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Artificial light and cloud cover interact to disrupt celestial migrations at night

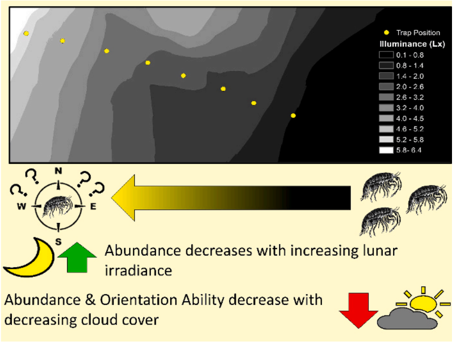
Leo M. Burke [a,*], Thomas W. Davies [b], David Wilcockson [c], Stuart Jenkins [d], Amy Ellison [a]

[a] Bangor University, School of Natural Sciences, Bangor LL57 2UW, UK
[b] University of Plymouth, School of Biological and Marine Sciences, Drake Circus, Plymouth PL4 8AA, UK
[c] Aberystwyth University, Department of Life Sciences, Edward Llywd Building, Aberystwyth SY23 3DA, UK
[d] Bangor University, School of Ocean Sciences, Menai Bridge LL59 5AB, UK

HIGHLIGHTS

- We studied the effects of ALAN on the navigation, movement and population ecology of *Talitrus saltator*.
- ALAN disrupts the migratory behaviour of *T. saltator*, altering the distribution of the species.
- The effects of ALAN were modulated by variations in lunar irradiance and cloud cover.
- Effects of ALAN differed between juveniles and adults.

GRAPHICAL ABSTRACT



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ABSTRACT

The growth of human activity and infrastructure has led to an unprecedented rise in the use of Artificial Light at Night (ALAN) with demonstrable impacts on ecological communities and ecosystem services. However, there remains very little information on how ALAN interacts with or obscures light from celestial bodies, which provide vital orientating cues in a number of species. Furthermore, no studies to date have examined how climatic conditions such as cloud cover, known to influence the intensity of skyglow, interact with lunar irradiance and ALAN over the course of a lunar cycle to alter migratory abilities of species.

Our night-time field study aimed to establish how lunar phase and climatic conditions (cloud cover) modulate the impact of ALAN on the abundance and migratory behaviour of *Talitrus saltator*, a key sandy beach detritivore which uses multiple light associated cues during nightly migrations. Our results showed that the number and size of individuals caught decreased significantly as ALAN intensity increased. Additionally, when exposed to ALAN more *T. saltator* were caught travelling parallel to the shoreline, indicating that the presence of ALAN is inhibiting their ability to navigate along their natural migration route, potentially impacting the distribution of the population. We found that lunar phase and cloud cover play a significant role in modifying the impact of ALAN, highlighting the importance of incorporating natural light cycles and climatic conditions when investigating ALAN impacts. Critically we demonstrate that light levels as low as 3 lx can have substantial effects on coastal

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* Corresponding author.
E-mail address: OSU266@bangor.ac.uk (L.M. Burke).

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invertebrate distributions. Our results provide the first evidence that ALAN impacted celestial migration can lead to changes to the distribution of a species.

1. Introduction

The widespread use of artificial light at night (ALAN) in recent history has transformed the night-time environment throughout a large proportion of the earth's surface (Longcore and Rich, 2004). Global urbanisation, which has been significantly linked to the spatial extent of ALAN, has nearly doubled over the last 20 years (Seto et al., 2012). Currently, roughly 60 % of the world's most populated cities are within 100 km of the coast (Tibbetts, 2002; Small and Nicholls, 2003) and over 20 % of coastlines are exposed to ALAN, with this predicted to increase at a rate of 2–6 % each year (Hölker et al., 2010; Kyba et al., 2017). The rapid increase in use of artificial lighting is leading to a gap between evolutionary adaptations and current environmental conditions for many organisms (Marangoni et al., 2022). In recent years the impacts of ALAN on natural environments have begun to receive greater attention, with studies documenting its wide-ranging impacts from the molecular level to entire ecosystems, modifying the abundance, distribution and behaviour of species across a range of biomes, taxa and spatial scales (Rich and Longcore, 2013; Gaston et al., 2013; Gaston and Bennie, 2014; Gaston et al., 2014). ALAN has been shown to alter the movement and orientational abilities of both terrestrial and marine organisms, from well publicised impacts on orientation related hatchling mortality (Peters and Verhoeven, 1994; Tuxbury and Salmon, 2005), to impacts on navigation (Le Corre et al., 2002; Merkel and Johansen, 2011), as well as behaviour and movement (Bird et al., 2004; Becker et al., 2013; Berge et al., 2020).

The role of celestial bodies, particularly the moon, in guiding nocturnal behaviours is well established in terrestrial (Prugh and Golden, 2014; Penteriani et al., 2010), marine (Ludvigsen et al., 2018; Righton et al., 2016; Shima et al., 2020) and freshwater (Grant et al., 2009; Corbet, 1958) environments. Lunar cues have been shown to be vital in determining a range of night-time behaviours including sea turtle hatchling migration (Salmon and Witherington, 1995), dung beetle orientation (Dacke et al., 2004), the timing and success of mating in moths (Storms et al., 2022), as well as nightly migrations of sandhoppers (Ugolini et al., 1999; Ugolini et al., 2003, 2005). Recent evidence suggests that ALAN inhibits lunar guided reproduction (Ayalon et al., 2021), orientation (Foster et al., 2021), migration (Torres et al., 2020) and foraging behaviour (Tidau et al., 2022) at intensities resembling that of natural moonlight.

The characteristics of ALAN depend on a host of variables including the distance to the light source, its power and spectral composition (Luginbuhl et al., 2014), the composition of the atmosphere, including the presence and altitude of clouds, as well as natural light regimes (lunar phase). Thus far investigations of ALAN impacts have generally failed to include sources of natural nocturnal light. Those studies that have aimed to incorporate lunar photobiology have primarily focused on the response of organisms exposed or not to simulated artificial light illuminances equivalent to dawn/dusk (Ugolini et al., 2005; Papi et al., 2007; Torres et al., 2020; Tidau et al., 2022), with very few considering the consequences of a gradient of in situ light pollution for celestial orientation (Foster et al., 2021). Understanding how natural light regimes and climatic conditions interact to alter the effect of ALAN at different spatial scales is vital in determining distances and thresholds at which organisms are affected.

We conducted an observational field experiment to investigate the impact of artificial light at night from a nearby town on the migrations, abundance and size distribution of *Talitrus saltator*, a common sandy shore detritivore which uses multiple light-based cues to undertake nightly migrations along a sea/land axis as well as orientate itself within its environment (Ugolini et al., 1999). The impacts of ALAN, lunar phase and cloud over, which is known to amplify artificial sky illuminance (Kyba et al., 2011), were assessed using directional pitfall trapping across an established light pollution gradient, encompassing two full lunar cycles and variable cloud conditions. We hypothesized that, at increased levels of light pollution, we would observe (1) greater disruption of expected migratory patterns leading to (2) reduced overall abundance of *T. saltator*, and (3) a shift in body size distributions, resulting from altered nocturnal foraging activity. Additionally we hypothesized that the (4) observed effects of ALAN would be greater under higher cloud coverage and increased lunar illuminance.

2. Methods

The impact of artificial light pollution on the migrations, abundance and body size of *T. saltator* was quantified over 18 nights from early June until the end of July 2021. Sampling was designed to capture *T. saltator* across three lunar phases (new moon, full moon and half-moon) as well as a range of cloud cover conditions (0–100 % cloud coverage). Over the course of the study period a total of 101,357 *T. saltator* were collected.

2.1. Study organism

Crustacean amphipods of the Talitridae family are among the most abundant and biomass-rich organisms in the upper layers of temperate sandy beaches (e.g., Dahl, 1952; Scapini et al., 1997; Schlacher et al., 2014). *T. saltator* has a well-defined nocturnal movement pattern, undertaking nightly seaward migrations to forage on strand-line algae before returning to the refuge of their burrows to avoid predation, desiccation and immersion. *T. saltator* represents one of the best-known biological examples of compass driven migration patterns in littoral arthropods. Since the mid-20th century various studies have demonstrated that when artificially or naturally displaced from their burrows, *T. saltator* uses multiple light-based cues to facilitate their recovery to their preferred shore height, following the most direct route (i.e. the sea – land axis; (Pardi and Scapini, 1983; Scapini et al., 1985; Ugolini and Scapini, 1988; Ugolini et al., 1999)). These migrations are heavily reliant on celestial cues and are vital in maintaining the fitness and survival of *T. saltator*. Previous studies have established the importance of a lunar compass in this behaviour (Ugolini and Scapini, 1988; Ugolini et al., 1999). As with all species that undergo light driven migration patterns, any disruption to these patterns of movement is likely to have severe impacts on the viability of populations.

2.2. Study site and light mapping

This study was conducted at Rhosneiger Traeth Llydan, a south facing, macrotidal sandy shore located on the North Wales coastline, UK (53.223°N, 4.517°W). Ground level illuminance (Lux) data was collected at night during a new moon and clear skies at 6 m resolution across five transects parallel to the shore and extending 300 m from the town of Rhosneiger (at approximately 20, 40, 60, 80 and 100 m from low water) using a Skye® LUX sensor (SpectroSense2+.GPS) logging every 5 s. These measures were GPS linked so that a prediction surface map of illuminance could be interpolated from the data using an exponential kriging model in ArcGIS 10.8.1. The town of Rhosneiger is located at the western end of the beach and a combination of direct street lighting and skyglow produces a gradient of decreasing illumination from west to east (Fig. 1). The generated light map was used to select the locations of the pitfall traps aimed at determining the abundance, size distribution and migration direction of captured *T. saltator*.

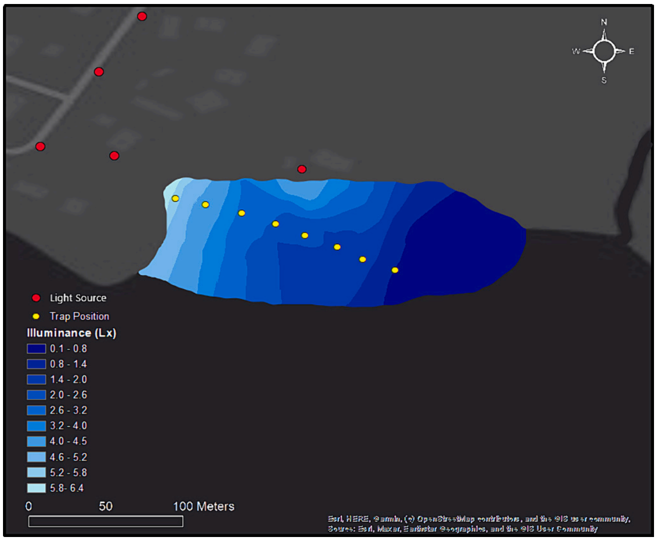

Fig. 1. The distribution of artificial light at night from High Pressure Sodium and LED street lighting across Rhosneiger's Broad Beach, Anglesey, North Wales. CRS = WGS84.

2.3. Survey design

Pitfall cross traps (Fig. S2; modified from Tongiorgi, 1963; Pardi et al., 1974; Scapini et al., 1992) were used to collect *T. saltator*. The traps were designed and placed to intercept animals travelling in four directions: seawards, landwards and from the two opposite directions parallel to the shoreline (East & West). Traps were placed in the same position each night along a transect located in the algal strandline of the eulittoral zone at GPS defined intervals to encapsulate the light gradient of the beach. Light measurements (lux) were also collected for every trap on each sampling night by taking a recording 2 h after setting the trap and 2 h before trap collection using Skye® LUX sensor (SpectroSense2+. GPS). Cloud cover, temperature and lunar phase data were recorded using the visual crossing database for each sampling night (https://www.visualcrossing.com/weather-history/rhosneiger/us/2021-06-01/2021-08-31). All data was obtained from Valley (ID: 03302099999) and EGOV (ID:EGOV) weather stations located 2 km from the study site at RAF Valley, Anglesey airport.

Traps were set at dusk (~23:00 h) and were collected 6 h later. Each trap was filled to a depth of 2 cm with 5 % sea water-formalin solution to preserve captured organisms. These animals were returned to the laboratory to be counted, measured and divided into size groups. Individuals were size sorted to investigate whether ALAN impacts differ with ontogeny. Based on previous studies (Williams, 1976, 1978; Scapini et al., 1992), specimens with a body length >8 mm were considered to be adults, whereas those equal to or <8 mm were placed in the juvenile size categories (<4 mm, 4–8 mm).

2.4. Data analysis

The impact of night-time light intensity (lux), lunar phase and cloud cover (Ground level illuminance * Cloud cover * Lunar Disk illuminance) on abundance was analysed using Generalised Linear Models with a Poisson error distribution and log link function (GLM; CRAN: lme4; Bolker et al., 2009). The variables cloud cover and lunar illuminance were included as continuous variables for the purposes of data analysis and separated into categories for graphical presentation (Cloud cover percentage: 0–33 % = Clear skies, 33–66 % = Partially cloudy, 66–100 % = Overcast). Lunar illuminance was obtained from a look up table (1 min resolution) of Zenith Sky Brightness modelled for Rhosneiger, Anglesey. Modelling followed Davies et al. (2013) in which the moon's sky position and phase angle were calculated from the time, date and geocentric coordinates of location (CRAN: astrolib). The Zenith Sky Brightness was then modelled accounting for lunar phase, altitude, opposition, parallax and atmospheric scattering according to Krisciunas and Schaefer (1991). We then took the median value from our 6 h sampling windows and used this in our analysis. We selected the 25th percentile, median and 75th percentile to present the effect of lunar illuminance ranging from 0 to 0.002 cd/m^2. We used linear regression modelling to quantify the relationship between abundance and night-time light intensity for each size category. We then used lstrends in the lsmeans package to perform a Tukey pairwise comparison test between size class responses to increasing light intensity (Lenth, 2016; R Core Team, 2018).

An index (the orientation index) summarising the propensity of *T. saltator* to move in a seaward/landward direction (as opposed to a direction parallel to the sea, East/West) was calculated by dividing the number of captured *T. saltator* recovered from the two quadrants parallel to the shoreline by the total caught per trap. The impact of light intensity on the orientation index was analysed using Generalised Linear Models with a binomial error distribution and logit link function (GLM; CRAN: lme4; Bolker et al., 2009). The most parsimonious combination of predictor variables nested within a global model, including all 2nd and 3rd order interactions (~Ground level illuminance * Lunar Illuminance * Cloud cover), was identified as that with the lowest value of Akaike's Information Criterion (AIC) using [CRAN: MuMIn (Dredge)]. Model selection was further validated using AIC weights, and the significance of the selected model was tested against a null intercept only model and individual model terms tested for significance. Bonferroni's post-hoc test was used to perform comparisons between traps, lunar illuminance and cloud cover. All statistical analyses were carried out in R version 3.5.1 (R Core Team, 2018).

3. Results

3.1. Total abundance

The distribution and movements of *T. saltator* across the study site were strongly associated with ALAN illuminance. The abundance of captured *T. saltator* was significantly lower under high artificial light illuminances, with the number of individuals caught increasing as the distance from the light source increased. Lux was included in the top 10 out of 15 candidate models (Table S2). All predictor variables, and the interaction between artificial light and cloud cover (Artificial light intensity * Cloud cover + Lunar illuminance), were included in the most parsimonious model describing the variance in abundance (Table S1). The selected model was 2.17 AIC points lower than the next ranking candidate model, had a high relative likelihood (0.58; Table S1) compared to remaining candidate models (from 0 to 0.20), and described significantly more variance in the total abundance of *T. saltator* than a null intercept only model ($\chi^2 = 677.45$, $p < 0.001$). The selected model contained a negative effect of increasing lux ($Z_{123} = -12.70$, $p < 0.001$) and a significant interaction between cloud cover and lux ($Z_{123} = 2.23$, $p = 0.02$) meaning that fewer individuals were caught under lower cloud cover, particularly for those traps located closer to the source of light pollution (Fig. 2). Lunar illuminance also altered the abundance of *T. saltator* with significantly fewer individuals caught as lunar illuminance increased ($Z_{123} = -3.03$, $p = 0.002$; Fig. 3).

3.2. Migration direction

The presence of ALAN disrupted the migration patterns of *T. saltator*, resulting in a higher proportion travelling parallel to the shore as ground level illuminance increased (Fig. 5). The most parsimonious model describing the variation in migration direction of *T. saltator* included interactive effects between artificial light illuminance and cloud cover (Lux * Cloud cover). The selected model was 2.14 AIC points lower than the next ranking candidate model, had a high relative likelihood (0.61;

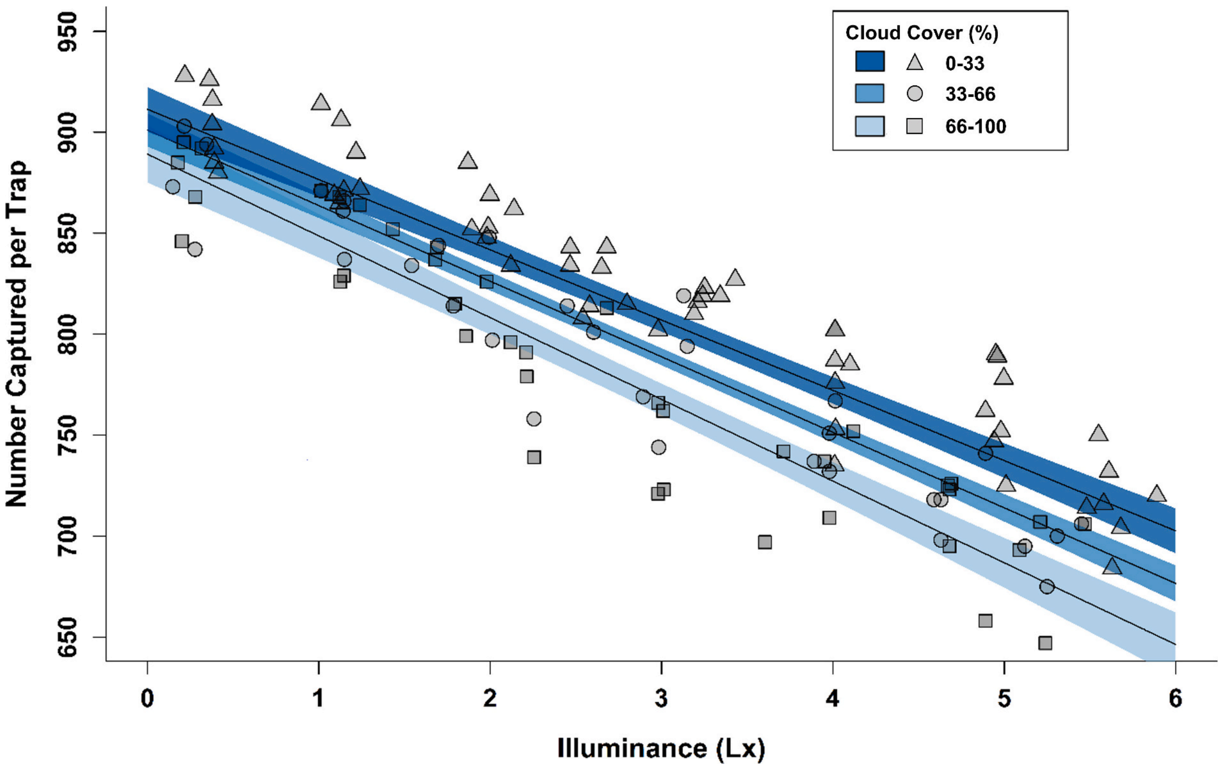

Fig. 2. The effect of increasing illuminance (lux) from artificial light pollution on the total number of *T. saltator* caught per pitfall trap. The interaction between artificial light illuminance and cloud cover has been plotted along with the confidence intervals for each level of cloud cover.

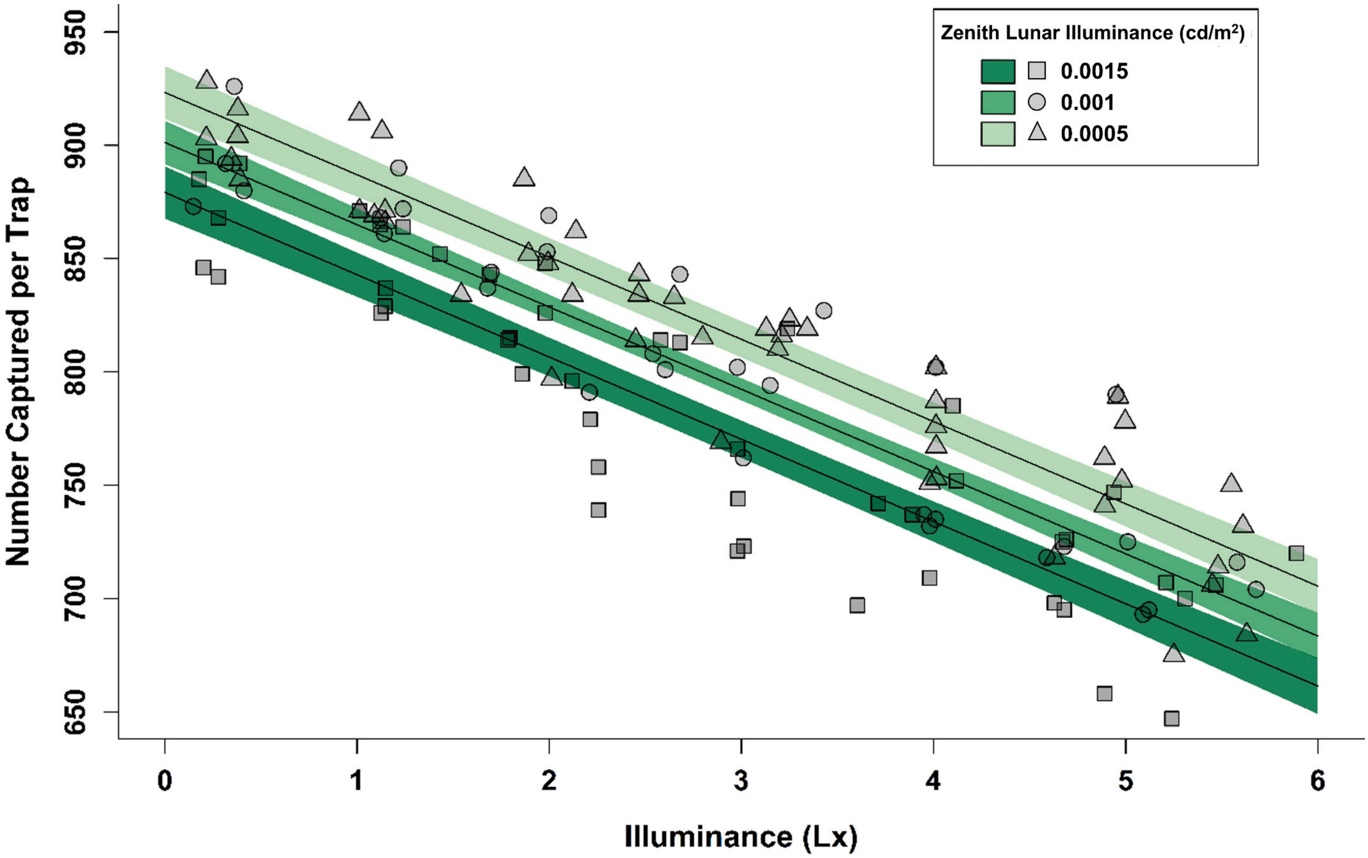

Fig. 3. The effect of increasing illuminance (lux) from artificial light pollution on the total number of *T. saltator* caught per pitfall trap. The additive effect of lunar phase has been plotted along with the confidence intervals for three levels of lunar disk illumination corresponding to lunar phase.

Table S2) compared to remaining candidate models (from 0 to 0.21), and described significantly more variance in the movement direction of *T. saltator* than a null intercept only model ($\chi^2 = 3422.8, p < 0.001$). Lux was included in the top 10 out of 15 candidate models, with all models not containing lux scoring higher than a null intercept only model (Table S2). Significantly more *T. saltator* migrated in an east/west direction as artificial light illuminance increased ($Z_{124} = 27.037$; $p < 0.0001$). The selected model also contained a significant interaction between lux and cloud cover meaning that the number of *T. saltator* caught travelling parallel to the shoreline significantly increased as cloud cover decreased ($Z_{124} = -2.38$, $p = 0.01$). Despite not being significant across all traps it is worth noting that the prevailing migration direction shifted as lux increased. Trap 1 to 3, located closest to the source of artificial light pollution, captured more sandhoppers moving eastwards compared to any other direction, with this result significant for trap 1 ($F(1) = 53.281$, $p < 0.001$). This effect diminishes as distance from the light source increases with traps 4–8 failing to record a predominant migration direction.

3.3. Size distribution

The impact of increasing artificial light illuminance differed significantly between juvenile (<8 mm body length) and adult groups (t (596) = −7.21, p < 0.001). Increasing illuminance resulted in a significant decrease in the abundance of *T. saltator* across all adult size classes ($F(1) = 924.38$, $p < 0.001$). The strongest effect of increasing illuminance was recorded for the 14–18 mm size class ($y = 241.67–22.17x$; Fig. 5). In contrast, the abundance of the two juvenile (<8 mm body length) size classes increased with increasing illuminance ($y = 173.15 + 3.06x$; Fig. 5), with the smallest of these groups (<4 mm) increasing significantly ($F(1) = 82.66$, $p < 0.001$).

4. Discussion

Evidence of the impact of ALAN on lunar guided processes is increasing, with known effects on phenology (Ayalon et al., 2021), movement (Torres et al., 2020; Foster et al., 2021) and community composition (Willems et al., 2022). The results from our study demonstrate the negative impact of ALAN on the orientating and migratory ability of *T. saltator* and how, when combined with variations in lunar irradiance and cloud coverage, this effect alters the distribution and size structure of populations. Critically, we demonstrate even modest levels of artificial light pollution (~3 lx) can have dramatic effects on coastal invertebrate distributions.

The negative impact of ALAN on an organism's ability to navigate and orientate themselves within their environment is widespread and well documented in several different systems, from well know occurrences such as bird strikes on artificially lit vessels at sea (Merkel and Johansen, 2011), to terrestrial invertebrates (Warrant and Dacke, 2010, 2011), and commercially important fish (Marchesan et al., 2005; Oppedal et al., 2011; Becker et al., 2013). Previous studies aimed at measuring the perception of polarised lunar light, a key orientating cue in dung beetles and other insects (Dacke et al., 2003, 2011), established that urban skyglow pollutes the lunar signal to such a degree that on most nights, lunar polarisation-based animal navigation is no longer expected to be possible (Kyba et al., 2011). Additionally, ALAN has been shown to impact lunar guided migrations across systems and at a range of scales, from interrupting the lunar guided diel vertical migration (DVM) of *Daphnia* (Moore et al., 2000), to changes in dung beetle orientation behaviour (Foster et al., 2021).

Despite growing evidence across systems that ALAN is capable of disrupting an organism's orientation abilities, no studies have aimed to establish how ALAN impacted lunar orientation translates to changes in a species' distribution. Our results revealed a strong relationship between ground level illuminance and the movement direction and abundance of captured *T. saltator*. As ground level illuminance increased, more *T. saltator* were captured travelling parallel to the shoreline, deviating from their normal perpendicular migratory pattern. Previous studies have established avoidance behaviours, as well as changes in the timing and duration of activity periods, in response to high artificial light illuminance across a range of systems and species (Bird et al., 2004; Pulgar et al., 2019; Duarte et al., 2019). Our results indicate a possible avoidance response for those traps located closest to the town of Rhosneiger, as more *T. saltator* were captured moving in an easterly direction away from the source of light pollution. However, given that we only recorded a prevailing migratory direction for trap 1 it is unlikely that an avoidance response to light is driving the trends observed throughout the remainder of the study site. Additionally, we recorded disrupted migratory patterns under light as low as 3 lx, indicating that, while high ALAN illuminances (>5 lx; Fig. 4) may trigger an avoidance response, the decline in abundance observed across the study site is likely a result of ALAN impacted orientation and movement. The results from this study build on previous research revealing negative effects of ALAN on the locomotor activity and lunar orientating ability of *T. saltator* under simulated skyglow (Torres et al., 2020). We also provide the first evidence that ALAN illuminances bright enough to obscure celestial navigation cues inhibit normal migratory behaviour potentially leading to changes in the distribution of species.

Our results highlight the importance of investigating the effects of ALAN across natural cycles of night-time light, namely lunar phases. Under full moon conditions less *T. saltator* were caught irrespective of ground level illuminance differences across the study site, indicating that, despite a background effect of ALAN, lunar irradiance still influences the abundance of active *T. saltator*. For other species, the light intensity of a full moon has been shown to suppress activity (Jaramillo et al., 2003; Prugh and Golden, 2014; Beltran et al., 2021; Willems et al., 2022; Tidau et al., 2022), a common pattern driven by trade-offs between foraging success and predator avoidance, and could explain the trends in the number of captured *T. saltator* observed here. Interestingly, the migration direction of *T. saltator* was not associated with lunar illuminance, possibly indicating that the presence of ALAN is obscuring the detection of lunar light and any potential effect of lunar phase on the migratory direction of *T. saltator*. Equally, it could be suggested that, despite relying on celestial queues to guide nightly migrations, the amount of lunar light is less critical to these migrations than the spectral characteristics or polarisation of the light, both of which are known to be influenced by climatic conditions such as cloud cover.

The effect of ALAN was greater under lower cloud coverage, with fewer *Talitrus* captured under clearer skies. We expected to record higher ground level illuminance levels under higher cloud cover as cloud coverage is known to increase the brightness of artificial skyglow (Kyba et al., 2011; Davies et al., 2014). However, in the present study, we recorded a change in ground level illuminance across the study site of just 0.4 lx in relation to cloud cover percentage (0–100 %). The relatively low change in ground level illuminance indicates that the observed effect is being driven by more than just a change in illuminance. The influence of polarised light has been gaining more attention with regards to ALAN impacted light cycles, and indeed could explain some of the observed effects of cloud cover and lunar phase presented here. It has been suggested that for some organisms the polarisation of light (or lack thereof) is equally or more important than the presence of the light itself. For example, migratory birds are known to be more strongly attracted to lights on nights with low cloud coverage (Rich and Longcore, 2013). Furthermore, a recent study confirmed that, in the absence of other celestial cues, *T. saltator* uses the skylight radiance gradient as a chronometric compass orienting reference, and that the detection of polarised light is key in determining the perception of these radiance and spectral gradients (Ugolini et al., 2023). Our results highlight the complexity involved when investigating the effects of ALAN, and the importance of incorporating climatic conditions known to influence the intensity of both natural and artificially introduced light.

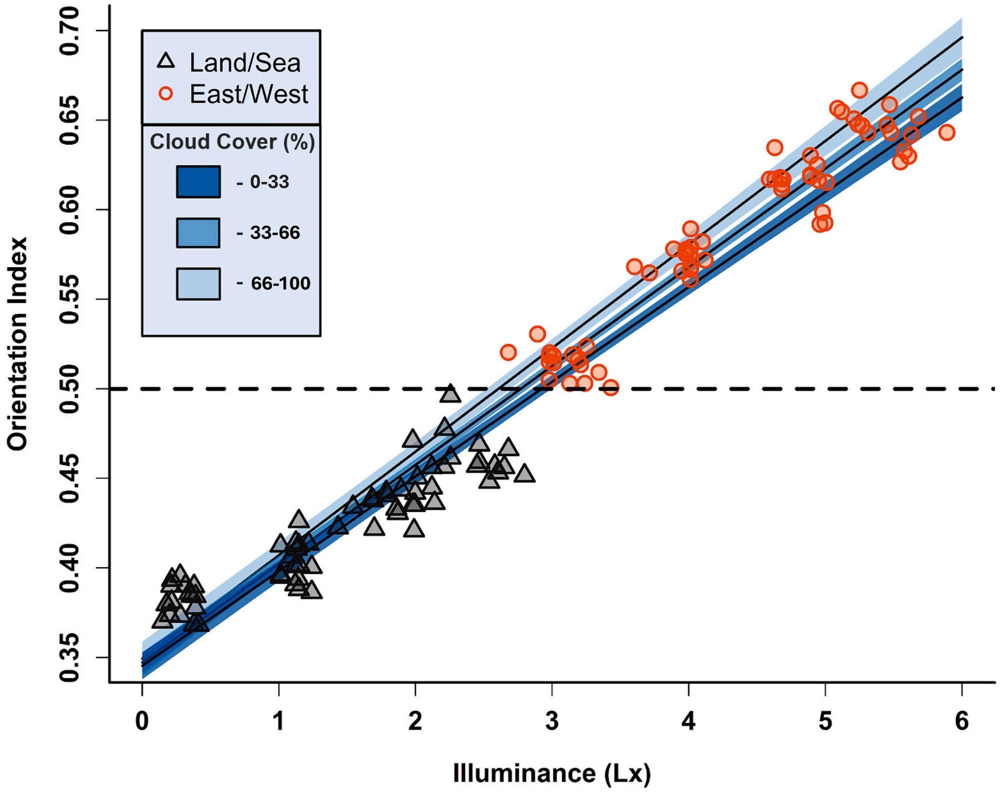

Fig. 4. The effect of increasing illuminance (Lux) from artificial light pollution on the migration direction of *T. saltator*. Migration index indicates the proportion of total individuals caught while moving along an East/West axis vs Land/Sea. The interaction between illuminance and cloud cover has been plotted along with the confidence intervals for each level of cloud cover percentage.

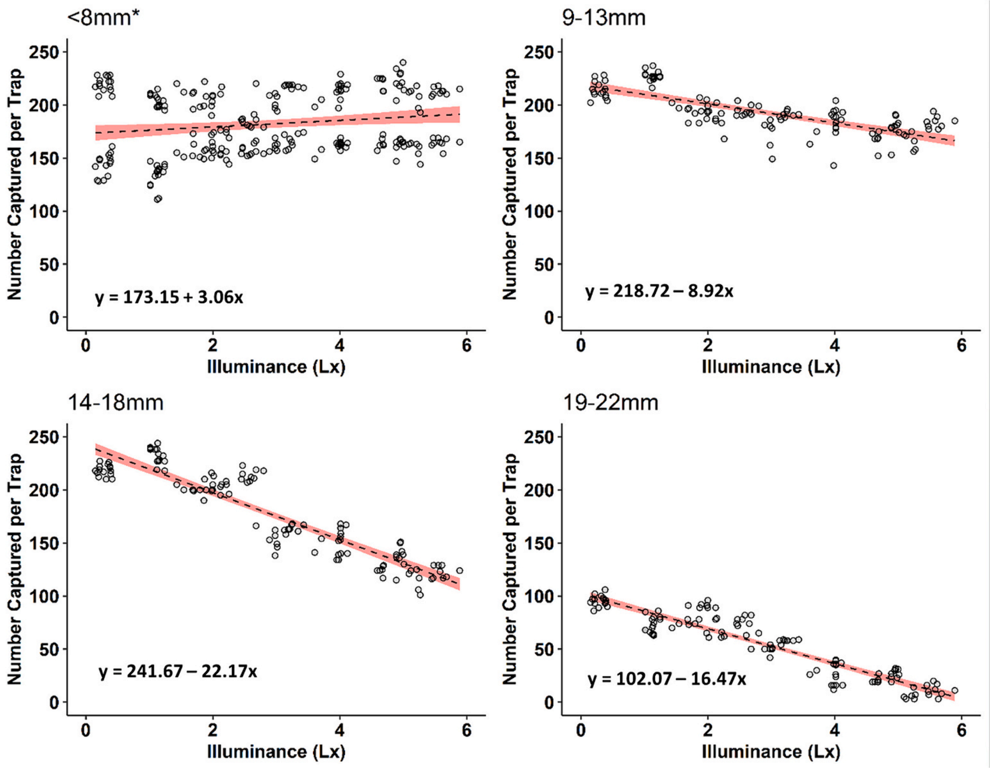

Fig. 5. The effect of increasing illuminance (lux) from artificial light pollution on the abundance of *T. saltator* across body size classes (mm). Black lines show a linear model fitted to the data, and the red shaded region show the 95 % confidence intervals.

The body size distribution of *T. saltator* populations varied significantly with the level of ALAN exposure. Adults, particularly the two largest size classes, exhibited a much steeper gradient of declining abundance as ALAN illuminance increased. Differences in the timing of activity between adult and juvenile populations are well documented in a range of terrestrial and aquatic species (Cardoso, 2002; Nardi et al., 2003; Pavesi et al., 2007; Gerrish et al., 2009). However, given that our traps were placed before dusk and left until dawn, it is unlikely that any potential differences in the timing of activity between juveniles and adults observed in other studies (Scapini et al., 1992; Duarte et al., 2019; Lynn et al., 2021) is leading to the trends observed here. Fewer large individuals under higher ALAN illuminance may be a result of a number of processes. Firstly, our data and other studies (Torres et al., 2020) indicate altered orientation and migratory patterns under ALAN, which conceivably may reduce foraging efficiency and lead to reduced growth rates and/or survival as documented for other species (Luarte et al., 2016; Dananay and Benard, 2018; Schligler et al., 2021). Alternatively, there are specific differences between juveniles and adults in response to artificial light resulting from ontogenetic shifts in morphology and physiology. For other species of crustaceans, juveniles with eyes differing to those of adults in both structure and function, often exhibit differing patterns of movement, behaviour and space utilisation (Meyer-Rochow, 1975, 2001; Hines et al., 1995). For many species, differences in the timing of activity and space utilisation between juveniles and adults serve to reduce intraspecific competition and cannibalism. Therefore, any alteration to the movement and space utilisation between juveniles and adults could have profound impacts on intraspecific competition and predation. For example, ALAN has been shown to increase the predation of juveniles by adults in the South American burrowing crab *Neohelice granulate* (Nuñez et al., 2021). Additionally, observations suggest that juveniles of some species are more sensitive to polarised light than adults (Meyer-Rochow, 1975). It is therefore possible that the differences observed between adults and juveniles in response to artificial light could lie within the ontogeny of the species. Currently no evidence exists regarding the differences between the perception of light in adult and juvenile *T. saltator*, but given the known sensitivity of other species of juvenile crustaceans to changes in the spectral characteristics of light, it could be proposed that juvenile navigation may be less impacted by the introduction of artificial light than adults. Impacts to different ontogenetic phases will likely enhance the potential for population level effects of ALAN.

Overall the findings of this study indicate that ALAN as low as 3 lx has the ability to alter the distribution and behaviour of a key invertebrate detritivore. Critically we provide the first evidence of ALAN impacted celestial migration translating into changes in the distribution of a species. The results of this study also highlight the importance of including climatic and lunar conditions when investigating the effects of ALAN. Additionally, we show that ALAN has the potential to impact various life stages in different ways meaning that the viability of populations could potentially hinge on understanding these impacts. Varying physiological conditions and requirements along the ontogeny of *T. saltator* and other invertebrates are likely to promote different responses to ALAN or other environmental factors (Benítez et al., 2016; Farnworth et al., 2018). If ALAN disrupts ontogenetic differences in timing of activity and space utilisation, intended to separate juveniles and adults, then greater intraspecific competition and cannibalism could lead to substantial population declines.

Our results reveal the potential for ALAN impacted celestial navigation and migration to translate to changes in the distribution and population structure of a species. The ability of ALAN to alter the population dynamics and biogeographical distribution of organisms that rely on celestial guided migrations is evident and is likely to increase given that the spatial extent of ALAN is expanding yearly. Our study highlights the pressing need for more information on how natural variables interact with ALAN to produce anthropogenic impacts to species, populations and systems.

CRediT authorship contribution statement

Leo M. Burke: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas W. Davies:** Writing – review & editing, Supervision, Methodology, Funding acquisition. **David Wilcockson:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Stuart Jenkins:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Amy Ellison:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, 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

I have shared my data at the attach file step.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.173790.

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