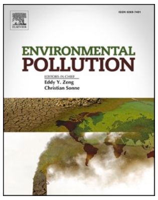
Environmental Pollution 385 (2025) 127155

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol



Artificial light at night alters seaweed reproductive phenology[☆]

Emma Moyse [a,*], Louise B. Firth [a,b], Tim Smyth [c,d], Thomas W. Davies [a]

[a] School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK
[b] School of Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, Cork, T23 N73K, Ireland
[c] Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK
[d] Centre for Geography and Environmental Science, Department of Earth and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9EZ, UK

ARTICLE INFO

Keywords:
Artificial light at night
Intertidal ecology
Global change ecology
Light pollution
Macroalgae
Phenology
Seaweeds
Urbanisation

ABSTRACT

Artificial light at night (ALAN) is a growing, globally prevalent environmental stressor. It is known to disrupt biological processes across taxa and biomes, including reproductive phenology in terrestrial plants, but its potential to alter reproductive timings in marine macroalgae remains unexplored. We used reflectance spectrometry to quantitatively assess changes in receptacle ripeness of three fucoid macroalgae species at four field sites along an ALAN gradient in Plymouth Sound, UK over a six-month period. At sites with elevated ALAN (measured using Sky Quality Meters, range 16.15–18.76 mag arcsec^{-2}, equivalent to 3.75×10^{-2}–3.38×10^{-3} cd/m^2), expected seasonal patterns of receptacle ripening in *Ascophyllum nodosum* were reversed, causing receptacles to continue ripening into the winter months as opposed to peaking during the summer. *Fucus serratus* also continued to ripen in winter when exposed to the highest ALAN levels (16.15 mag arcsec^{-2}, 3.75×10^{-2} cd m^{-2}). Our results provide some of the first evidence that ALAN disrupts reproductive timings in fucoid macroalgae. Given the critical role of fucoids in coastal ecosystems worldwide, ALAN should be recognised as a potential driver of ecological change in these species. Incorporating ALAN into conservation strategies is essential for protecting these foundational habitats.

1. Introduction

Artificial light at night (ALAN) is a major anthropogenic pollutant that has transformed the nocturnal environment, but its ecological impacts are frequently overlooked. It is a global phenomenon, affecting at least 80 % of the world's human population (Falchi et al., 2016), and is rapidly expanding, with its area and intensity increasing annually by approximately 2.2 % and 1.8 %, respectively (Kyba et al., 2017). Contrary to popular belief, ALAN impacts are not restricted to terrestrial biomes but are also far-reaching in the marine environment (e.g., Garratt et al., 2019; Marangoni et al., 2022; Smyth et al., 2022), as biologically meaningful levels of light can penetrate to up to 50 m depth (Smyth et al., 2021). ALAN originates primarily from urban and peri-urban sources such as street lighting, illuminated buildings, and coastal infrastructure, all of which have proliferated with global urbanisation (Gaston et al., 2012; Kyba et al., 2017; United Nations, 2019). As urbanisation expands, both the spatial extent and intensity of ALAN increase, particularly along coastlines where residential and industrial development are concentrated (Smyth et al., 2022). These emissions contribute not only to direct illumination of coastal habitats but also to skyglow, which spreads artificial brightness far beyond the immediate vicinity of light sources (Kyba & Hölker, 2013). The intensity and spectral composition of ALAN therefore vary regionally, reflecting differences in population density, lighting technology, and management practices, as well as the geomorphological features of coastlines (Gaston et al., 2012; Smyth et al., 2022). Coastal ecosystems are particularly affected: over 1.9 million km^2 of coastal seas are impacted globally (Smyth et al., 2021), and ALAN exposure intensifies other, more frequently investigated urbanisation impacts such as habitat fragmentation (Aguilera & González, 2023). The biological and ecological impacts span taxa and levels of biological organisation, altering everything from cellular physiology to species assemblage composition (Davies & Smyth, 2018; Garratt et al., 2019; Sanders et al., 2021).

While the vast majority of studies to date have focused on animals, the impacts of ALAN on plants are also well-documented, including negative effects on pollination (Knop et al., 2017), diversity (Bucher

---

[☆] This paper has been recommended for acceptance by Dr Parvaiz Ahmad.
[*] Corresponding author.
E-mail address: emma.moyse@postgrad.plymouth.ac.uk (E. Moyse).

https://doi.org/10.1016/j.envpol.2025.127155
Received 15 May 2025; Received in revised form 8 September 2025; Accepted 22 September 2025

et al., 2023), leaf physiology and chemistry (Segrestin et al., 2021), and, crucially, phenology. Illumination at levels equivalent to street lighting can alter flowering times and vegetation composition in grasslands (Bennie et al., 2018), while large-scale analyses demonstrate both earlier budburst and delayed leaf senescence in trees exposed to ALAN (Lian et al., 2021; Zheng et al., 2021; Meng et al., 2022). These shifts are of comparable magnitude to climatic drivers and may interact with them in complex ways, underscoring the importance of ALAN as a driver of terrestrial phenological change. Algae, however, are significantly understudied, despite light being among the most influential factors governing their growth, physiology, and community structures (Grubisic, 2018). ALAN research relating to algae focuses on the use of artificial lighting in a cultivation context (e.g., Blanken et al., 2013; Brzychczyk et al., 2020), and/or overwhelmingly concerns microalgae (Grubisic et al., 2017; Ayalon et al., 2021; Diamantopoulou et al., 2021). ALAN impacts on macroalgae remain almost entirely unexplored, and while it may be tempting to extrapolate potential effects from terrestrial plant studies, such comparisons, while common, are likely to be misleading due to a host of fundamental environmental and biological differences between the two groups (Schiel & Foster, 2006). Clearly there is an urgent need for macroalgae-specific ALAN research.

Fucoid macroalgae are among the most widely distributed foundation species in the marine environment. Globally estimated to cover a total area of up to 2.57 million km^2, they are potentially the largest mapped marine biome (Fragkopoulou et al., 2022). Their tendency towards large sizes and long lifespans – possibly over a century for *Ascophyllum nodosum* (Åberg, 1992) – means they can be ecologically dominant, and therefore shape their ecosystems over large timeframes (Åberg, 1992; Menge et al., 2017). They provide complex and varied habitats for vast numbers of species, acting as nurseries and feeding grounds for turtles, small cetaceans, and fish (Witherington et al., 2012; Miller, 2015; James & Whitfield, 2023), and as substrate, food source, and camouflage for intertidal invertebrates (Wilbur & Steneck, 1999; Crothers, 2012). In the northeast Atlantic, they are frequently the foundation of entire rocky shore food webs and ecosystems (Lewis, 1964). Other ecosystem services provided by fucoids include acting as major primary producers (Mann, 1973; Pessarrodona et al., 2022), increasing biodiversity (Coleman & Wernberg, 2017; Thomsen et al., 2022), acting as ecosystem engineers by modifying rocky environments (Bellgrove et al., 2017), sequestering carbon (Buck-Wiese et al., 2023), buffering thermal extremes (Coombes et al., 2013), and filtering contaminants out of the water column (Roberts et al., 2006). Fucoids are also an economically valuable resource: *A. nodosum* is the most commercially important seaweed species in Canada, for example, where it is harvested for use in human nutritional supplements, as animal feed, and as fertiliser (Ugarte & Sharp, 2001). Fucoids can play a valuable role in the restoration of degraded ecosystems (Bellgrove et al., 2017), and their foundational role and range of services provided mean that managers sometimes use them as indicator species for overall ecosystem health (de Vasconcelos et al., 2019; Mannino & Micheli, 2020).

Fucoid reproductive phenology varies across species and large spatial scales but is consistently dependent on environmental conditions (Hatchett et al., 2022). Light is a key environmental factor, influencing both receptacle development, where photosynthesis drives periods of rapid apical growth, and the timing of gametogenesis and gamete release (Pearson & Brawley, 1996; Serrão et al., 1996). Constant exposure to light has been shown to disrupt gamete release in laboratory cultured fucoids (Pearson et al., 1998), while some wild populations of *Fucus vesiculosus* exhibit peaks in gamete release according to a semilunar pattern (Andersson et al., 1994). The interaction between circadian and tidal immersion cycles is accepted as a key cue that controls fucoid spawning (Pearson & Brawley, 1996; Ladah et al., 2003; Monteiro et al., 2012). Given the diversity of fucoid species and their habitats, however, their responses to ALAN are likely to be species-specific and locally variable, thus field-based research is urgently needed.

We conducted a six-month field investigation into the reproductive phenology of three fucoid species (*A. nodosum*, *Fucus serratus*, and *F. vesiculosus:* see Fig. 1) at four sites along an ALAN gradient. We used hyperspectral reflectance spectrometry to accurately measure receptacle colour at approximately two week intervals. This novel approach to measuring algal phenology allowed us to gather quantitative receptacle ripening data, avoiding the subjectivity inherent in assessing colour by eye, which may be impacted by location, ambient light and weather conditions, or variation between observers. We investigated whether trends in fucoid receptacle ripening differed between ALAN-exposed and ALAN-naïve sites. We predicted that increased ALAN exposure would disrupt seasonal phenology by extending perceived daylength and delaying morphological changes typically triggered by shortening days in autumn and winter. We hypothesised that ALAN exposure would delay receptacle ripening in all three species compared to low ALAN conditions.

2. Materials and methods

2.1. Study species

Ascophyllum nodosum, *Fucus serratus*, and *Fucus vesiculosus* are widely distributed fucoid macroalgae common on rocky shores around the UK. *A. nodosum* and *F. vesiculosus* characteristically occur on the mid shore, while *F. serratus* typically occurs slightly lower, beginning its range on the low-mid shore and extending into the low shore. All three species are more prevalent on sheltered to moderately exposed shores, but can tolerate a wide range of tidal strengths, and are robust to changes in salinity (Tyler-Walters et al., 2024). Their typical reproductive timings in the UK are listed below (*ibid*):

- *A. nodosum* receptacles begin growing in April and take 12 months to mature. Gamete production mainly occurs in March and April, and receptacles generally ripen in April to June.
- *F. serratus* may be reproductively active year-round, but reproduction is generally believed to peak between August and October.
- *F. vesiculosus* has a reproductive period of around 6 months, beginning in December and reaching peak fertility in May and June.

Fertilisation success depends on the synchronous release of gametes under optimal environmental conditions (Hatchett et al., 2022), of which light is a crucial example (Ladah et al., 2003; Monteiro et al., 2012).

2.2. Study sites

Four sites were identified along an ALAN gradient around Plymouth Sound, UK: Coxside (50.3659°N, 4.1302°W), Mountbatten (50.3566°N, 4.1267°W), Tinside (50.3633°N, 4.1414°W), and Wembury (50.3164°N, 4.0829°W). Sites were classified as high ALAN (Coxside, Tinside), medium ALAN (Mountbatten), or low ALAN (Wembury) based on representative night sky brightness measurements taken *in situ* before moon rise using a Unihedron Sky Quality Meter – L (SQM-L) under clear sky conditions during a waning crescent moon phase (see Fig. 2 and Table 1). All three of the target algae species were routinely present at all sites throughout the study period with the exception of Tinside, where only *Fucus serratus* was found consistently.

2.3. Data acquisition and processing

Sites were sampled at approximately 2-week intervals between July and December 2023, though sampling was not possible at 3 of the sites (Coxside, Mountbatten, Wembury) in November due to severe storms. Sampling dates were chosen to roughly correspond with spring tides (±3 days), which coincide with new and full lunar phases. Algae were sampled from horizontal, equally light-exposed areas of the mid-shore using 50 cm quadrats placed semi-randomly on areas with significant

Fig. 1. Images of the three target fucoid algae species in their non-reproductive (top row) and reproductive (bottom row) states. Left to right: *Ascophyllum nodosum, Fucus serratus, Fucus vesiculosus*.

fucoid algae cover (five quadrats per site, per sampling day). One representative, undamaged adult specimen of each of the study species present in each quadrat was sampled. This meant that for each site we obtained a minimum of 5 fucoid specimens (one per quadrat) per sampling day, but up to 15 if all three species occurred in every quadrat, with intermediate totals when species were patchily distributed.

Hyperspectral reflectance spectra of algae receptacles were measured *in situ* using a portable spectrometer (Ocean Insight OCEAN-HDX-XR) with a wavelength response from 200 to 1100 nm, at 0.5 nm resolution, fitted with a 3 m long 1000 μm fibre optic probe. Specimens were illuminated using an Ocean Optics ISP-REF integrating sphere with a built-in tungsten-halogen light source (colour temperature 3100 K) to ensure even surface illumination and to provide a standardised light environment, allowing us to take measurements in the field without variability in light conditions or cloud cover impacting accuracy. The sampling optic was manipulated via the ISP-REF to exclude specular reflectance. The spectrometer was calibrated between quadrats using a WS-1-SL Spectralon® diffuse reflectance standard. Measurements were taken with the aperture of the integrating sphere held 5 mm above the centre of each receptacle and pointing downwards.

Total brightness (B_1), sometimes also referred to as “total reflectance” (Örnborg et al., 2002) or “spectral intensity” (Andersson et al., 1998; Pryke et al., 2001) was calculated as a quantitative proxy for receptacle ripeness, since ripening in these species causes a gradual colour change from brownish green to a brighter yellow (see Fig. 1), and therefore a higher B_1 value. Reflectance spectra were standardised to a 1 nm resolution using the as.rspec function in the R package ‘pavo’ (Maia et al., 2019). Wavelengths outside the 500–675 nm range were excluded in order to isolate the triple peak in the green to orange portion of the colour spectrum characteristic of brown algae reflectance spectra (Uhl et al., 2013; Kotta et al., 2014), and B_1 was calculated for this wavelength range. B_1 is calculated using the formula:

$$B_1 = \int_{\lambda_{min}}^{\lambda_{max}} R_i \, d\lambda$$

Where λ_{max} and λ_{min} are the upper and lower wavelength limits respectively and R_i is the percentage reflectance at the ith wavelength (Endler, 1990) and can be summarised as the total amount of light reflected between these wavelengths (Saks et al., 2003).

2.4. Statistical analysis

Statistical analysis was conducted using R (RStudio version 2024.09.1 + 394; R Core Team, 2024). To test hypotheses relating to differences in total brightness over time between sites, and because the data were highly overdispersed, negative binomial generalised linear models (GLMs) were fitted for each species with the interaction between the serial day of the year surveyed (‘day’) and site (Coxside,

Fig. 2. Images of the field sites at night: (a) Coxside – very high ALAN; (b) Tinside – high ALAN; (c) Mountbatten – medium ALAN; (d) Wembury – low ALAN.

Table 1
Representative levels of light at night on the mid-shore at study sites. Note that as Sky Quality Meter units are on a negative logarithmic scale, smaller values indicate brighter skies. Typical values range between 16 for highly light polluted skies and 22 for extremely dark skies. Photon flux density (PPFD; μmol m^{-2} s^{-1}) values were estimated from luminance by first converting to illuminance (lux ≈ $\pi \cdot$cd m^{-2} for diffuse sky, Hänel et al., 2018) and then applying published lux–PPFD conversion factors for white LEDs (0.0144–0.0171 μmol m^{-2} s^{-1} per lux, depending on correlated colour temperature; Lang, 2019; cf. Thimijan & Heins, 1983). These values should be interpreted as approximate order-of-magnitude comparisons only, not direct measurements.

Site	Sky Quality Meter (mag arcsec^{-2})	Equivalent sky luminance (cd/m^2)	Estimated PPFD (μmol m^2 s^{-1})
Coxside	16.15	3.75×10^{-2}	$(1.7–2.0) \times 10^{-3}$
Tinside	17.25	1.36×10^{-2}	$(6.1–7.3) \times 10^{-4}$
Mountbatten	18.76	3.38×10^{-3}	$(1.5–1.8) \times 10^{-4}$
Wembury	19.97	1.11×10^{-3}	$(5.0–6.0) \times 10^{-5}$

Mountbatten, Wembury for A. nodosum and F. *vesiculosus*; Coxside, Mountbatten, Tinside, Wembury for *F. serratus*) as the independent variable: $B_1 \sim$ day*site (CRAN: MASS, Venables & Ripley, 2002). Since individual algae were not sampled repeatedly over time, there was no need to control for repeated measures. Unlike Poisson or Gaussian models, the negative binomial framework accommodates the additional variability observed in overdispersed data (where the variance is greater than the mean), ensuring greater flexibility and a better model fit. Impacts of day and site were investigated using a two-way analysis of covariance (ANCOVA) with serial day of the year as the covariate and site as the independent variable; trend differences were investigated using post-hoc pairwise comparisons via the emtrends function (CRAN: emmeans, Lenth, 2024). Predicted relationships between B_1 and time by site were calculated using the predict function (R Core Team, 2024).

3. Results

Nocturnal brightness varied markedly between sites. Coxside, the brightest site, was almost three times brighter than Tinside (3.75×10^{-2} vs. 1.36×10^{-2} cd m^{-2}), over ten times brighter than Mountbatten (3.38×10^{-3} cd m^{-2}), and more than thirty times brighter than Wembury (1.11×10^{-3} cd m^{-2}). Wembury was therefore substantially darker than all other sites and served as the low-ALAN control (see Table 1).

For *A. nodosum,* the rate of change in receptacle brightness differed significantly between sites, as indicated by a negative binomial generalised linear model ($X^2 = 8.29$, *d.f.* $= 2$, $p < 0.05$). At Wembury (low ALAN), mean *A. nodosum* receptacle brightness followed the expected seasonal pattern for the species, decreasing by over 25 % between July and December (Fig. 3a). Mean total brightness declined from 3502 on serial day 190 (9th July) to 2624 on serial day 340 (6th December) (see Table 2). In contrast, at ALAN-exposed sites, this pattern was reversed. Mean receptacle brightness increased by over 26 % at Mountbatten (medium ALAN), rising from 2562 on serial day 190–3238 on serial day 340 (Fig. 3b), and by over 54 % at Coxside (high ALAN) increasing from 2308 to 3565 over the same period (Fig. 3c). Post-hoc pairwise comparisons revealed significant differences ($p < 0.05$) in receptacle brightness trends between the low ALAN site (Wembury) and both ALAN-exposed sites (Coxside and Mountbatten). However, no significant difference was found between the two ALAN-exposed sites (see Table 2).

The rate of change in *F. serratus* receptacle brightness also differed significantly between sites, as indicated by a negative binomial generalised linear model ($X^2 = 17.01$, *d.f.* $= 3$, $p < 0.001$). At Wembury (low ALAN), Mountbatten (medium ALAN), and Tinside (high ALAN), mean *F. serratus* receptacle brightness remained relatively stable throughout the study period, consistent with the capacity of *F. serratus* to remain reproductively active year-round (Fig. 4). However, at Coxside (the highest ALAN site), mean receptacle brightness increased by over 101 %, rising from 1418 on serial day 190–2861 on serial day 340 (Fig. 4d). Post-hoc comparisons revealed significant differences ($p < 0.05$) in brightness trends between Coxside and both Tinside and Mountbatten. The comparison between Coxside and Wembury, while not statistically significant at the $p < 0.05$ level, was also approaching significance ($p = 0.061$; see Table 2).

There was no significant difference in the rate of change of *F. vesiculosus* receptacle brightness between sites ($X^2 = 1.27$, *d.f.* $= 2$, $p = 0.529$) (Fig. 5). Receptacle brightness was not significantly influenced by day of the year ($X^2 = 1.18$, *d.f.* $= 1$, $p = 0.278$) or site ($X^2 = 5.18$, *d.f.*

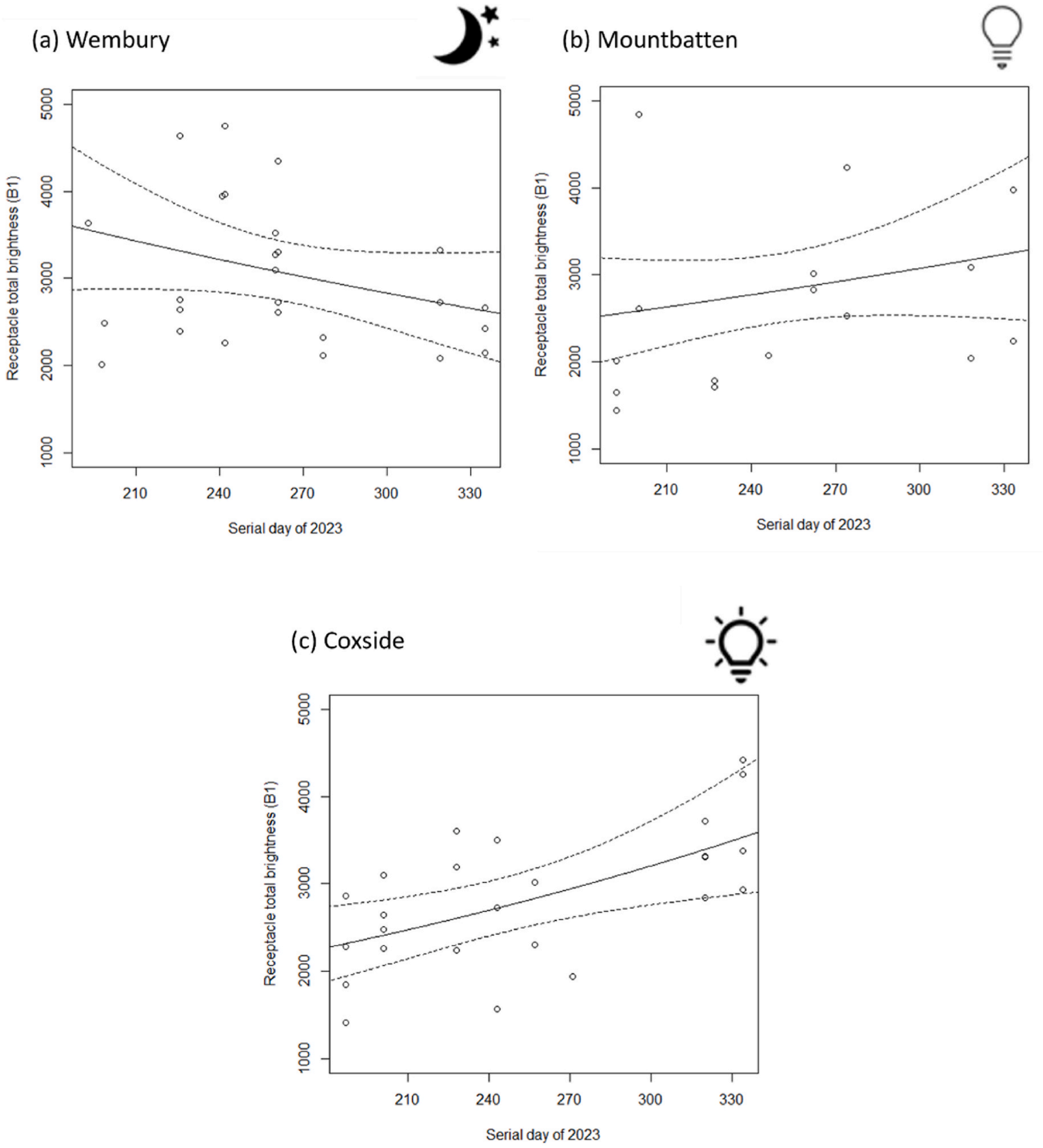


Fig. 3. Predicted trends in total brightness (B_1) of *Ascophyllum nodosum* receptacles as a function of time at sites along an artificial light at night (ALAN) gradient: (a) Wembury – low ALAN; (b) Mountbatten – medium ALAN; (c) Coxside – high ALAN. Circular points show actual B_1 calculated from wavelengths in the 500–675 nm range of hyperspectral reflectance spectrometry measurements of *A. nodosum* receptacles. Dotted lines represent 95 % confidence intervals.

= 2, $p = 0.075$).

4. Discussion

ALAN is known to disrupt reproductive phenology in terrestrial plants (Bennie et al., 2016, 2018; Lian et al., 2021; Zheng et al., 2021; Meng et al., 2022). To explore whether similar disruptions occur in fucoid macroalgae, we conducted a field study along a coastal ALAN gradient. Our results provide some of the first evidence that ALAN alters reproductive timing in these species and suggests that responses are species-specific. In *A. nodosum,* ALAN exposure reversed the expected seasonal pattern of receptacle ripening, while in *F. serratus* exposure to the highest ALAN levels led to greater increases in receptacle ripening compared to lower ALAN levels.

As predicted, ALAN exposure delayed receptacle ripening in *A. nodosum,* with receptacles ripening into winter rather than starting in a ripened state and reducing in ripeness over time, as seen at the low-ALAN site. This may be due to ALAN prolonging the perceived day length during autumn and winter, extending the photoperiod and triggering or extending gametogenesis. This has previously been observed in deciduous trees, for which ALAN exposure delays leaf production and flowering (Lian et al., 2021), as well as leaf colouration (Meng et al., 2022). The release of these late-developed gametes may also be inhibited during the winter storm season, as successful spawning requires calm water conditions (Brawley & Johnson, 1992; Berndt et al., 2002; Gordon & Brawley, 2004). *A. nodosum* is a long-lived, low-recruitment species whose reproductive success is vulnerable to environmental disruption (Printz, 1959; Vadas et al., 1990; Åberg, 1992). Our finding that

Table 2
Results of post-hoc pairwise comparisons of trends in *Ascophyllum nodosum* and *Fucus serratus* receptacle total brightness by site. Significant main effects and interactions are in italics, with significant p-values indicated by asterisks.

Species	Site comparison	Estimate	SE	z ratio	*p*
Ascophyllum nodosum	Coxside - Mountbatten	0.001	0.002	0.648	0.517
	Coxside - Wembury	*0.005*	*0.002*	*2.958*	*0.003**
	Mountbatten - Wembury	*0.004*	*0.002*	*1.969*	*0.049**
Fucus serratus	*Coxside - Mountbatten*	*0.005*	*0.001*	*3.708*	*0.0002**
	Coxside - Tinside	*0.004*	*0.001*	*3.298*	*0.001**
	Coxside - Wembury	0.003	0.002	1.873	0.061
	Mountbatten - Tinside	−0.001	0.001	−1.070	0.285
	Mountbatten - Wembury	−0.003	0.002	−1.564	0.118
	Tinside - Wembury	−0.001	0.001	−0.796	0.426

reproductive phenology patterns were reversed for this species at both high- and medium-ALAN sites suggests that changes to the light environment should be considered important for reproductive processes in this species. If these phenological shifts cause sporelings to be released into suboptimal environmental conditions, recruitment is likely to decline further. This could lead to shifts in macroalgal assemblages with more ALAN-tolerant species outcompeting and replacing *A. nodosum*.

Our hypothesis predicted delayed ripening under ALAN, but this was not supported for *F. serratus*, for which our results present a less clear picture than for *A. nodosum.* Since *F. serratus* can reproduce year-round, site-wide trends in receptacle ripening may be less pronounced. However, the significantly higher level of ripening observed at Coxside remains noteworthy. Coxside is exposed to extremely high levels of ALAN, even compared to Tinside, our second "high-ALAN" site (see Fig. 2). This suggests that ALAN levels at Coxside may exceed a threshold below which *F. serratus* is not significantly affected. Aside from this extreme case, however, the fact that there was no significant difference in ripening trends between our other high-, medium-, and low-ALAN sites may indicate that *F. serratus* is more robust to changes in its light environment than *A. nodosum*. This may be due to its slightly lower position on the shore relative to other fucoid species offering some protection from ALAN exposure (Fig. 4).

Contrary to our expectations, we did not observe any impact of ALAN on *F. vesiculosus*. This may be explained by the narrower reproductive window of this species, which typically occurs in the first half of the year (Tyler-Walters et al., 2024), falling outside our study period. Including *F. vesiculosus* nevertheless provides a useful negative result, as it demonstrates that ALAN-induced phenological disruption is not detectable year-round across all fucoids. This highlights the importance of considering species-specific reproductive schedules when assessing ALAN impacts, and suggests that future studies timed to coincide with the main reproductive season of *F. vesiculosus* may reveal effects not captured here.

The localised nature of the observed changes is also noteworthy. As with any field study, these results should be interpreted in the context of natural variability among sites and species. However, while fucoid reproductive timings are known to differ between locations, this variation is typically reported over much larger spatial scales (see Hatchett et al., 2022; Tyler-Walters et al., 2024). Such high phenological variability within the same species across a comparatively small area is unexpected and suggests a need for a much more site-specific approach to the investigation and management of these species. Such localised effects of ALAN may contribute even further to the habitat fragmentation so commonly associated with ALAN's main driver, urbanisation (Falchi et al., 2016; Kyba et al., 2017).

Light conditions, particularly light intensity and photoperiod, are widely accepted as key factors in algal reproductive timing (Dring, 1988; Andersson et al., 1994; de Bettignies et al., 2018). Photoperiod, the aspect of natural lighting regimes perhaps most altered by ALAN, is the most reliable cue for macroalgal gametogenesis (Brawley & Johnson, 1992), and light intensity is frequently cited as an important factor for gamete release (see de Bettignies et al., 2018). While ALAN specifically remains largely unexplored, other factors that alter perceived photoperiod, such as turbidity or cover by other plant canopies can disrupt reproductive phenology (Breeman et al., 1984). Gametogenesis is more commonly thought to be induced by perceived short-day conditions, but perceived long-day conditions, which ALAN can induce, can also trigger it (Dring, 1984; Kain & Norton, 1990). Clearly, the light environment is a crucial and complex determinant of reproductive timing in algae and research into the impact of ALAN is long overdue. Our results indicate that ALAN can alter the timing of fucoid reproduction, possibly via disruption of light-based cues such as photoperiod perception and circadian regulation. While the precise mechanisms (e.g. the role of photoreceptive pigments or downstream metabolic pathways) remain to be determined, they represent an important avenue for future experimental work.

In addition to light regimes, one of the most important environmental factors for the timing of algal gamete release is water movement, with calm conditions generally required for successful spawning (Brawley & Johnson, 1992; Serrão et al., 1996; Berndt et al., 2002). We selected sites with similar levels of wave exposure, either contained within the Plymouth Breakwater (Coxside, Tinside, and Mountbatten), or behind the Great Mewstone, (Wembury). so it is unlikely that water movement will have differed significantly enough between our sites to meaningfully impact the algae's reproduction.

Salinity was long believed to be an important limiting factor for fucoid reproduction, though this has been challenged in the last decade (Ardehed et al., 2016; Kinnby et al., 2019). While there is some salinity variation between our study sites, all are typically well over 30 practical salinity units (PSU), and thus far removed from the brackish conditions (<5 PSU) in which fucoid reproduction has been shown to falter (Serrão et al., 1996, 1999), so we are confident we can discount any major effect of salinity for the purposes of this study.

Elevated temperature due to urban heat island effects is sometimes considered a complicating factor in ALAN studies relating to terrestrial plant phenology (ffrench-Constant et al., 2016)., but in a systematic review of 81 papers concerning algal reproductive phenology, de Bettignies et al. (2018) found just two in which temperature was demonstrated to be a strong predictor of gamete release, both of which involved degrees of temperature variation exceeding that expected between our study sites at any one time (Norton, 1981; Bacon & Vadas, 1991), so it seems unlikely that any slight temperature variation between sites could drive such dramatic shifts in reproductive timing.

Coxside's proximity to a marina also raises the possibility of localised differences in nutrient levels or contaminants. While such factors can influence algal physiology and growth (e.g. Van Alstyne & Pelletreau, 2000; Steen and Rueness, 2004; Colvard and Helmuth, 2017), there is little evidence that they act as proximate drivers of fucoid reproductive timing (Hatchett et al., 2022). The scale and direction of the phenological shifts we observed are instead most consistent with the gradient in nocturnal light exposure.

If ALAN-induced changes in algal phenology reduce reproductive success, there are likely to be significant ecological implications. As key habitat-forming species, fucoids provide food, shelter, nurseries, and camouflage for countless other species, many of which rely on particular fucoids for their survival, for example the flat periwinkle *Littorina obtusata,* which is almost exclusively associated with intertidal fucoids (Wilbur & Steneck, 1999), and obligate epiphytes such as *Vertebratalanosa,* a red alga that colonises *A. nodosum* (Lewis, 1964). Any disruption to the population stability of these long-lived foundation species may also lead to a decline in associated biodiversity, particularly

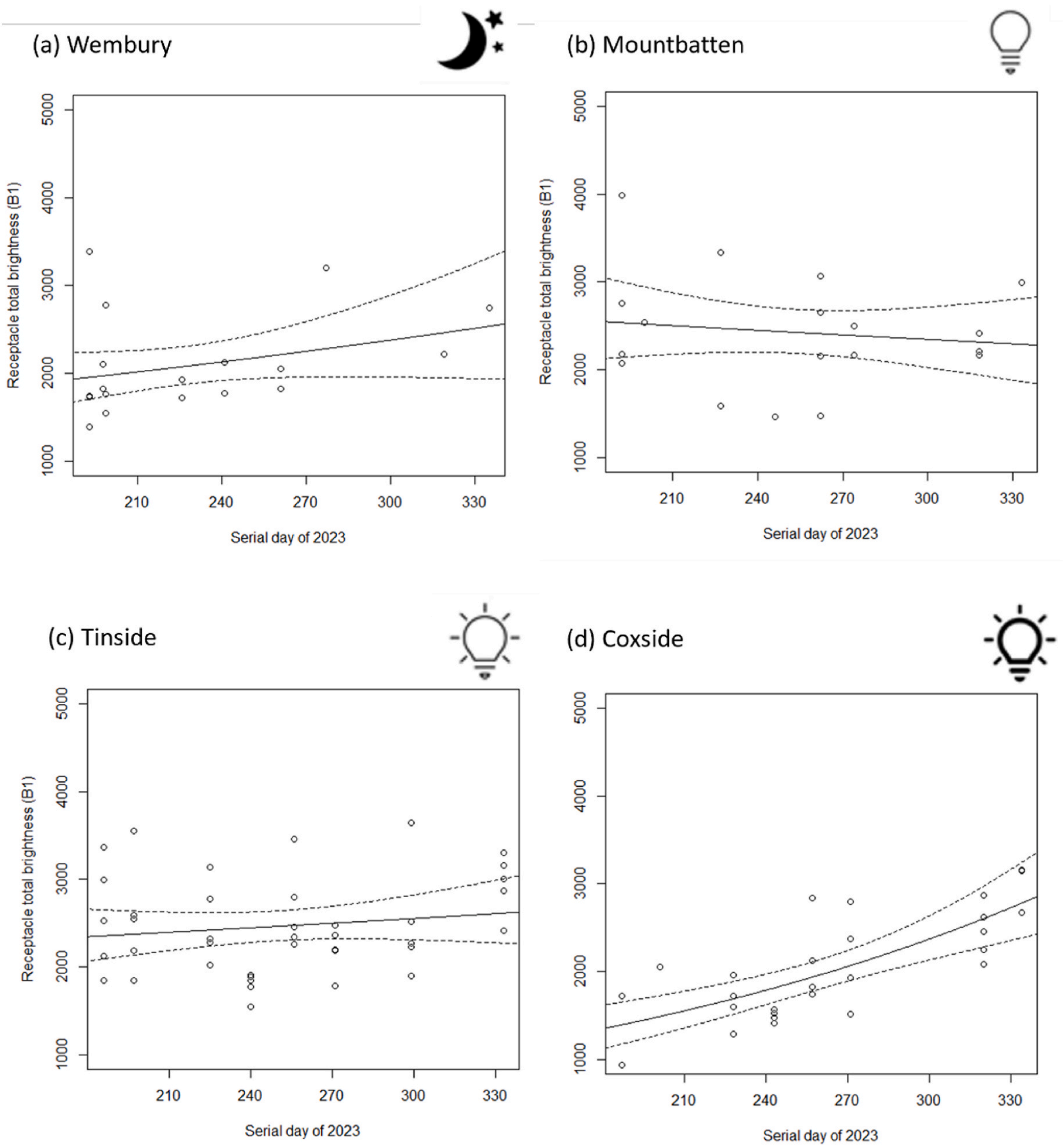


Fig. 4. Predicted trends in total brightness (B_1) of *Fucus serratus* receptacles as a function of time at sites along an artificial light at night (ALAN) gradient: (a) Wembury – low ALAN; (b) Mountbatten – medium ALAN; (c) Tinside – high ALAN; (c) Coxside – high ALAN. Circular points show actual B_1 calculated from wavelengths in the 500–675 nm range of hyperspectral reflectance spectrometry measurements of *F. serratus* receptacles. Dotted lines represent 95 % confidence intervals.

if assemblages become more homogenous as more ALAN-tolerant species dominate (Coleman & Wernberg, 2017; Thomsen et al., 2022). Similarly, given their role as key foundation species, any reduction in complex habitat-forming macroalgae in particular could disrupt trophic interactions and reduce productivity across entire coastal ecosystems (Coleman & Wernberg, 2017; Pessarrodona et al., 2022). Clearly, further research is urgently needed to determine whether these phenological shifts translate into long-term changes in reproductive success and macroalgal assemblage structure.

Our study provides some of the first field-based evidence that ALAN can disrupt the reproductive phenology of fucoid macroalgae. Given the foundational role of fucoids in providing habitat, food, and ecosystem services worldwide, any consequent disruptions to their reproductive success could have cascading ecosystem effects. While further work will be needed before detailed management recommendations can be made, these results establish a basis for future research into the ecological consequences of ALAN for fucoids. As ALAN continues to expand globally with urbanization (Falchi et al., 2016; Kyba et al., 2017), the effects of this pervasive environmental stressor are only likely to increase. Understanding these effects will be critical for the conservation and management of these foundational but often-overlooked species.

CRediT authorship contribution statement

Emma Moyse: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Louise B. Firth:** Writing – review & editing, Conceptualization. **Tim Smyth:** Writing – review & editing, Conceptualization. **Thomas W. Davies:** Writing – review & editing, Supervision, Conceptualization.

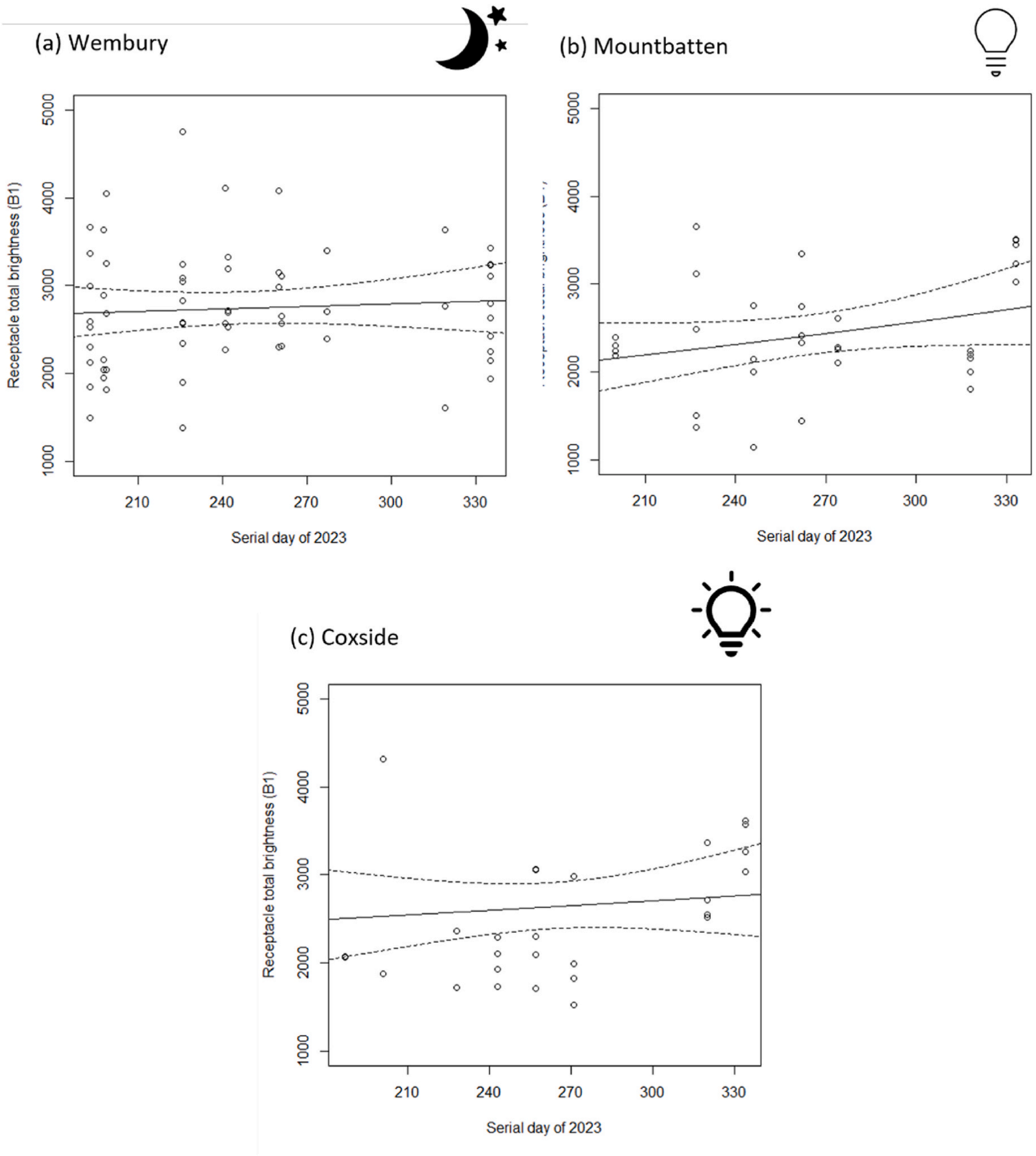


Fig. 5. Predicted trends in total brightness (B_1) of *Fucus vesiculosus* receptacles as a function of time at sites along an artificial light at night (ALAN) gradient: (a) Wembury – low ALAN; (b) Mountbatten – medium ALAN; (c) Coxside – high ALAN. Circular points show actual B_1 calculated from wavelengths in the 500–675 nm range of hyperspectral reflectance spectrometry measurements of *F. vesiculosus* receptacles. Dotted lines represent 95 % confidence intervals.

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.

Acknowledgements

This work was supported by the Natural Environment Research Council (grant numbers NE/S003533/2 and NE/S003568/1 awarded to T.W.D. and T.S.), and a PhD studentship awarded to E.M. by the School of Biological and Marine Sciences, University of Plymouth, UK.

Data availability

Data will be available via the Plymouth Electronic Archive and Research Library (PEARL)

References

Åberg, P., 1992. A demographic study of two populations of the seaweed *Ascophyllum nodosum.* Ecology 73 (4), 1473–1487. https://doi.org/10.2307/1940691.

Aguilera, M.A., González, M.G., 2023. Urban infrastructure expansion and artificial light pollution degrade coastal ecosystems, increasing natural-to-urban structural connectivity. Landsc. Urban Plann. 229, 104609. https://doi.org/10.1016/j.landurbplan.2022.104609.

Andersson, S., Kautsky, L., Kalvas, A., 1994. Circadian and lunar gamete release in *fucus Vesiculosus* in the atidal Baltic sea. Mar. Ecol. Prog. Ser. 195–201. https://doi.org/10.3354/meps110195.

Andersson, S., Örnborg, J., Andersson, M., 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. Proc. R. Soc. London, B 265 (1395), 445–450. https://doi.org/10.1098/rspb.1998.0315.

Ardehed, A., Johansson, D., Sundqvist, L., Schagerström, E., Zagrodzka, Z., Kovaltchouk, N.A., Bergström, L., Kautsky, L., Rafajlovic, M., Pereyra, R.T., 2016. Divergence within and among seaweed siblings (*fucus Vesiculosus* and *F. radicans*) in the Baltic sea. PLoS One 11 (8), e0161266. https://doi.org/10.1371/journal.pone.0161266.

Ayalon, I., Benichou, J.I.C., Avisar, D., Levy, O., 2021. The Endosymbiotic Coral Algae *Symbiodiniaceae* Are Sensitive to a Sensory Pollutant: Artificial Light at Night, ALAN [Original Research]. Front. Physiol. 12. https://doi.org/10.3389/fphys.2021.695083.

Bacon, L.C., Vadas, R.L., 1991. A model for gamete release in *Ascophyllum nodosum* (phaeophyta). J. Phycol. 27 (2), 166–173. https://doi.org/10.1111/j.0022-3646.1991.00166.x.

Bellgrove, A., McKenzie, P.F., Cameron, H., Pocklington, J.B., 2017. Restoring rocky intertidal communities: lessons from a benthic macroalgal ecosystem engineer. Mar. Pollut. Bull. 117 (1), 17–27. https://doi.org/10.1016/j.marpolbul.2017.02.012.

Bennie, J., Davies, T.W., Cruse, D., Bell, F., Gaston, K.J., 2018. Artificial light at night alters grassland vegetation species composition and phenology. J. Appl. Ecol. 55 (1), 442–450. https://doi.org/10.1111/1365-2664.12927.

Bennie, J., Davies, T.W., Cruse, D., Gaston, K.J., 2016. Ecological effects of artificial light at night on wild plants. J. Ecol. 104 (3), 611–620. https://doi.org/10.1111/1365-2745.12551.

Berndt, M., Callow, J.A., Brawley, S.H., 2002. Gamete concentrations and timing and success of fertilization in a rocky shore seaweed. Mar. Ecol. Prog. Ser. 226, 273–285. https://doi.org/10.3354/meps226273.

Blanken, W., Cuaresma, M., Wijffels, R.H., Janssen, M., 2013. Cultivation of microalgae on artificial light comes at a cost. Algal Res. 2 (4), 333–340. https://doi.org/10.1016/j.algal.2013.09.004.

Brawley, S.H., Johnson, L.E., 1992. Gametogenesis, gametes and zygotes: an ecological perspective on sexual reproduction in the algae. Br. Phycol. J. 27 (3), 233–252. https://doi.org/10.1080/00071619200650241.

Breeman, A.M., Bos, S., van Essen, S., van Mulekom, L.L., 1984. Light-dark regimes in the intertidal zone and tetrasporangial periodicity in the red alga *Rhodochorton purpureum*. Helgol. Meeresunters. 38 (3), 365–387. https://doi.org/10.1007/BF02027687.

Brzychczyk, B., Hebda, T., Pedryc, N., 2020. The influence of artificial lighting systems on the cultivation of algae: the example of *Chlorella vulgaris*. Energies 13 (22), 5994. https://doi.org/10.3390/en13225994.

Bucher, S.F., Uhde, L., Weigelt, A., Cesarz, S., Eisenhauer, N., Gebler, A., Kyba, C., Römermann, C., Shatwell, T., Hines, J., 2023. Artificial light at night decreases plant diversity and performance in experimental grassland communities. Phil. Trans. Biol. Sci. 378 (1892), 20220358. https://doi.org/10.1098/rstb.2022.0358.

Buck-Wiese, H., Andskog, M.A., Nguyen, N.P., Bligh, M., Asmala, E., Vidal-Melgosa, S., Liebeke, M., Gustafsson, C., Hehemann, J.-H., 2023. Fucoid brown algae inject fucoidan carbon into the ocean. Proc. Natl. Acad. Sci. 120 (1), e2210561119. https://doi.org/10.1073/pnas.2210561119.

Coleman, M.A., Wernberg, T., 2017. Forgotten underwater forests: the key role of fucoids on Australian temperate reefs. Ecol. Evol. 7 (20), 8406–8418. https://doi.org/10.1002/ece3.3279.

Colvard, N., Helmuth, B., 2017. Nutrients influence the thermal ecophysiology of an intertidal macroalga: multiple stressors or multiple drivers? Ecol. Appl. 27 (2), 669–681. https://doi.org/10.1002/eap.1475.

Coombes, M.A., Naylor, L.A., Viles, H.A., Thompson, R.C., 2013. Bioprotection and disturbance: seaweed, microclimatic stability and conditions for mechanical weathering in the intertidal zone. Geomorphology 202, 4–14. https://doi.org/10.1016/j.geomorph.2012.09.014.

Crothers, J., 2012. Snails on Rocky Sea Shores, vol. 30. Pelagic Publishing.

Davies, T.W., Smyth, T., 2018. Why artificial light at night should be a focus for global change research in the 21st century. Glob. Change Biol. 24 (3), 872–882. https://doi.org/10.1111/gcb.13927.

de Bettignies, T., Wernberg, T., Gurgel, C.F.D., 2018. Exploring the influence of temperature on aspects of the reproductive phenology of temperate seaweeds. Front. Mar. Sci. 5. https://doi.org/10.3389/fmars.2018.00218 [Review].

de Vasconcelos, E.R.T.P.P., Vasconcelos, J.B., Reis, T.N.d.V., Cocentino, A.d.L.M., Mallea, A.J.A., Martins, G.M., Neto, A.I., Fujii, M.T., 2019. Macroalgal responses to coastal urbanization: relative abundance of indicator species. J. Appl. Phycol. 31 (2), 893–903. https://doi.org/10.1007/s10811-018-1639-3.

Diamantopoulou, C., Christoforou, E., Dominoni, D.M., Kaiserli, E., Czyzewski, J., Mirzai, N., Spatharis, S., 2021. Wavelength-dependent effects of artificial light at night on phytoplankton growth and community structure. Proc. Biol. Sci. 288 (1953), 20210525. https://doi.org/10.1098/rspb.2021.0525.

Dring, M., 1984. Photoperiodism and phycology. Prog. Phycol. Res. 3, 159–192.

Dring, M.J., 1988. Photocontrol of development in algae. Annu. Rev. Plant Biol. 39, 157–174. https://doi.org/10.1146/annurev.arplant.39.1.157. Volume 39, 1988.

Endler, J.A., 1990. On the measurement and classification of colour in studies of animal colour patterns. Biol. J. Linn. Soc. 41, 315–352. https://doi.org/10.1111/j.1095-8312.1990.tb00839.x.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., Portnov, B. A., Rybnikova, N.A., Furgoni, R., 2016. The new world atlas of artificial night sky brightness. Sci. Adv. 2 (6), e1600377. https://doi.org/10.1126/sciadv.1600377.

Fragkopoulou, E., Serrão, E.A., De Clerck, O., Costello, M.J., Araújo, M.B., Duarte, C.M., Krause-Jensen, D., Assis, J., 2022. Global biodiversity patterns of marine forests of brown macroalgae. Global Ecol. Biogeogr. 31 (4), 636–648. https://doi.org/10.1111/geb.13450.

ffrench-Constant, R.H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A., McGregor, P.K., 2016. Light pollution is associated with earlier tree budburst across the United Kingdom. Proc. Biol. Sci. 283 (1833), 20160813. https://doi.org/10.1098/rspb.2016.0813.

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.

Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. Reducing the ecological consequences of night-time light pollution: options and developments. J. Appl. Ecol. 49 (6), 1256–1266.

Gordon, R., Brawley, S.H., 2004. Effects of water motion on propagule release from algae with complex life histories. Mar. Biol. 145 (1), 21–29. https://doi.org/10.1007/s00227-004-1305-y.

Grubisic, M., 2018. Waters under artificial lights: does light pollution matter for aquatic primary producers? Limnol. Oceanogr. Bull. 27 (3), 76–81. https://doi.org/10.1002/lob.10254.

Grubisic, M., Singer, G., Bruno, M.C., van Grunsven, R.H.A., Manfrin, A., Monaghan, M. T., Hölker, F., 2017. Artificial light at night decreases biomass and alters community composition of benthic primary producers in a sub-alpine stream. Limnol. Oceanogr. 62 (6), 2799–2810. https://doi.org/10.1002/lno.10607.

Hänel, A., Posch, T., Ribas, S.J., Aubé, M., Duriscoe, D., Jechow, A., Kollath, Z., Lolkema, D.E., Moore, C., Schmidt, N., Spoelstra, H., Wuchterl, G., Kyba, C.C.M., 2018. Measuring night sky brightness: methods and challenges. J. Quant. Spectrosc. Radiat. Transf. 205, 278–290. https://doi.org/10.1016/j.jqsrt.2017.09.008.

Hatchett, W.J., Coyer, J.A., Sjøtun, K., Jueterbock, A., Hoarau, G., 2022. A review of reproduction in the seaweed genus fucus (ochrophyta, fucales): background for renewed consideration as a model organism. Front. Mar. Sci. 9. https://doi.org/10.3389/fmars.2022.1051838 [Review].

James, N.C., Whitfield, A.K., 2023. The role of macroalgae as nursery areas for fish species within coastal seascapes. Cambridge Prisms: Coastal Futures 1, e3. https://doi.org/10.1017/cft.2022.3.

Kain, J.M., Norton, T.A., 1990. Marine ecology. In: Cole, K.M., Sheath, R.G. (Eds.), Biology of the Red Algae. Cambridge University Press.

Kinnby, A., Pereyra, R.T., Havenhand, J.N., De Wit, P., Jonsson, P.R., Pavia, H., Johannesson, K., 2019. Factors affecting formation of adventitious branches in the seaweeds *fucus Vesiculosus* and *F. radicans*. BMC Ecol. 19, 1–10. https://doi.org/10.1186/s12898-019-0239-7.

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., Fontaine, C., 2017. Artificial light at night as a new threat to pollination. Nature 548 (7666), 206–209. https://doi.org/10.1038/nature23288.

Kotta, J., Remm, K., Vahtmäe, E., Kutser, T., Orav-Kotta, H., 2014. In-air spectral signatures of the Baltic sea macrophytes and their statistical separability. J. Appl. Remote Sens. 8 (1), 083634. https://doi.org/10.1117/1.JRS.8.083634.

Kyba, C.C.M., Hölker, F., 2013. Do artificially illuminated skies affect biodiversity in nocturnal landscapes? Landsc. Ecol. 28 (9), 1637–1640. https://doi.org/10.1007/s10980-013-9936-3.

Kyba, C.C.M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C.D., Gaston, K.J., Guanter, L., 2017. Artificially lit surface of Earth at night increasing in radiance and extent. Sci. Adv. 3 (11), e1701528. https://doi.org/10.1126/sciadv.1701528.

Ladah, L., Bermudez, R., Pearson, G., Serrão, E., 2003. Fertilization success and recruitment of dioecious and hermaphroditic fucoid seaweeds with contrasting distributions near their southern limit. Mar. Ecol. Prog. Ser. 262, 173–183. https://doi.org/10.3354/meps262173.

Lang, S., 2019. Photometry and photosynthesis. Retrieved 27/08/25 from. https://www.allthingslighting.org/photometry-and-photosynthesis/.

Lenth, R., 2024. Estimated marginal means, Aka least-squares means [R package version 1.10.2]. https://CRAN.R-project.org/package=emmeans.

Lewis, J.R., 1964. The Ecology of Rocky Shores. The English Universities Press Ltd.

Lian, X., Jiao, L., Zhong, J., Jia, Q., Liu, J., Liu, Z., 2021. Artificial light pollution inhibits plant phenology advance induced by climate warming. Environ. Pollut. 291, 118110. https://doi.org/10.1016/j.envpol.2021.118110.

Maia, R., Gruson, H., Endler, J.A., White, T.E., 2019. Pavo 2: new tools for the spectral and spatial analysis of colour in R. Methods Ecol. Evol. 10 (7). https://doi.org/10.1111/2041-210X.13174.

Mann, K.H., 1973. Seaweeds: their productivity and strategy for growth. Science 182 (4116), 975–981. https://doi.org/10.1126/science.182.4116.975.

Mannino, A.M., Micheli, C., 2020. Ecological function of phenolic compounds from mediterranean fucoid algae and seagrasses: an overview on the genus *cystoseira sensu lato* and *Posidonia oceanica* (L.) delile. J. Mar. Sci. Eng. 8 (1), 19. https://doi.org/10.3390/jmse8010019.

Marangoni, L.F., 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. Change Biol. 28 (18), 5346–5367. https://doi.org/10.1111/gcb.16264.

Meng, L., Zhou, Y., Román, M.O., Stokes, E.C., Wang, Z., Asrar, G.R., Mao, J., Richardson, A.D., Gu, L., Wang, Y., 2022. Artificial light at night: an underappreciated effect on phenology of deciduous woody plants. PNAS Nexus 1 (2). https://doi.org/10.1093/pnasnexus/pgac046.

Menge, B.A., Bracken, M.E.S., Lubchenco, J., Leslie, H.M., 2017. Alternative state? Experimentally induced fucus canopy persists 38 yr in an *Ascophyllum*-dominated community. Ecosphere 8 (3), e01725. https://doi.org/10.1002/ecs2.1725.

Miller, E.J., 2015. *Ecology of Hector's Dolphin (Cephalorhynchus Hectori): Quantifying Diet and Investigating Habitat Selection at Banks Peninsula* [Doctoral Dissertation. University of Otago]. https://ourarchive.otago.ac.

nz/esploro/outputs/doctoral/Ecology-of-Hectors-dolphin-Cephalorhynchus-hectori/9926480222001891#file-0.

Monteiro, C.A., Serrão, E.A., Pearson, G.A., 2012. Prezygotic barriers to hybridization in marine broadcast spawners: reproductive timing and mating system variation. PLoS One 7 (4), e35978. https://doi.org/10.1371/journal.pone.0035978.

Norton, T.A., 1981. Gamete expulsion and release in *Sargassum muticum*. Bot. Mar. 24 (8), 465–470. https://doi.org/10.1515/botm.1981.24.8.465.

Örnborg, J., Andersson, S., Griffith, S.C., Sheldon, B.C., 2002. Seasonal changes in a ultraviolet structural colour signal in blue tits, *Parus caeruleus*. Biol. J. Linn. Soc. 76 (2), 237–245. https://doi.org/10.1111/j.1095-8312.2002.tb02085.x.

Pearson, G.A., Brawley, S.H., 1996. Reproductive ecology, of *fucus Distichus* (phaeophyceae): an intertidal alga with successful external fertilization. Mar. Ecol. Prog. Ser. 143, 211–223. https://doi.org/10.3354/meps143211.

Pearson, G.A., Serrão, E.A., Brawley, S.H., 1998. Control of gamete release in fucoid algae: sensing hydrodynamic conditions via carbon acquisition. Ecology 79 (5), 1725–1739. https://doi.org/10.1890/0012-9658(1998)079[1725:COGRIF]2.0.CO;2.

Pessarrodona, A., Assis, J., Filbee-Dexter, K., Burrows, M.T., Gattuso, J.-P., Duarte, C.M., Krause-Jensen, D., Moore, P.J., Smale, D.A., Wernberg, T., 2022. Global seaweed productivity. Sci. Adv. 8 (37), eabn2465. https://doi.org/10.1126/sciadv.abn2465.

Printz, H.S., 1959. Investigations of the failure of recuperation and re-populating in cropped *ascophyllum* areas. In: Avhandlinger Utgitt Av Det Norske Videnskap-Akademi I Oslo, vol. 3.

Pryke, S.R., Lawes, M.J., Andersson, S., 2001. Agonistic carotenoid signalling in Male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. Anim. Behav. 62 (4), 695–704. https://doi.org/10.1006/anbe.2001.1804.

R Core Team, 2024. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.

Roberts, D.A., Poore, A.G.B., Johnston, E.L., 2006. Ecological consequences of copper contamination in macroalgae: effects on epifauna and associated herbivores. Environ. Toxicol. Chem. 25 (9), 2470–2479. https://doi.org/10.1897/05-661R.1.

Saks, L., McGraw, K., Hõrak, P., 2003. How feather colour reflects its carotenoid content. Funct. Ecol. 17 (4), 555–561. https://doi.org/10.1046/j.1365-2435.2003.00765.x.

Sanders, D., Frago, E., Kehoe, R., Patterson, C., Gaston, K.J., 2021. A meta-analysis of biological impacts of artificial light at night. Nature Ecology & Evolution 5 (1), 74–81. https://doi.org/10.1038/s41559-020-01322-x.

Schiel, D.R., Foster, M.S., 2006. The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. Annual review of ecology, evolution, and systematics 37, 343–372. https://doi.org/10.1146/annurev.ecolsys.37.091305.110251. Volume 37, 2006.

Segrestin, J., Mondy, N., Boisselet, C., Guigard, L., Lengagne, T., Poussineau, S., Secondi, J., Puijalon, S., 2021. Effects of artificial light at night on the leaf functional traits of freshwater plants. Freshw. Biol. 66 (12), 2264–2271. https://doi.org/10.1111/fwb.13830.

Serrão, E.A., Kautsky, L., Brawley, S.H., 1996. Distributional success of the marine seaweed *fucus vesiculosus* L. in the brackish Baltic sea correlates with osmotic capabilities of Baltic gametes. Oecologia 107, 1–12. https://doi.org/10.1007/bf00582229.

Serrão, E.A., Brawley, S.H., Hedman, J., Kautsky, L., Samuelsson, G., 1999. Reproductive success of *fucus Vesiculosus* (phaeophyceae) in the Baltic sea. J. Phycol. 35 (2), 254–269. https://doi.org/10.1046/j.1529-8817.1999.3520254.x.

Smyth, T.J., Wright, A.E., McKee, D., Tidau, S., Tamir, R., Dubinsky, Z., Iluz, D., Davies, T.W., 2021. A global atlas of artificial light at night under the sea. Elementa: Science of the Anthropocene 9 (1). https://doi.org/10.1525/elementa.2021.00049.

Smyth, T.J., Wright, A.E., Edwards-Jones, A., McKee, D., Queirós, A., Rendon, O., Tidau, S., Davies, T.W., 2022. Disruption of marine habitats by artificial light at night from global coastal megacities. Elementa: Science of the Anthropocene 10 (1). https://doi.org/10.1525/elementa.2022.00042.

Steen, H., Rueness, J., 2004. Comparison of survival and growth in germlings of six fucoid species (fucales, Phaeophyceae) at two different temperature and nutrient levels. Sarsia 89 (3), 175–183. https://doi.org/10.1080/00364820410005818.

Thimijan, R.W., Heins, R.D., 1983. Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. Hortscience 18 (6), 818–822. https://doi.org/10.21273/HORTSCI.18.6.818.

Thomsen, M.S., Altieri, A.H., Angelini, C., Bishop, M.J., Bulleri, F., Farhan, R., Frühling, V.M.M., Gribben, P.E., Harrison, S.B., He, Q., Klinghardt, M., Langeneck, J., Lanham, B.S., Mondardini, L., Mulders, Y., Oleksyn, S., Ramus, A.P., Schiel, D.R., Schneider, T., Siciliano, A., Silliman, B.R., Smale, D.A., South, P.M., Wernberg, T., Zhang, S., Zotz, G., 2022. Heterogeneity within and among co-occurring foundation species increases biodiversity. Nat. Commun. 13 (1), 581. https://doi.org/10.1038/s41467-022-28194-y.

Tyler-Walters, H., Hiscock, K., Tillin, H.M., Stamp, T., Readman, J.A.J., Perry, F., Ashley, M., De-Bastos, E.S.R., D'Avack, E.A.S., Jasper, C., Gibb, N., Mainwaring, K., McQuillan, R.M., Wilson, C.M., Gibson-Hall, E., Last, E.K., Grady (nee Robson), L.M., Garrard, S.L., Williams, E., Graves, K.P., Taylor, J., Molloy, L., Ridgeway, A., Matear, L., Taylor, J., Nikolova, C., Dinwoodie, K., Perry, J., Molloy, L., Baron-Cohen, L., Fergusson, M., Savage, J., Bull, G., Serpetti, N., Narayanaswamy, B., Hughes, D., Burdett, E.G., Lloyd, K.A., Mardle, M.J., Watson, A., Granö, E., Nash, R. A., Roche, C., Budd, G.C., Hill, J.M., Jackson, A., White, N., Rayment, W.J., Wilding, C.M., Marshall, C.E., Wilson, E., Riley, K., Neal, K.J., Sabatini, M., Durkin, O.C., Ager, O.E.D., Bilewitch, J., Carter, M., Hosie, A.M., Mieszkowska, N., Lear, D.B., 2024. Marine life information network: biology and sensitivity key information review database [on-line]. www.marlin.ac.uk.

Ugarte, R.A., Sharp, G., 2001. 6. A new approach to seaweed management in eastern Canada: the case of *Ascophyllum nodosum*. Cah. Biol. Mar. 42 (1/2), 63–70.

Uhl, F., Oppelt, N., Bartsch, I., 2013. Spectral mixture of intertidal marine macroalgae around the island of helgoland (germany, north sea). Aquat. Bot. 111, 112–124. https://doi.org/10.1016/j.aquabot.2013.06.001.

United Nations, 2019. World Urbanization Prospects: the 2018 Revision (ST/ESA/SER.A/420). United Nations, Department of Economic and Social Affairs, New York, NY. Population Division.

Vadas, R., Wright, W.A., Miller, S.L., 1990. Recruitment of *ascophyllum Nodosum*: wave action as a source of mortality. Mar. Ecol. Prog. Ser. 61 (3), 263. https://doi.org/10.3354/meps061263.

Van Alstyne, K.L., Pelletreau, K.N., 2000. Effects of nutrient enrichment on growth and phlorotannin production in *fucus Gardneri* embryos. Mar. Ecol. Prog. Ser. 206, 33–43. https://doi.org/10.3354/meps206033.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, fourth ed. Springer https://www.stats.ox.ac.uk/pub/MASS4/.

Wilbur, A.K., Steneck, R.S., 1999. Polychromatic patterns of *Littorina obtusata* on *ascophyllum Nodosum*: are snails hiding in intertidal seaweed? Northeast. Nat. 6 (3), 189–198. https://doi.org/10.2307/3858593.

Witherington, B., Hirama, S., Hardy, R., 2012. Young sea turtles of the pelagic *Sargassum*-dominated drift community: habitat use, population density, and threats. Mar. Ecol. Prog. Ser. 463, 1–22. https://doi.org/10.3354/meps09970.

Zheng, Q., Teo, H.C., Koh, L.P., 2021. Artificial light at night advances spring phenology in the United States. Remote Sens. 13 (3), 399. https://doi.org/10.3390/rs13030399.