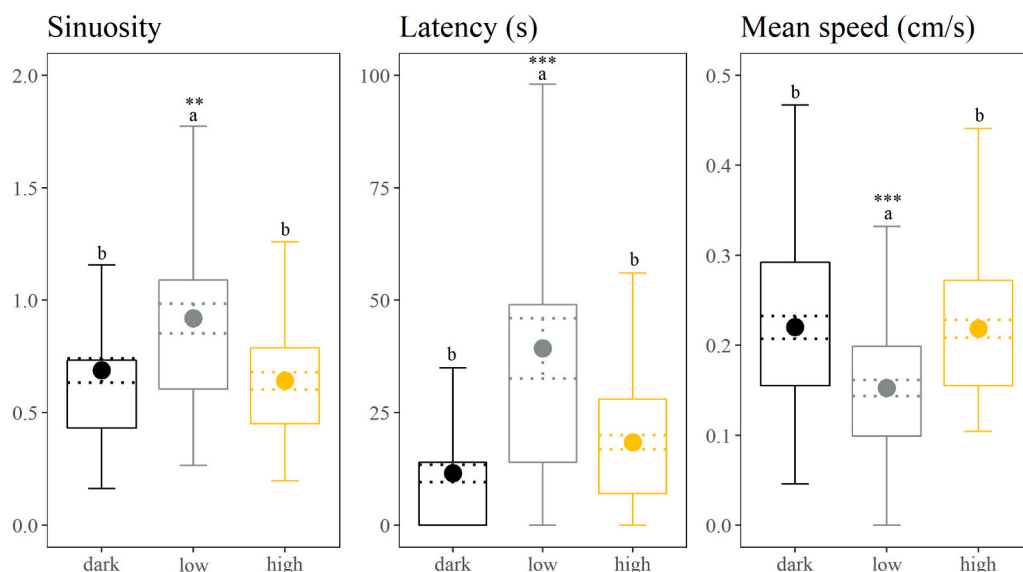


Fig. 2. Boxplots representing (a) sinuosity, (b) latency (s) and (c) mean speed (cm/s), for sea urchins in each site, Dark, Low and High. Boxes represent the Interquartile Range (IQR), and the whiskers the Minimum (25th percentile $-1.5 \times \text{IQR}$) and Maximum (75th percentile $+1.5 \times \text{IQR}$) Value in the Data. The big dot with dotted lines represents the mean \pm SE. Significance of probability associated with effects is shown as follows: *** $p < 0.001$, ** $p < 0.01$. Different letters denote significant difference between sites.

Table 1

Results of mixed linear models on the effect of ALAN on latency, mean speed and sinuosity. Coefficient estimates with standard errors (within brackets) are shown. Significance of probability associated with effects is shown as follows: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Effects	Mean speed (cm/s)	Latency (s)	Sinuosity
Intercept	0.26 (0.04)***	-5.52 (17.18)	
Low vs. Dark	-0.065 (0.02)***	28.02 (6.62)***	0.5 (0.22)* 0.27 (0.08)**
High vs. Dark	-0.005 (0.02)	8.01 (6.97)	-0.05 (0.08)
Size	-0.001 (0.001)	0.35 (0.37)	0.004 (0.005)
<u>A posteriori contrast</u>			
Low vs. High	-0.07 (0.014)***	20.00 (6.04)***	0.319 (0.074)***

laboratory conditions (3.68 ± 0.35 cm/min on horizontal surfaces, Domenici et al., 2003; ~ 8 cm/min under unmanipulated conditions, Pagès et al., 2021).

In the naturally dark environment, large variability in directions among *P. lividus* individuals corroborated our expectations of a uniform pattern of movements, confirming a lack of directionality in absence of light stimuli. On the contrary, when exposed to artificial light, either at high or low intensity, individuals showed negative phototaxis. Negative phototaxis induced by high light intensity in sea urchin has been well documented both in laboratory and in the field (Holmes, 1912; Ullrich-Lüter et al., 2011; Sun et al., 2019). In this study, the direction of trajectories in the Low and High sites was non-uniform, and it was in a direction opposite to the light source(s). This can be further validated by the fact that at the Low site, where there was only one dominant direction of the artificial light source, the mean vector length r was the greatest, while at the High site, where there were two intense artificial light sources, the mean vector length r was lower, which reflected the presence of two modes in the trajectories, each one oriented away from one of the lights. Circular bimodality is common in natural behavior when animals are stimulated by two sources (Batschelet, 1981). Our result is in accordance with those found in the littoral amphipod *Talitrus saltator*, that shows two prevalent phototactic directions when subjected

to two different light sources (Ercolini and Scapini, 1976). These results combined show that, even under low artificial light conditions, sea urchins tend to move away from the light source, and that when exposed to two different light sources they chose a preferred path to follow.

Previous works have shown that light can affect the behavior of *Paracentrotus lividus*. Both covering behavior (Verling et al., 2002), feeding behavior (Bauer et al., 2022) and activity (Domenici et al., 2003) can be affected by light conditions. In particular, the speed of locomotion of individuals exposed to a direct light source was found to be higher than under diffuse light (Domenici et al., 2003). Based on this information, we hypothesized that in environments artificially lit at night, *P. lividus* would tend to move away from the light source(s) with a higher locomotor performance in the highest light level. As expected, at higher light intensity sea urchins started crawling sooner, moved faster and in a straighter line. It is worth noting, however, that the different results between low and high light treatments may be due to different light sources in the two conditions. (1) The High light condition was provided by two light sources versus one in the Low light condition. It is not known what the effect of the number of light sources might have on the locomotor response of sea urchins. (2) The percentage of blue in the light spectrum was significantly higher at the High site and this may have caused a greater impact of ALAN. This hypothesis is in accordance with the findings by Yang et al. (2021), who reported that long-term blue light radiation decreased fitness-related behavior of the sea urchin *S. intermedius*. Finally, in absence of any light stimuli, sea urchins also crawled with a similar latency, speed and sinuosity as the high light condition. This can be interpreted as a behavior typical of refuge seeking, unrelated to a reaction to light, but rather a consequence of being in the center of a flat surface that provides no protection as in the case of the arenas we used.

As an alternative, not mutually exclusive explanation, observed results might be interpreted from an adaptive perspective. Under this scenario, a parabolic pattern in latency, speed and sinuosity should be visualized starting from the dark condition up to high light intensity. As soon as a light appears, the environment acquires directionality, and the animal start exhibiting an adaptive behavior to a stressful condition. Even under low light intensity, individuals of *P. lividus* aim to get away from the stress source (the light) rather than to explore, but are slower, with high latency and sinuosity, as expected in an environment poorly defined. When the environment starts to be clearly legible, as under high

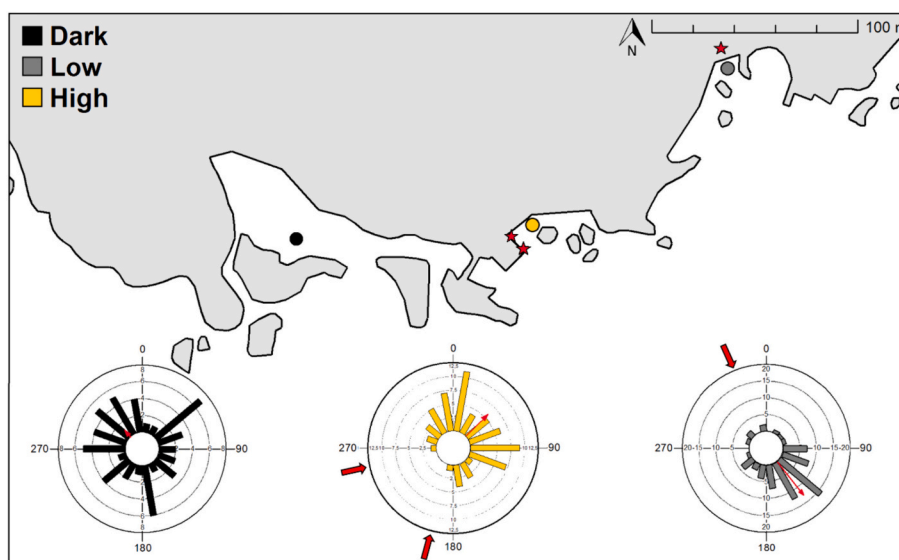


Fig. 3. Map of the study area (Castiglioncello, Italy), showing the three sites characterized by naturally dark conditions (Dark, 0 lx, black), by low (Low, 1.5 lx, grey) and high intensity (High, 18 lx, yellow) of artificial light at night, and their respective circular histograms representing frequency of the direction of trajectories for *P. lividus*. 0°, 90°, 180°, 270° represent North, East, South and West, respectively. The thin red arrows indicate the mean orientation, and its length is the mean vector (r , from 0 to 1; $r = 1$ is represented by an arrow that reaches the edge of the outer circle). Concentric circles represent the frequency of observations. The thick red arrows indicate the direction of artificial light sources. The red stars represent the artificial light sources. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Analysis of variance (Two Way ANOVA) on direction data (Harrison and Kanji, 1988) based on circular statistics.

ANOVA	df	Chi ²
Date	6	10.25
Site	4	59.23***
Pairwise multiple comparisons		
Dark vs. High	2	14.013***
Dark vs. Low	2	36.017***
High vs. Low	2	40.816***

*** $p < 0.001$.

ALAN intensity, an effective escape response is implemented, and individuals become faster and move straight away from the light source(s). Finally, it is worth mentioning that the reduced locomotor activity at low ALAN intensity might mimic the natural behavior of individuals during full moon nights, as observed in another sea urchin species (*Echinometra viridis*; Shulman, 2020).

The study of the effects of artificial light pollution has advanced over the past decade, during which various aspects of this pollutant have been investigated, particularly in the field (Sanders et al., 2021, Marangoni et al., 2022). Assessing the effects of light pollution in the field, however, imposes several difficulties related to the potential alternative sources of disturbance that can be found on site, to the fact that often it is not possible to directly control the type and amount of light disturbance present, and to difficulties in recording behavior in freely moving animals underwater under dark conditions. Here, we carried out observations in semi-controlled conditions, using a set up that represents a trade-off solution that facilitates the recording of sea urchin motion in circular arenas, while maintaining realistic ALAN disturbance levels found in the field. We recognize the limits of our semi-natural approach, and future work should attempt to investigate the variables investigated here into field conditions. We observed a clear negative phototactic behavior in sea urchins exposed to ALAN, with a direction of movement opposite to the light source(s) and decreased latency and sinuosity of path, and increased speed at increasing light intensity. These motion

characteristics are typical of *P. lividus* behavior when exposed to predatory cues (Pagès et al., 2021); a similar effect of ALAN and predator cue has been observed on feeding rates in the Chilean predator *Concholepas concholepas*. Interestingly, no increase in refuge seeking or predation risk has been observed in this species under ALAN conditions (Manríquez et al., 2021), but light pollution resulted in decreased feeding activity. Similarly, prolonged exposure to ALAN disrupted the circadian rhythm and altered foraging behavior of dogwhelks (*Nucella lapillus*) (Underwood et al., 2017). Under field conditions, if ALAN causes *P. lividus* to move away from light sources, this might interfere with its feeding activity, too. For example, in an attempt to escape from nocturnal light, individuals may change their spatial distribution, thereby forming aggregations in areas less subjected to ALAN, which can cause greater competition for space and food. If food resources are scarce in these areas, a reduction in feeding activity and rates might result in lower growth rates and development, with a consequent lower impact on macroalgae and seagrass beds. Cascading effects at the benthic ecosystem level have been observed in other coastal marine systems, such as a significant increase in diversity of the microscopic photoautotrophic component on intertidal rocky shores (Maggi et al., 2019b), and a change in benthic assemblage structure as an indirect consequence of ALAN effect on predator fish success and abundance (Bolton et al., 2017).

Future studies in the field will help to clarify the potential effects on *P. lividus* behavior when exposed to artificial light at night. For example, the interaction of ALAN exposure with predation pressure and food availability will increase our knowledge of the ecology of complex benthic systems in urbanized areas. Finally, further studies investigating the effect of different intensities and spectra of artificial light, as well as ALAN effects in combination with moon-tuned behaviors are needed, to better predict potential changes in shallow subtidal communities and to shed light on potential synergistic effects between ALAN and other urban-related stressors.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

CRediT authorship contribution statement

Giorgia Sanna: Writing – original draft, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Paolo Domenici:** Writing – review & editing, Software, Methodology, Conceptualization. **Elena Maggi:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, 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 after acceptance.

Acknowledgements

Thanks are due to Prof. Iacopo Bertocci, Dr. Francesca Rossi, Dr. Serena Como, Mr. Davide Di Bari, Ms. Ilaria Antoni, Ms. Asia Batini, Ms. Giulia Borghi for nocturnal field activities, and to Antonio Olita for his help with the analysis of circular data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2024.116782>.

References

- Aubé, M., Roby, J., Kocifaj, M., 2013. Evaluating potential spectral impacts of various artificial lights on melatonin suppression, photosynthesis, and star visibility. *PLoS ONE* 8 (7), e67798. <https://doi.org/10.1371/journal.pone.0067798>.
- Barnes, D., Verling, E., Crook, A., Davidson, I., O'Mahoney, M., 2002. Local population disappearance follows (20 yr after) cycle collapse in a pivotal ecological species. *Mar. Ecol. Prog. Ser.* 226, 311–313. <https://doi.org/10.3354/meps226311>.
- Batschelet, E., 1981. *Circular Statistics in Biology*. Amsterdam University Press.
- Bauer, F., Ritter, M., Šiljeg, A., Gretschel, G., Lenz, M., 2022. Effects of artificial light at night on the feeding behaviour of three marine benthic grazers from the Adriatic Sea are species-specific and mostly short-lived. *Mar. Pollut. Bull.* 185, 114303 <https://doi.org/10.1016/j.marpolbul.2022.114303>.
- Benhamou, S., 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *J. Theor. Biol.* 229 (2), 209–220. <https://doi.org/10.1016/j.jtbi.2004.03.016>. Jul 21.
- Benedetti-Cecchi, L., Cinelli, F., 1995. Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west coast of Italy (western Mediterranean). *Mar. Ecol. Prog. Ser.* 126, 203–212. <https://doi.org/10.3354/meps126203>.
- Berens, P., 2009a. CircStat: a MATLAB toolbox for circular statistics. *J. Stat. Softw.* 3, 1–21. <https://doi.org/10.18637/jss.v031.i10>.
- Berens, P., 2009b. CircStat: AMATLABToolbox for circular statistics. *J. Stat. Softw.* 31 <https://doi.org/10.18637/jss.v031.i10>.
- Berry, M., Booth, D.T., Limpus, C.J., 2013. Artificial lighting and disrupted sea-finding behavior in hatchling loggerhead turtles (*Caretta caretta*) on the Woongarra coast, south-East Queensland, Australia. *Aust. J. Zool.* 61, 137. <https://doi.org/10.1071/zo13028>.
- Bolton, D., Mayer-Pinto, M., Clark, G., Dafforn, K., Brassil, W., Becker, A., Johnston, E., 2017. Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. *Sci. Total Environ.* 576, 1–9. <https://doi.org/10.1016/j.scitotenv.2016.10.037>.
- Boudouresque, C.F., Verlaque, M., 2013. *Paracentrotus lividus*. *Dev. Aquac. Fish. Sci.* 297–327 <https://doi.org/10.1016/b978-0-12-396491-5.00021-6>.
- Bourgeois, S., Gilot-Fromont, E., Viallefont, A., Boussamba, F., Deem, S.L., 2009. Influence of artificial lights, logs and erosion on leatherback sea turtle hatchling orientation at Pongara National Park, Gabon. *Biol. Conserv.* 142, 85–93. <https://doi.org/10.1016/j.biocon.2008.09.028>.
- Brundu, G., Farina, S., Domenici, P., 2020. Going back into the wild: the behavioural effects of raising sea urchins in captivity. *Conserv. Physiol.* 8 <https://doi.org/10.1093/conphys/coaa015>.
- Cho, S.K., Cha, B.J., Bae, B.S., Park, S.W., 2014. A laboratory study of the correlation between texture and the speed of locomotion by the sea urchin *Hemicentrotus pulcherrimus*. *Mar. Freshw. Behav. Physiol.* 47, 329–334. <https://doi.org/10.1080/10236244.2014.944817>.
- Cinzano, P., Falchi, F., Elvidge, C., 2001. The first world atlas of the artificial night sky brightness. *Mon. Not. R. Astron. Soc.* 328, 689–707. <https://doi.org/10.1046/j.1365-8711.2001.04882.x>.
- Cirino, P., Ciaravolo, M., Paglialonga, A., Toscano, A., 2017. Long-term maintenance of the sea urchin *Paracentrotus lividus* in culture. *Aquacult. Rep.* 7, 27–33. <https://doi.org/10.1016/j.aqrep.2017.04.003>.
- Cohen-Rengifo, M., Agüera, A., Detrain, C., Bouma, T.J., Dubois, P., Flammang, P., 2018. Biomechanics and behaviour in the sea urchin *Paracentrotus lividus* (Lamarck, 1816) when facing gradually increasing water flows. *J. Exp. Mar. Biol. Ecol.* 506, 61–71. <https://doi.org/10.1016/j.jembe.2018.05.010>.
- Crook, A.C., Long, M., Barnes, D.K., 2000. Quantifying daily migration in the sea urchin *Paracentrotus lividus*. *J. Mar. Biol. Assoc. U. K.* 80, 177–178. <https://doi.org/10.1017/s0025315499001721>.
- Davies, T., Smyth, T., 2017. Why artificial light at night should be a focus for global change research in the 21st century. *Glob. Chang. Biol.* 24, 872–882. <https://doi.org/10.1111/gcb.13927>.
- Davies, T., Duffy, J., Bennie, J., Gaston, K., 2014. The nature, extent, and ecological implications of marine light pollution. *Front. Ecol. Environ.* 12, 347–355. <https://doi.org/10.1890/130281>.
- Davies, T.W., Coleman, M., Griffith, K.M., Jenkins, S.R., 2015. Night-time lighting alters the composition of marine epifaunal communities. *Biol. Lett.* 11, 20150080. <https://doi.org/10.1098/rsbl.2015.0080>.
- Dimitriadis, C., Fournari-Konstantinidou, I., Sourbès, L., Koutsoubas, D., Mazaris, A.D., 2018. Reduction of sea turtle population recruitment caused by nightlight: evidence from the Mediterranean region. *Ocean Coast. Manag.* 153, 108–115. <https://doi.org/10.1016/j.ocecoaman.2017.12.013>.
- Domenici, P., González-Calderón, D., Ferrari, R., 2003. Locomotor performance in the sea urchin *Paracentrotus lividus*. *J. Mar. Biol. Assoc. U. K.* 83, 285–292. <https://doi.org/10.1017/s0025315403007094h>.
- Duarte, C., Quintanilla-Ahumada, D., Anguita, C., Manríquez, P.H., Widdicombe, S., Pulgar, J., Silva-Rodríguez, E.A., Miranda, C., Manríquez, K., Quijón, P.A., 2019. Artificial light pollution at night (ALAN) disrupts the distribution and circadian rhythm of a sandy beach isopod. *Environ. Pollut.* 248, 565–573. <https://doi.org/10.1016/j.envpol.2019.02.037>.
- Ercolini, A., Scapini, F., 1976. Sensitivity and response to light in the laboratory of the littoral amphipod *Talitrus saltator* Montagu. *Monitore Zoologico Italiano-Italian J. Zool.* 10, 293–309. <https://doi.org/10.1080/00269786.1976.10736274>.
- Fobert, E.K., Miller, C.R., Swearer, S.E., Mayer-Pinto, M., 2023. The impacts of artificial light at night on the ecology of temperate and tropical reefs. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 378, 20220362. <https://doi.org/10.1098/rstb.2022.0362>.
- Garratt, M.J., Jenkins, S.R., Davies, T.W., 2019. Mapping the consequences of artificial light at night for intertidal ecosystems. *Sci. Total Environ.* 691, 760–768. <https://doi.org/10.1016/j.scitotenv.2019.07.156>.
- Harrison, D., Kanji, G.K., 1988. The development of analysis of variance for circular data. *J. Appl. Stat.* 15, 197.
- Hereu, B., 2005. Movement patterns of the sea urchin *Paracentrotus lividus* in a marine reserve and an unprotected area in the NW Mediterranean. *Mar. Ecol.* 26, 54–62. <https://doi.org/10.1111/j.1439-0485.2005.00038.x>.
- Holmes, S.J., 1912. Phototaxis in the sea urchin, *Arbacia punctulata*. *J. Anim. Behav.* 2, 126–136. <https://doi.org/10.1037/h0076037>.
- Landler, L., Ruxton, G.D., Malkemper, E.P., 2019. The Hermans-Rasson test as a powerful alternative to the Rayleigh test for circular statistics in biology. *BMC Ecol.* 19, 30. <https://doi.org/10.1186/s12898-019-0246-8>.
- Laur, D.R., Ebeling, A.W., Reed, D.C., 1986. Experimental evaluations of substrate types as barriers to sea urchin (*Strongylocentrotus* spp.) movement. *Mar. Biol.* 93, 209–215. <https://doi.org/10.1007/bf00508258>.
- Lawrence, J.M., 1976. Covering response in sea urchins. *Nature* 262, 490–491. <https://doi.org/10.1038/262490a0>.
- Lawrence, J.M., 2013. *Sea Urchins: Biology and Ecology (Volume 38) (Developments in Aquaculture and Fisheries Science)*. Academic Press.
- Luarte, T., Bonta, C., Silva-Rodríguez, E., Quijón, P., Miranda, C., Farias, A., Duarte, C., 2016. Light pollution reduces activity, food consumption and growth rates in a sandy beach invertebrate. *Environ. Pollut.* 218, 1147–1153. <https://doi.org/10.1016/j.envpol.2016.08.068>.
- Maggi, E., Benedetti-Cecchi, L., 2018. Trophic compensation stabilizes marine primary producers exposed to artificial light at night. *Mar. Ecol. Prog. Ser.* 606, 1–5. <https://doi.org/10.3354/meps12769>.
- Maggi, E., Bertocci, I., Benedetti-Cecchi, L., 2019a. Light pollution enhances temporal variability of photosynthetic activity in mature and developing biofilm. *Hydrobiologia* 847, 1793–1802. <https://doi.org/10.1007/s10750-019-04102-2>.
- Maggi, E., Bongiorno, L., Fontanini, D., Capocchi, A., dal Bello, M., Giacomelli, A., Benedetti-Cecchi, L., 2019b. Artificial light at night erases positive interactions across trophic levels. *Funct. Ecol.* 34, 694–706. <https://doi.org/10.1111/1365-2435.13485>.
- Manríquez, P.H., Jara, M.E., González, C.P., Seguel, M., Quijón, P.A., Widdicombe, S., Duarte, C., 2021. Effects of artificial light at night and predator cues on foraging and predator avoidance in the keystone inshore mollusc *Concholepas concholepas*. *Environ. Pollut.* 280, 116895. <https://doi.org/10.1016/j.envpol.2021.116895>.
- Marangoni, L.F.B., Davies, T., Smyth, T., Rodríguez, A., Hamann, M., Duarte, C., Pendoley, K., Berge, J., Maggi, E., Levy, O., 2022. Impacts of artificial light at night in marine ecosystems—a review. *Glob. Chang. Biol.* 28, 5346–5367. <https://doi.org/10.1111/gcb.16264>.
- Millot, N., 1955. The covering reaction in a Tropical Sea urchin. *Nature* 175, 561. <https://doi.org/10.1038/175561a0>.

- Millott, N., Takahashi, K., 1963. The shadow reaction of *Diadema antillarum* Philippi. IV. Spine movements and their implications. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 246, 437–469. <https://doi.org/10.1098/rstb.1963.0011>.
- Pagès, J.F., Bartumeus, F., Romero, J., Alcoverro, T., 2021. The scent of fear makes sea urchins go ballistic. *Mov. Ecol.* 9 <https://doi.org/10.1186/s40462-021-00287-1>.
- Parnell, P.E., Fumo, J.T., Lennert-Cody, C.E., Schroeter, S.C., Dayton, P.K., 2017. Sea urchin behavior in a Southern California kelp forest: food, fear, behavioral niches, and scaling up individual behavior. *J. Shellfish Res.* 36, 529–543. <https://doi.org/10.2983/035.036.0224>.
- Pearse, J.S., 2006. Ecological role of purple sea urchins. *Science* 314, 940–941. <https://doi.org/10.1126/science.1131888>.
- Pulgar, J., Zeballos, D., Vargas, J., Aldana, M., Manriquez, P.H., Manriquez, K., Quijón, P.A., Widdicombe, S., Anguita, C., Quintanilla, D., Duarte, C., 2019. Endogenous cycles, activity patterns and energy expenditure of an intertidal fish is modified by artificial light pollution at night (ALAN). *Environ. Pollut.* 244, 361–366. <https://doi.org/10.1016/j.envpol.2018.10.063>.
- R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rivas, M.L., Santidrián Tomillo, P., Diéguez Uribeondo, J., Marco, A., 2015. Leatherback hatchling sea-finding in response to artificial lighting: interaction between wavelength and moonlight. *J. Exp. Mar. Biol. Ecol.* 463, 143–149. <https://doi.org/10.1016/j.jembe.2014.12.001>.
- Rodríguez, S.R., Ojeda, F.P., 1998. Behavioral responses of the sea urchin *Tetrapygus nigerto* predators and food. *Mar. Freshw. Behav. Physiol.* 31, 21–37. <https://doi.org/10.1080/10236249809387060>.
- Sanders, D., Frago, E., Kehoe, R., Patteron, C., Gaston, K.J., 2021. *Nat. Ecol. Evol.* 5, 74–81. <https://doi.org/10.1038/s41559-020-01322-x>.
- Shulman, M., 2020. Echinometra Sea urchins on Caribbean coral reefs: diel and lunar cycles of movement and feeding, densities, and morphology. *J. Exp. Mar. Biol. Ecol.* 530–531, 151430 <https://doi.org/10.1016/j.jembe.2020.151430>.
- Small, C., Nicholls, R.J., 2003. A global analysis of human settlement in coastal zones. *J. Coast. Res.* 19, 584–599. <http://www.jstor.org/stable/4299200>.
- Sun, J., Chi, X., Yang, M., Ding, J., Shi, D., Yu, Y., Chang, Y., Zhao, C., 2019, November 8. Light intensity regulates phototaxis, foraging and righting behaviors of the sea urchin *Strongylo-centrotus intermedius*. *PeerJ* 7, e8001. <https://doi.org/10.7717/peerj.8001>.
- Tuya, F., Martín, J.A., Luque, A., 2004. Patterns of nocturnal movement of the long-spined sea urchin *Diadema antillarum* (Philippi) in gran Canaria (the Canary Islands, central East Atlantic Ocean). *Helgol. Mar. Res.* 58, 26–31. <https://doi.org/10.1007/s10152-003-0164-0>.
- Ullrich-Lüter, E.M., Dupont, S., Arboleda, E., Hausen, H., Arnone, M.I., 2011, May 2. Unique system of photoreceptors in sea urchin tube feet. *Proc. Natl. Acad. Sci.* 108, 8367–8372. <https://doi.org/10.1073/pnas.1018495108>.
- Underwood, C.N., Davies, T.W., Queirós, A.M., 2017. Artificial light at night alters trophic interactions of intertidal invertebrates. *J. Anim. Ecol.* 86, 781–789. <https://doi.org/10.1111/1365-2656.12670>.
- Verling, E., Crook, A., & Barnes, D. K. A. (2002). Covering behaviour in *Paracentrotus lividus*: is light important? *Mar. Biol.* 140, 391–396. doi:<https://doi.org/10.1007/s002270100689>.
- Yang, M., Hu, F., Leng, X., Chi, X., Yin, D., Ding, J., Li, X., Zuo, R., Chang, Y., Zhao, C., 2021. Long-term effects of light spectra on fitness related behaviors and growth of the sea urchin *Strongylocentrotus intermedius*. *Aquaculture* 537, 736518. <https://doi.org/10.1016/j.aquaculture.2021.736518>.
- Yoshida, M., 1956. On the light response of the chromatophore of the sea-urchin, *Diadema setosum* (Leske). *J. Exp. Biol.* 33, 119–123. <https://doi.org/10.1242/jeb.33.1.119>.