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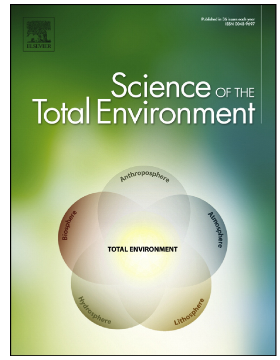

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Mapping the consequences of artificial light at night for intertidal ecosystems

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Abstract

Widespread coastal urbanization has resulted in artificial light pollution encroaching into intertidal habitats, which are highly valued by society for ecosystem services including coastal protection, climate regulation and recreation. While the impacts of artificial light at night in terrestrial and riparian ecosystems are increasingly well documented, those on organisms that reside in coastal intertidal habitats are less well explored. The distribution of artificial light at night from seaside promenade lighting was mapped across a sandy shore, and its consequences for macroinvertebrate community structure quantified accounting for other collinear environmental variables known to shape biodiversity in intertidal ecosystems (shore height, wave exposure and organic matter content). Macroinvertebrate community composition significantly changed along artificial light gradients. Greater numbers of species and total community biomass were observed with increasing illumination, a relationship that was more pronounced (increased effects size) with increasing organic matter availability.. Individual taxa exhibited different relationships with artificial light illuminance; the abundances of 27% of non-rare taxa [including amphipods (Amphipoda), catworms (*Nephtys* spp.), and sand mason worms (*Lanice conchilega*)] decreased with increasing illumination, while 20% [including tellins (*Tellinidae* spp.), lugworms (*Arenicola marina*) and ragworms (*Nereididae* spp.)] increased. Possible causes of these relationships are discussed, including direct effects of artificial light on macroinvertebrate behaviour and indirect effects via trophic interactions. With increasing light pollution in coastal zones around the world, larger scale changes in intertidal ecosystems could be occurring.

Key Words

Artificial light at night, illuminance, High Pressure Sodium, intertidal ecosystems, sandy shore, macroinvertebrates, community structure.

Introduction

Today around a quarter of the Earth's surface is polluted by artificial light at night (Falchi et al., 2016), originating from industry, residential areas and transportation networks (Bennie et al., 2014; Gaston et al., 2015). A wide range of ecological impacts of this pollution have been identified, including effects on physiology (Navara & Nelson, 2007; Dominoni et al., 2013), navigation (Tuxbury & Salmon, 2005; Rodríguez et al., 2012), reproductive behaviour (Jokiel et al., 1985; van Geffen et al., 2015), predation success (Santos et al., 2010; Underwood et al., 2017), community structure (Davies et al., 2012; Bolton et al., 2017) and ecosystem services (Lyytimäki, 2013).

With widespread coastal urbanization, the impact of artificial light at night on marine ecosystems has become a topic of increasing concern (Becker et al., 2013; Davies et al., 2014; Davies et al., 2016; Bolton et al., 2017). 75% of the world's megacities (populations > 10 million) are now located in coastal regions (Luijendijk et al., 2018), and more than 22% of shorelines worldwide are light-polluted (Davies et al., 2014). The effects of artificial light on shallow marine species, including fish (Becker et al., 2013), amphipods (Navarro-Barranco & Hughes, 2015) and sessile invertebrates (Davies et al., 2015), have been documented in recent years. The consequences of lighting intertidal habitats – which provide valuable ecosystem services globally (Costanza et al., 1997; Barbier et al., 2011) and are likely most exposed among marine ecosystems to light pollution –have more recently become a focus for research (Luarte et al., 2016; Duarte et al., 2019)..

Daily, monthly and seasonal natural light cycles play an important role in intertidal ecosystems, synchronising mass spawning and hatching events, partitioning feeding and swimming activity, and regulating migrations (Jansson & Källander, 1968; Forward, 1986; Robles et al., 1989; Naylor, 2001). Species interactions across trophic levels are also guided by light availability, determining the timing and success of predatory activity and the ability of prey to avoid predation (Viherluoto & Viitasalo, 2001; Santos et al., 2010; Underwood et al., 2017). Perhaps most importantly, intertidal invertebrate larvae are guided by light during settlement site selection, which determines subsequent survival and reproductive success (Thorson, 1964; Davies et al., 2014). These key ecological processes that shape intertidal ecosystems are likely affected by light pollution from streets, promenades, piers, jetties, harbours and marinas (Davies et al., 2014). Recent data has demonstrated strong evidence of artificial light impacts including reduced activity and growth rates on individual species that reside in sandy shores (Luarte et al., 2016; Duarte et al., 2019), which are the most widespread of intertidal ecosystems (Brown & McLachlan, 2002), with potential larger scale implications for macroinvertebrate assemblages. The consequences of artificially lighting beaches for the structure and composition of intertidal macroinvertebrate communities, however, remains unquantified.

We mapped the exposure of intertidal organisms in a sandy shore ecosystem to artificial light from promenade High Pressure Sodium lighting, and demonstrate for the first time its consequences for intertidal macroinvertebrate community composition and structure.

Methods

Summary

Ground level night-time artificial illuminance (Lux) was measured across Llandudno West Shore beach in North-West Wales, UK (53.320°N, 3.846°W) and the data used to produce a 6 m resolution light map. Macroinvertebrate communities, sediment grain size (a good proxy of wave exposure [Burt et al., 2010]), and organic matter content were sampled at low, mid and high shore elevations across a gradient in illumination parallel to the shoreline.

The relationships between response variables (macroinvertebrate community composition, species richness, species dominance, the total number of individuals, total community biomass, and the presence of individual taxa) and artificial light exposure were quantified accounting for potentially collinear gradients in shore height, median grain size and organic matter concentration.

Study site

This study was conducted at Llandudno West Shore Beach, a west-facing, macrotidal, sandy beach on the North Wales coast. The northern half of the shore is illuminated by adjacent High Pressure Sodium promenade lighting such that gradients of decreasing illumination are established from high to low shore, and north to south (Figure 1). The site contains two fish-tail groynes, the larger of which (Gogarth Breakwater) brackets the northern limit of the shore.

Light mapping

Ground level illuminance was mapped at night at 6 m resolution across 4 transects parallel to the shore (at approximately 0, 40, 100 and 200 m from the sea wall) using a Skye® LUX sensor logging every 5 seconds. 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. The light data was collected between 12:30 and 2:30 am on the 11th of June 2018 during a new moon to avoid moonlight intereference.

Shore sampling

One macroinvertebrate and two sediment samples were extracted from 54 sampling stations across the measured illumination gradient along horizontal transects (approximately

900 m in length) at three shore heights representative of the full gradient of zonation (Figure 1). Each transect occupied a 50 cm elevation zone, relative to Ordnance Datum Newlyn: high shore (1 to 1.5 m), middle shore (-0.25 to 0.25 m) and low shore (-1.5 to -1 m); and contained 18 sampling stations positioned randomly within 40 m intervals along the transect. Sampling was undertaken either side of the smaller groyne to control for effects of potentionally colinear variables known to influence community composition (grain size and organic matter content) (Bull et al., 1998; French & Livesey, 2000; Walker et al., 2008; Fanini et al., 2009). 89% of the samples (16 stations on each transect) were collected over 3 consecutive days (20th - 22nd June 2018), with the final 11% collected 10 days later on a day with comparable weather conditions, using the same equipment and consistent methods. All sampling was undertaken at low/retreating tide.

At each station a macroinvertebrate sample (0.1 m^2 to 0.2 m depth) was dug and wet sieved through a 1 mm mesh, and two small sediment cores (0.008 m^2 to 0.2 m depth) were extracted for grain size and organic matter content analysis . Macroinvertebrate samples were preserved in 70% Industrial Methylated Spirit with rose bengal pending lab analysis, and all specimens were identified to the lowest practicible taxonomic resolution, counted and weighed. One sediment sample from each station, after washing and drying, was shaken for 15 minutes through a stack of brass sieves with decreasing mesh sizes (4 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, 63 µm). The remaining sediment in each sieve was weighed, and median grain size was calculated using GRADISTAT v 8.0 (Blott & Pye, 2001). The remaining sediment samples were dried and then heated in a muffle furnace at 450°C for 4 hours to burn off any organic matter, with the resulting differences in the weights of the samples used to calculate organic matter concentrations (Cambardella et al., 2001).

Statistical analysis

Data analysis was performed using R statistical software. The relationship between macroinvertebrate community composition and artificial light exposure (ground-level illuminance) was examined using a permutational multivariate analysis of variance (adonis, CRAN: vegan), performed on Bray-Curtis dissimilarity matrices calculated from log-transformed species abundance and biomass, accounting for shore height, particle size and organic matter. All first order effects and second order interactions with light were included in the model.

The relationships between macroinvertebrate community metrics (total number of individuals [*n* m^{-2}], total biomass [g m^{-2}], species richness [species count] and species dominance [1 – Pielou's evenness]) and environmental variables (artificial illuminance, shore height, particle size, organic matter) were quantified using multiple regression models fitted using either spatially autocorrelated mixed effects models (corrHLfit, CRAN: spaMM) or generalised linear models with appropriate error distributions where spatial autocorrelation was not identified in the response variable of interest (determined using Mantel tests).

Model selection (model.sel, CRAN: MuMIn) was used to compare the small-sample-size corrected values of Akaike's Information Criterion (AIC) of a series of candidate regression models, including the global model (~ illuminance * shore height + illuminance * particle size + illuminance * organic matter), all possible nested models of the global model, and a null (~ intercept only) model (Table 2). The most parsimonious models were tested for significance by comparing to a null model using a likelihood ratio test. Where the most parsimonious models were significantly different from the null, and included the illuminance predictor variable, the significance of this variable was further tested using a likelihood ratio test comparing the model with a nested model in which the illuminance variable was omitted. If the model included a second order effect of illuminance, the significance of the effect was determined by testing the model against itself but with the interaction removed.

The relationships between the abundances of individual macroinvertebrate species and environmental variables were also examined using multiple regression model selection, as previously described, identifying the most parsimonious model for each species and testing the significance of illuminance when present as a predictor variable. The abundances of rarer species were summed by genus or family (Table 3) to reduce zero inflation. Analyses were performed on numerical abundance data for taxa present in more than 50% of samples, and presence-absence data for taxa present in less than 50% of samples, with appropriate error distributions fitted in each case Any taxa that were present in less than 10% of the samples were deemed too rare to be reliably incorporated in the analysis.

Results

The light data displayed an exponentially decreasing gradient in illuminance from high to low shore adjacent to the lamp-posts (Figure 1), ranging from 5 lux on the promenade, equivalent to a typical residential side street (Gaston et al., 2013), to 0.006 lux, with the lowest values found in the far south and on the low shore directly next to Gogarth Breakwater. Median grain size on the intertidal shore ranged from 142 to 169 μm (fine sand), with the organic matter concentration of the sediment between 0.3 and 0.9%. Gradients in grain size and organic matter were not collinear with illuminance (variance inflation factor [VIF] values < 3).

The beach contained an abundance of intertidal macroinvertebrates (median: 180 n m^{-2}), with a total of 1984 individuals collected, representing 45 species and 26 families. The macroinvertebrate assemblages on the shore predominately consisted of crustaceans (70%), polychaetes (26%) and bivalves (3%) [percentages by abundance]. There was no significant difference in the structure of the community sampled between different survey days, with regard to abundance ($F_{(3,50)} = 1.29$, p = 0.29), biomass ($F_{(3,50)} = 0.84$, p = 0.48), species richness ($F_{(3,50)} = 1.84$, p = 0.15) or species dominance ($F_{(3,48)} = 0.94$, p = 0.43).

Macroinvertebrate community composition across the shore was significantly related to the degree of exposure to artificial light at night, accounting for other environmental variables (shore height, particle size and organic matter), and regardless of whether abundance or biomass was used (*n* individuals m^{-2}: $F_{(44,53)} = 2.26$, $p < 0.05$; g m^{-2}: $F_{(44,53)} = 2.52$, $p < 0.01$; Table 1).

Artificial illuminance (lux) was included in the most parsimonious models describing the species richness and total community biomass of macroinvertebrates (Table 2). The relationship between light and these responses was modulated by organic matter content (Species richness: $x^2 = 46.90$, $p < 0.01$; Biomass: $x^2 = 8.42$, $p < 0.01$). The selected model (Lux * Organic) described significantly more of the variability in these responses compared to a null (~ intercept only) model (Species richness: $x^2 = 81.56$, $p < 0.01$; Biomass: $x^2 = 2.72$, $p < 0.001$). Species richness and biomass (Figure 2) increased with increasing illuminance; relationships that became more positive with increasing organic matter availability (Figure 3). The cumulative abundance and species dominance of the macroinvertebrate community were not strongly related to artificial light exposure, with the illuminance model (~ Lux) describing no more variation in the responses than the null model (~ intercept only) (Abundance: $x^2 = 0.56$, $p = 0.11$; Dominance: $x^2 = 0.01$, $p = 0.67$).

Out of the 15 common taxa of macroinvertebrates found on the shore, the abundances of 7 taxa (47%) displayed significant relationships with artificial light exposure accounting for other environmental variables (Table 3). Four of these taxa decreased in either abundance or probability of occurrence with increasing illuminance, including amphipods (*Bathyporeia elegans* and *Haustorius arenarius*), catworms (*Nephtys* spp.) and sand mason worms (*Lanice conchilega*), while the remaining 3 taxa increased in probability of occurance with increasing illuminance: *Tellinidae* spp., *Arenicola marina* and *Nereididae* spp. (Figure 4).

Discussion

Macroinvertebrate community composition is known to be affected by artificial light at night in a variety of ecosystems, including terrestrial ground-dwelling communities (Davies et al., 2012; Davies et al., 2017; Manfrin et al., 2017), sessile marine epifaunal communities (Davies et al., 2015; Bolton et al., 2017) and riparian ecosystems (Meyer & Sullivan, 2013). To our knowledge the results presented here represent the first evidence of artificial light altering macroinvertebrate community structure and composition in a sandy shore ecosystem. Macroinvertebrate assemblages in sandy shore habitats - which make up around 75% of the world's ice-free coastlines (Brown & McLachlan, 2002) - are critical to ecosystem functioning and connectivity. They contribute to sediment aeration, facilitating organic matter mineralisation and nutrient cycling, form planktonic linkages between distant habitats, and provide important resources for top consumers such as birds and fish (Brauns, 2008; Schlacher et al., 2008).

Our study found changes in the community composition, species richness and cumulative biomass of macroinvertebrates that were related to the level of exposure to artificial light pollution from adjacent High Pressure Sodium promenade lighting with illuminances equivalent to residential side streets (Gaston et al., 2013). While our study was limited to one shore line, the relationships between macroinvertebrate community descriptors and artificial illumination were quantified accounting for e key structural drivers in intertidal ecosystems (shore elevation, and wave exposure), which are also strongly linked with groyne proximity, hence we are confident that the results presented constitute evidence of artificial light impacts in the focal study system.

The effects of anthropogenic structures such as groynes on sandy shore ecosystems are well established (French & Livesey, 2000; Martin et al., 2005; Walker et al., 2008; Fanini et al., 2009). Reduced wave exposure on the intertidal shore due to sheltering by anthropogenic structures often leads to changes in the sediment characteristics of the beach with regard to particle sizes and organic content, which in turn drive changes in macroinvertebrate assemblages (Martin et al., 2005; Rodil et al., 2007; Walker et al., 2008). These effects were given careful consideration during study design, and controlled for by sampling either side of the groyne structures, and in the analysis by including median grain size and organic matter content as candidate variables during the model selection procedure. We are therefore confident that the results reported here are not artefacts of groyne effects.

47% of non-rare taxa were individually found to either increase or decrease in abundance (or the probability of occurrence) with increasing illumination, accounting for shore height and sediment characteristics, including common intertidal species such as polychaetes (*Nephtys* spp., *Lanice conchilega*, *Arenicola marina*, *Nereididae* spp.), amphipods (*Bathyporeia elegans*, *Haustorius arenarius*) and bivalves (*Tellinidae* spp.). Although the mechanisms responsible for these relationships are uncertain, there are a range of possible explanations based on the known influences of light in intertidal systems, which encompass direct effects of artificial light on macroinvertebrate life cycles, and indirect effects due to trophic interactions.

Multiple aspects of marine macroinvertebrate reproductive biology are guided by natural light cues, including synchronised broadcast spawning, larval phototaxis, and recruitment (Thorson, 1964; Bentley et al., 2001; Naylor, 2001). The adult stages of mobile marine macroinvertebrates can also be highly photosensitive with taxa displaying both positive and negative phototaxis (Tranter et al., 1981; Del Portillo & Dimock Jr, 1982; Adams, 2001). Marine amphipods, for example, are known to be strongly attracted to artificial lights (Meekan et al., 2001; Hughes & Ahyong, 2016), with assemblages of subtidal amphipods aggregating in halogen light traps with intensities equivalent to average levels of coastal light pollution (Navarro-Barranco & Hughes, 2015). As is the case for many taxa displaying this aggregation response (for example Lepidoptera, Araneae and Coleoptera), the mechanism of disruption remains unclear. Orientation using the lunar and solar compass is, however, common in some intertidal amphipod species (Ugolini et al., 2005; Ugolini et al., 2012), and artificial light disruption of this compass is plausible.

As with many other groups (Rydell, 1992; Becker et al., 2013), aggregation in illuminated areas will increase the vulnerability of intertidal macroinvertebrates to predation. Increases in the abundance of predators as a result of artificial light has been previously reported in a variety of ecosystems and species, from coastal fish (Becker et al., 2013) to bats (Rydell & Racey, 1995) and ground-dwelling insects and arachnids (Davies et al., 2012), and can lead to significant changes in the composition of prey communities within illuminated areas (Bolton et al., 2017). In the same manner that bats target moths and other flying insects around streetlights (Rydell, 1992; Acharya & Fenton, 1999; Minnaar et al., 2015), wading birds are attracted to the nocturnal foraging opportunity posed by light-polluted intertidal shores (Santos et al., 2010). Taking advantage of artificial illumination, these birds alter their feeding strategy from tactile to sight-based foraging (Dwyer et al., 2013), displaying increased intake rates of macroinvertebrate prey compared to non-illuminated regions (Santos et al., 2010).

The negative effect of artificial light exposure on the prevalence of amphipods (*Bathyporeia elegans* and *Haustorius arenarius*) in the current study, which constitute the prey of wading birds (Goss-Custard & Jones, 1976; Evans et al., 1980), could be due to light-attracted aggregations being targeted by foragers. Similarly, two polychaete taxa also displayed negative relationships to artificial illuminance: catworms (*Nephtys* spp.) and sand mason worms (*Lanice conchilega*), which are two of the most common prey groups in the diet of intertidal foraging birds (Goss-Custard & Jones, 1976; Yates et al., 1993; Petersen & Klaus-Michael, 1999).

Intertidal macroinvertebrates are known to be threatened by a variety of anthropogenic pressures, such as coastal development, pollution discharge and climate change (Brown & McLachlan, 2002; Schlacher et al., 2007; Defeo et al., 2009). However the impact of artificial light pollution remained unconsidered until recent years (Luarte et al., 2016; Duarte et al., 2019). This study demonstrates that artificial light pollution can alter intertidal macroinfaunal communities in sandy beach ecosystems. With 75% of the world's megacities located near coastlines (Luijendijk et al., 2018), the potential for widespread artificial light at night in coastal regions (Davies et al. 2014) to alter the biogeographical distributions of intertidal organisms is clear. It may prove possible to reduce these impacts by limiting the period, intensity and dispersal of lighting, as well as altering the types of lights used and their spectral composition (Gaston et al., 2012; Rajkhowa, 2012).

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CRediT author statement

Matthew J. Garratt: Methodology, Formal Analysis, Investigation, Writing-Original Draft, Visualisation. **Stuart R. Jenkins:** Writing-Review & Editing, Supervision, Project Administration, Funding Acquisition. **Thomas W. Davies:** Conceptualization, Methodology, Formal Analysis, Writing-Review & Editing, Visualisation, Supervision, Project Administration, Funding Acquisition.

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Figure 1. The distribution of artificial light at night form High Pressure Sodium promenade lighting across Llandudno West Shore Beach, North Wales.

Figure 2. Macroinvertebrate community structure metrics that were significantly related to artificial light exposure from High Pressure Sodium promenade lighting: **A)** species richness (species count); **B)** cumulative biomass (g m^{-2}).

Figure 3. The effects of artificial light at night from High Pressure Sodium lighting on macroinvertebrate species richness and biomass at high (a-b), medium (c-d), and low (e-f) organic matter content in a sandy shore ecosystem. Relationships (dashed lines) are presented from the most parsimonious generalised linear models (Table 2) which included artificial light exposure and were significantly different from a null (intercept only) model. A significant interaction between artificial light exposure and organic matter content was present in both cases, presented here using the lower quartile, median and upper quartile values of organic matter concentration (%). Grey regions indicate the 95% confidence intervals of these relationships.

Figure 4. Intertidal macroinvertebrate taxa with abundances or occurrences significantly related to artificial light at night from High Pressure Sodium promenade lighting in a sandy shore ecosystem. The relationship between artificial light exposure and each abundance measure (dashed lines) were identified as the most parsimonious generalised linear models that were significantly different from a null (intercept only) model. Grey regions indicate the 95% confidence intervals of these relationships. *Nephtys* spp. and *Haustorius arenarius* were analysed using poisson GLMs performed on abundance data, while binomial GLMs performed on presence/absence data were used for the remaining taxa.

Table 1. The relationship between macroinvertebrate community composition and artificial light exposure from High Pressure Sodium promenade lighting in a sandy shore ecosystem. Permutational multivariate analysis of variances were performed on Bray-Curtis dissimilarity matrices calculated from log-transformed species abundance and biomass data. The tested model included first order effects of all physical variables, and interactions with illuminance.

	Community composition response			
	Abundance		**Biomass**	
Predictor	$F_{(44,53)}$	p	$F_{(44,53)}$	p
Illuminance (lux)	2.26	$\underline{<0.05}$	2.52	$\underline{<0.01}$
Shore height	5.97	$\underline{<0.001}$	3.71	$\underline{<0.001}$
D50 (μm)	1.90	0.089	1.98	$\underline{<0.05}$
Organic matter (%)	3.10	$\underline{<0.01}$	2.33	$\underline{<0.01}$
Lux:Shore height	1.50	0.120	1.35	0.117
Lux:D50	0.74	0.589	1.39	0.139
Lux:Organic	1.23	0.321	1.62	0.076

Table 2. Selection of the most parsimonious models describing how macroinvertebrate abundance (*n* m^{-2}), biomass (g m^{-2}), species richness (species count) and species dominance (1 - J') vary with exposure to High Pressure Sodium promenade lighting, and other physical variables in a sandy shore ecosystem. AICc values of the most parsimonious models are underlined and bolded.

Model	**AICc**			
	Abundance [a]	Biomass [a]	Richness [b]	Dominance [c]
Lux * Shore height + Lux * D50 + Lux * Organic	67.8	58.5	269.4	-24.4
Lux * Shore height + Lux * Organic	63.0	55.8	266.5	-20.4
Lux * D50 + Lux * Organic	74.6	50.2	259.9	-21.9
Lux * Shore heigth + Lux * D50	63.4	60.3	267.8	-25.3
Lux * Shore height	59.6	61.3	267.4	-16.8
Lux * D50	78.4	53.2	262.0	-17.2
Lux * Organic	70.8	<u>**49.5**</u>	<u>**256.8**</u>	-17.7
Lux	76.5	54.4	260.2	-9.8
Shore height + D50 + Organic	58.0	60.4	264.2	-26.7
Shore height + D50	59.3	59.2	261.7	-23.3
Shore height + Organic	55.5	62.5	265.5	<u>**-26.1**</u>
Shore height	<u>**56.9**</u>	62.3	263.1	-21.3
D50 + Organic	72.6	62.9	266.4	-24.1
D50	75.5	61.3	264.3	-19.6
Organic	72.1	62.3	265.0	-19.0
Null	76.8	61.6	262.9	-11.6

[a] Gaussian GLM performed on $\log_{10}(x+1)$ transformed data
[b] Gaussian GLM performed on raw data
[c] Poisson GLM performed on raw data

Table 3. Examining the relationships between the abundances of common macroinvertebrate taxa and exposure to High Pressure Sodium promenade lighting in a sandy shore ecosystem. Commonality is defined as the percentage of samples individual taxa were found in. The percentage contribution of each taxon to the total abundance and biomass of the macroinvertebrate community is also displayed, along with the formula of the most parsimonious model describing those predictor variables which shaped either the abundance or presence of each taxon. Taxa affected by artificial light underlined.

Taxon	Proportion of samples (%)	Proportion of abundance (%)	Proportion of biomass (%)	Model formula
Nephtys spp. [a]	70.4	8.7	9.9	Lux * Organic + D50
Bathyporeia pilosa [a]	66.7	49.9	4.0	Shore height
Spionidae spp. [b]	50.0	4.8	3.6	Shore height
Orbiniidae spp. [b]	37.0	2.4	7.5	Null
Crangon crangon [b]	35.2	2.6	1.5	Organic
Tellinidae spp. [b]	35.2	2.3	14.3	Lux * Organic + D50
Lanice conchilega [b]	33.3	6.4	4.8	Lux + Organic
Bathyporeia elegans [b]	25.9	3.8	0.2	Lux + Shore height
Haustorius arenarius [b]	24.1	2.7	2.8	Lux * Organic
Phyllodocidae spp. [b]	22.2	0.8	0.04	Shore height
Eurydice pulchra [*]	18.5	10.5	1.2	Shore height
Cerastoderma edule [b]	14.8	0.7	34.1	Null
Arenicola marina [b]	13.0	0.5	11.9	Lux
Nereididae spp. [b]	13.0	1.2	1.7	Lux
Semelidae spp. [b]	11.1	0.4	0.01	Null
Sum	*NA*	97.6	97.6	*NA*

[a] Poisson GLM performed on raw abundance (n m^{-2}) data
[b] Binomial GLM performed on presence/absence data
* Spatially autocorrelated binomial model (corrHLfit) performed on presence/absence data

Highlights

- Our coasts are increasingly polluted by artificial light at night (ALAN).
- We studied the potential effects of ALAN in an intertidal sandy shore ecosystem.
- Macrofaunal community structure significantly changed across a gradient in ALAN.
- 47% of non-rare taxa displayed significant relationships to illuminance.
- Relationships with key environmental drivers were accounted for.

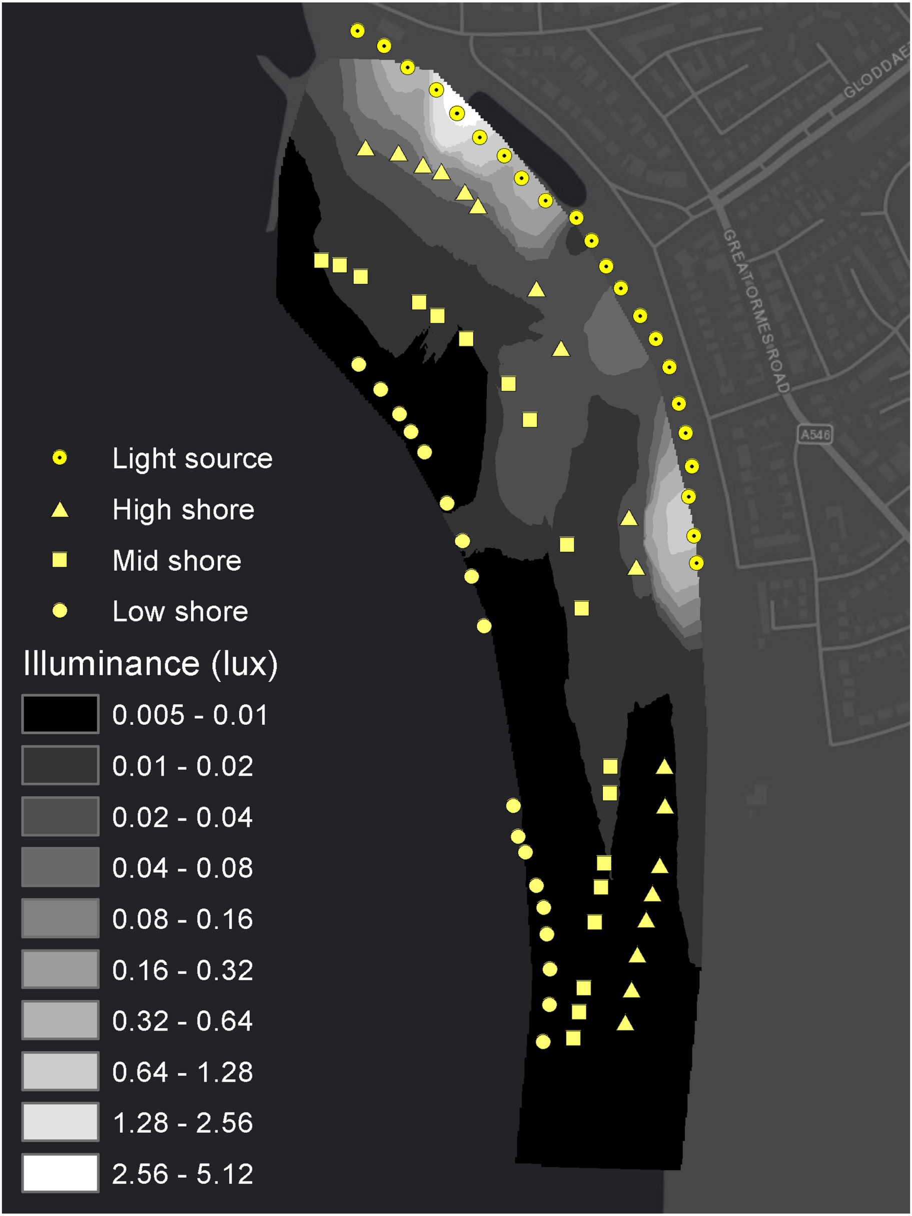

Light source
High shore
Mid shore
Low shore
Illuminance (lux)
0.005 - 0.01
0.01 - 0.02
0.02 - 0.04
0.04 - 0.08
0.08 - 0.16
0.16 - 0.32
0.32 - 0.64
0.64 - 1.28
1.28 - 2.56
2.56 - 5.12
GREAT ORMES ROAD
A546

Figure 1

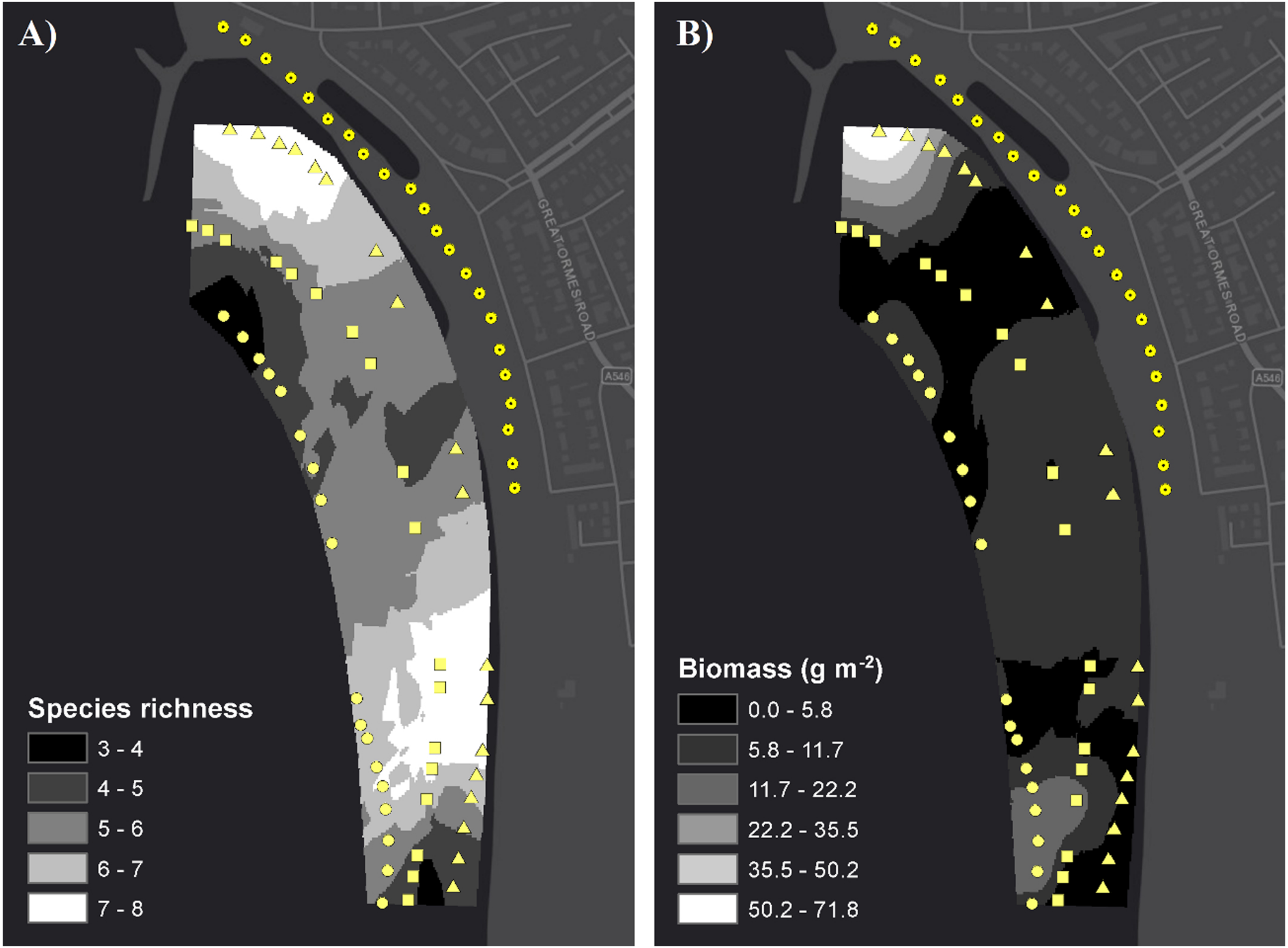
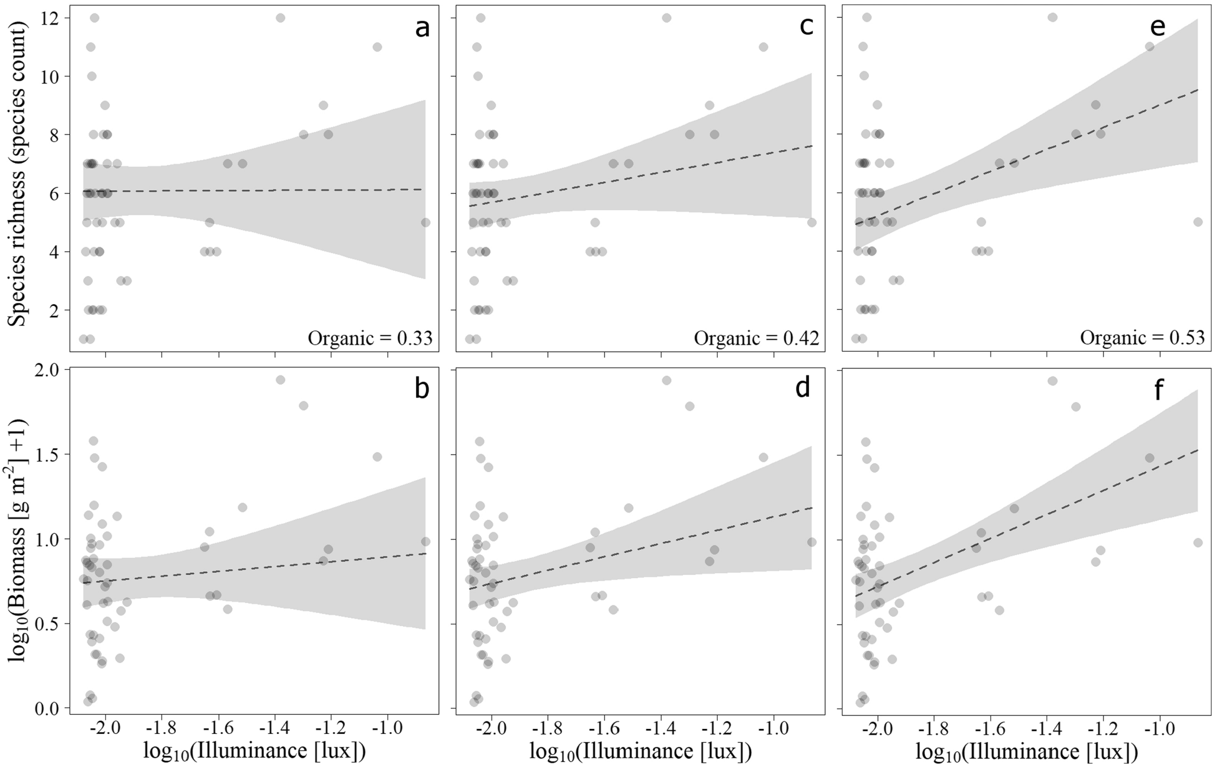
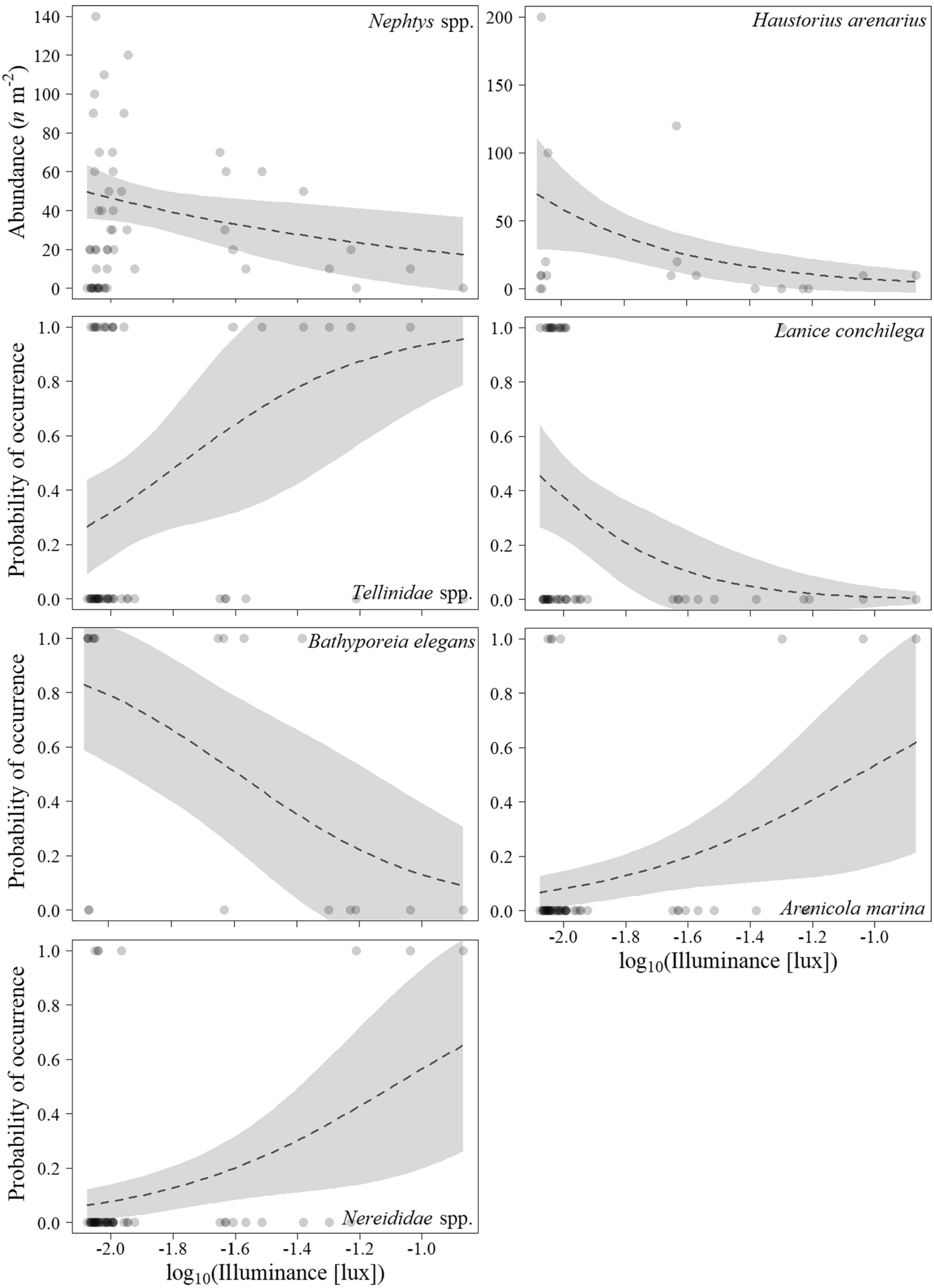

A)
Species richness
3 - 4
4 - 5
5 - 6
6 - 7
7 - 8
B)
Biomass (g m-2)
0.0 - 5.8
5.8 - 11.7
11.7 - 22.2
22.2 - 35.5
35.5 - 50.2
50.2 - 71.8
GREAT ORMES ROAD
A546

Figure 2



Species richness (species count)
12
10
8
6
4
2
a
Organic = 0.33
c
Organic = 0.42
e
Organic = 0.53
log$_{10}$(Biomass [g m^{-2}] +1)
2.0
1.5
1.0
0.5
0.0
b
d
f
-2.0
-1.8
-1.6
-1.4
-1.2
-1.0
log$_{10}$(Illuminance [lux])
log$_{10}$(Illuminance [lux])
log$_{10}$(Illuminance [lux])

Figure 3



Nephtys spp.
Haustorius arenarius
Tellinidae spp.
Lanice conchilega
Bathyporeia elegans
Arenicola marina
Nereididae spp.
Abundance (n m-2)
Probability of occurence
log10(Illuminance [lux])

Figure 4