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Marine artificial light at night: An empirical and technical guide

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1 **Marine artificial light at night: An empirical and technical**
2 **guide**

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18

19 **Running headline:** A guide to marine light pollution research

20 **Abstract**

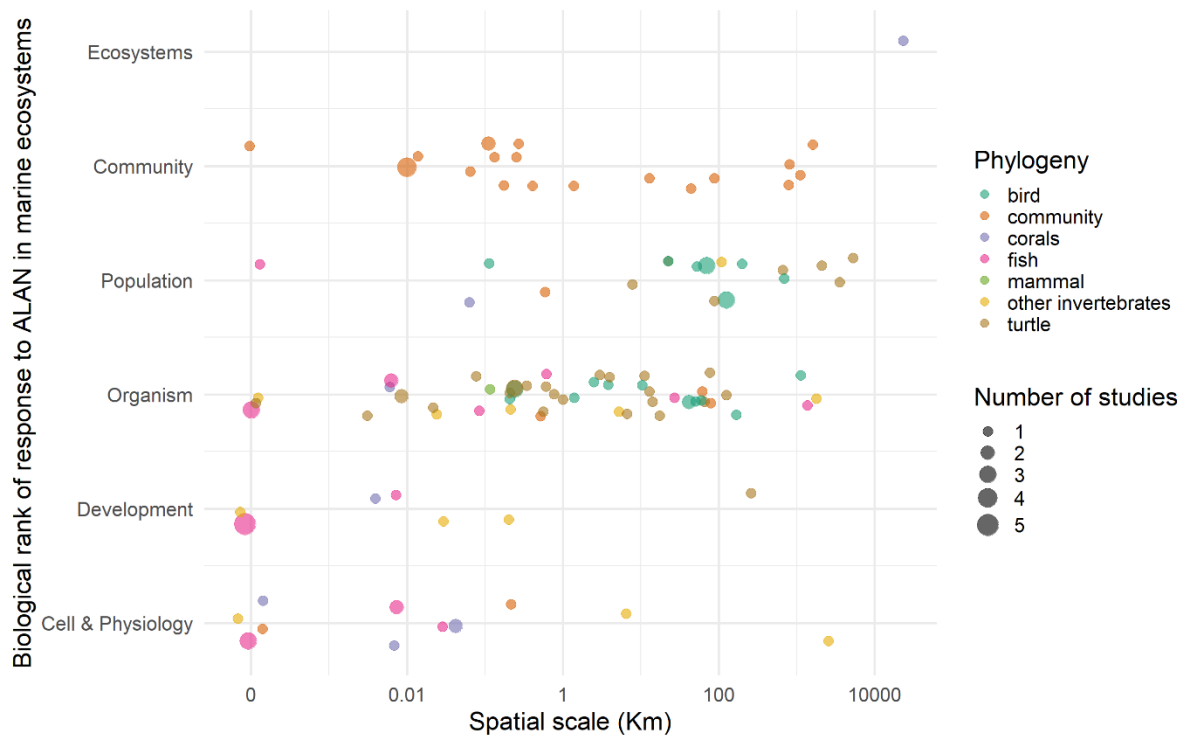
- 21 1. The increasing illumination of our world by artificial light at night (ALAN) has created a
22 new field of global change research with impacts now being demonstrated across taxa,
23 biological ranks and spatial scales. Following advances in terrestrial ecology, marine
24 ALAN has become a rapidly growing research area attracting scientists from across all
25 biomes. Limitations in technology, complexities of researching many coastal and marine
26 ecosystems, and the interdisciplinary nature of ALAN research present numerous
27 challenges.
- 28 2. Drawing on expertise from optical oceanographers, modellers, community ecologists,
29 experimental and molecular biologists, we share practical advice and solutions that have
30 proven useful for marine ALAN research. Discussing lessons learnt early on can help in
31 the effective and efficient development of a field.
- 32 3. The guide follows a sensory ecology approach to marine light pollution and consolidates
33 physics, ecology and biology. First, we introduce marine lightscapes highlighting how
34 these differ from terrestrial ones and provide an overview of biological adaptations to
35 them. Second, we discuss study design and technology to best quantify ALAN exposure
36 of and impacts on marine and coastal organisms including molecular tools and
37 approaches to scale-up marine ALAN research.
- 38 4. We conclude that the growing field of marine ALAN research presents opportunities not
39 only for improving our understanding of this globally widespread stressor, but also for
40 advancing fundamental marine photobiology, chronobiology, and night-time ecology.
41 Interdisciplinary research will be essential to gain insights into natural marine
42 lightscapes shaping the ecology and evolution coastal and marine ecosystems.

43 **Key-words:** Artificial light at night, chronobiology, coastal ecosystems, light pollution, marine
44 ecology, night-time ecology, nocturnality, photobiology, underwater lightscapes

45 **Introduction**

46 Artificial light at night (ALAN) is a rapidly expanding form of human-induced environmental change
47 altering environments at an unprecedented pace and scale (Sih et al., 2011). ALAN affects 80% of the
48 global human population (Falchi et al., 2016), expands in area by 2.2% and intensifies by 1.8%
49 annually (Kyba et al., 2017). Urbanisation exposes more than 22% of the world's nearshore
50 environment to ALAN (Davies et al., 2014). Shipping, sea-based oil and gas platforms and deep-sea
51 exploration extend direct lighting offshore. Artificial skyglow (direct lighting emitted or reflected
52 upwards, scattered in the atmosphere and reflected back to the ground; Kyba et al., 2011) can
53 spread light pollution hundreds of kilometres from its source (Luginbuhl et al., 2014). ALAN exposure
54 of marine and coastal ecosystems is likely to be further amplified by the societal transition towards
55 energy efficient, broadband Light Emitting Diodes (LEDs) (Zissis & Bertoldi, 2018). Emission spectra
56 (peak and range) vary greatly between lighting technology (Elvidge et al., 2010). Broadband white
57 LEDs are rich in short wavelengths to which many marine organisms are naturally sensitive to and
58 which penetrate deeper underwater (Tamir et al., 2017). With the expansion of LED usage, more
59 marine organisms are likely to be exposed to ALAN.

60 Marine light pollution has become a dynamic, fast evolving research field with impacts being
61 documented for an increasing range of biological responses and taxa at different spatial scales
62 (Figure 1, Table S1). Marine ALAN affects cell processes, physiology, behaviours, recruitment,
63 communities and entire ecosystems (Ayalon et al., 2020; Davies et al., 2015; Fobert et al., 2019;
64 Navarro-Barranco & Hughes, 2015; O'Connor et al., 2019). The interdisciplinary nature of ALAN
65 research, limitations in technology and complexities of researching most marine ecosystems present
66 numerous challenges that researchers should be aware of when entering the field. This guide is
67 intended to serve as an orientation for newcomers to marine ALAN research; those working on ALAN
68 with little experience of research in marine and coastal ecosystems; and the growing community of
69 scientists concerned with the prevalence and impacts of ALAN on the marine environment. Our
70 intention is to help improve the precision, accuracy and real-world application of results.



71

72 **Figure 1 Spatial, biological and phylogenetic focus of marine ALAN research over the last 35 years (based on**
 73 **peer reviewed publications retrieved by Web of Science keyword search and complemented by references**
 74 **from ALAN reviews and papers).**

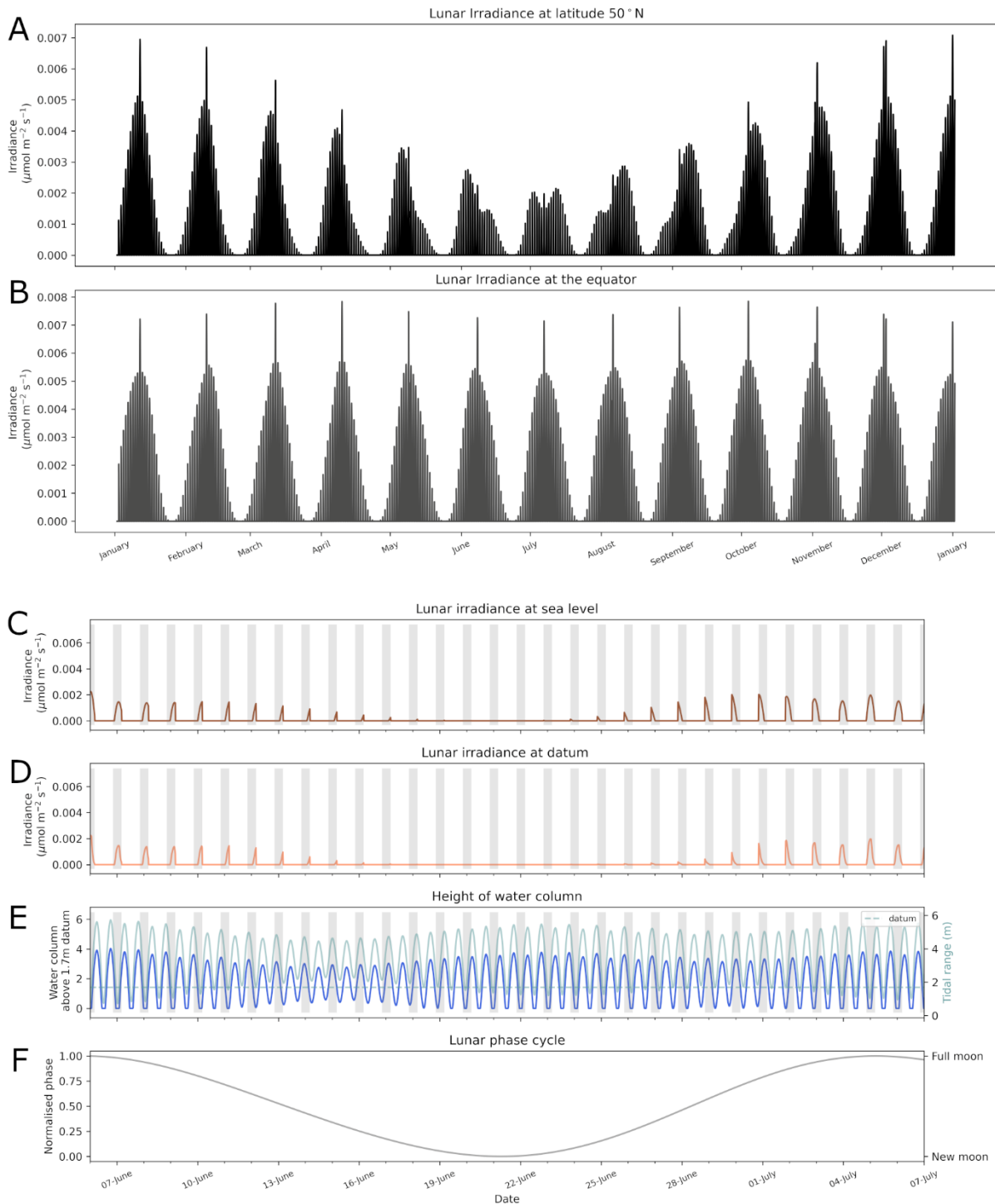
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76 This guide follows a sensory ecology approach: how organisms acquire, process, and respond to
 77 information from their environment including anthropogenic pollution (Sih et al., 2011). We
 78 combine expertise from optical oceanographers, environmental modellers, community, behavioural
 79 and molecular biologists to identify challenges and best practice in marine ALAN research design and
 80 implementation. Firstly, we briefly introduce basic characteristics of natural marine lightscapes and
 81 biological adaptations to them to prompt thinking about the potential of ALAN to disrupt coastal and
 82 marine ecosystems. Secondly, we discuss methods to quantifying marine ALAN exposure and
 83 impacts, which are the focus of this guide. Finally, we synthesise the most pressing challenges in
 84 marine ALAN research and the insights to be gained from integrating physics and biology. This guide
 85 also opens avenues for advancing research on natural marine lightscapes and fundamental
 86 ecological and evolutionary adaptations to them.

87 **Marine lightscapes**

88 As in terrestrial ecosystems, the moon and the sun govern marine lightscapes in the photic zone
89 (Warrant & Locket, 2004). The earth's rotation creates diurnal light-dark cycles (24 hours) including
90 twilight (Kronfeld-Schor & Dayan, 2003). The earth's axis of rotation and orbital plain around the sun
91 create seasonal (365.24 days) variations in day-night length (Helm et al., 2013). The orbit of the
92 moon around the earth, and changes in full moon altitude as the earth orbits the sun create 29.5 day
93 and annual lunar cycles in natural night-time lighting (Kronfeld-Schor et al., 2013). Lunar light cycles
94 create spatially discrete but temporally predictable mean nocturnal sea surface illuminances. Light
95 intensities diverge considerably: Full moon (0.1–0.3 lux) is around six orders of magnitude dimmer
96 than full sunlight (130 000 lux) but 1000 times brighter than a clear starry night (0.0001 lux) (for an
97 overview see Dick, 2020). Light-dark cycles vary with latitude exhibiting larger amplitude towards the
98 poles (Hut et al., 2013). For instance, full moon altitude and night-time sky brightness at high
99 latitudes peak annually during winter solstice (Figure 2A) and close to the equator biannually during
100 equinoxes (Figure 2B).

101 The properties of seawater, together with numerous meteorological, geographical and geological
102 factors, influence the spatiotemporal extent, intensity, and spectra of natural and artificial light
103 underwater (Figure 2C-F, Figure 3). Underwater lightscapes in the open ocean are relatively well
104 understood. Light in the wavelengths of 475 nm transmits best (Figure 3A; Mobley, 1994) and
105 penetrates down to 1000 m creating dim conditions similar to starlight (Warrant & Locket, 2004).
106 The high concentrations of optically active constituents such as Chlorophyll a, inorganic sediment
107 and coloured dissolved organic matter (CDOM) govern wavelength dependent light absorption and
108 scattering which makes measuring shallow coastal, estuarine and temperate underwater lightscapes
109 more complex (Ackleson, 2003; Mobley, 1994).



110
 111 **Figure 2 Moonlight cycles in and out of the sea.** The 2020 lunar calendar in zenith sky brightness detectable at
 112 the sea surface at (A) 50° latitude and (B) the equator. (C-F) Modelled seabed (datum 1.7m) moonlight
 113 irradiance in the intertidal through a synodic month accounting for the impact of the moon's phase angle (F)
 114 on sea surface irradiance (D), and tidal height above datum 1.7m (E) on the attenuation of sea surface
 115 moonlight (C) for Plymouth, UK (~50° latitude). Light-tidal interaction model based on Roberts et al. (2018) and
 116 extended to include lunar components.

117

118 Seasonally variable sea temperatures, sunlight, rainfall and nutrient availability change

119 concentrations of optically active constituents (e.g. high during spring phytoplankton bloom). Local

120 bathymetry and topography affect wave and tidal driven resuspension of sediments, algae and
121 detritus and thus the optical properties in coastal waters. Light in the spectrum of around 450 nm is
122 attenuated and suspended particles reflect wavelengths between 495–570 nm (green to human
123 eyes) and 570–590 nm (yellow) (Mobley, 1994). Benthic ecosystems (seagrass, kelp, corals) further
124 modify shallow underwater lightscapes (Ackleson, 2003). Tidal cycles change the path length of
125 natural (Roberts et al., 2018) and artificial (Davies et al., 2020) light on the seafloor and expose
126 intertidal marine organisms up to twice daily to direct light (Figure 2C-F). Tidal amplitudes vary
127 monthly (spring and neap tides) and annually (equinoctial tides) and can range from a few
128 centimetres up to more than 15 meters (Desplanque & Mossman, 2001).

129 **Biological adaptations to marine lightscapes**

130 Evolutionary adaptations of coastal and marine organisms to light cycles, intensity and spectra
131 manifest themselves in various morphological, molecular, physiological and behavioural traits
132 influencing populations, communities and ecosystems. Exploring the diverse marine photobiology of
133 the study system of interest can serve as a starting point for formulating hypotheses about marine
134 ALAN impacts, and designing studies to quantify them.

135 Table 1 showcases common photosensory systems, the information captured, biological responses
136 to light and taxonomic occurrence. Light sensing abilities range from the detection of light, shade or
137 darkness via single photoreceptor cells and eye spots to monochromatic imaging and complex, high-
138 resolution multi-colour vision via compound or camera-type eyes (Land & Nilsson, 2012).

139 Photopigments and receptor cells are the fundamental structures to detect and convert a photon of
140 light into an electrochemical signal (Nilsson, 2009). This process depends on the spectral absorbance
141 of molecules such as opsins and cryptochromes (Figure 3B; Kaniewska et al., 2015; Luehrmann et al.,
142 2020). In animals, non-visual photoreception relies either on cryptochromes or opsins but opsin
143 photopigments are solely responsible for vision (Nilsson, 2009).

144 An animal's photosensitivity is described by its minimal light sensitivity (intensity) and spectral
 145 sensitivity (measured as peak sensitivity, λ -max). To perceive colour, organisms need at least two
 146 photoreceptor cells with different spectral sensitivities (Land & Nilsson, 2012). In most cases, more
 147 photoreceptors mean more colours can be discriminated (up to twelve in mantis shrimp; Thoen et
 148 al., 2014). However, as the generation and integration of electrical signals varies between species,
 149 the widespread colour-opponent coding system is not always applicable (Thoen et al., 2014). The
 150 visual biology of marine animals is a fast moving research field and essential to inform how ALAN can
 151 disrupt or mask natural cues and signals (Figure 3B). Tables S2 and S3 provide a non-exhaustive
 152 overview on taxa, sensitivity measurements and methods. Table 1 presents optical sensor analogues
 153 that best resemble organisms' visual system to quantify its photosensitivity.

154 **Table 1 Overview of marine photobiology. Common photosensory systems in marine animals, the**
 155 **information it captures, biological responses to light (showcasing taxonomic occurrence) and the sensor**
 156 **analogue that best resemble organisms' visual system. The categorisation of the photosensory system is not**
 157 **comprehensive but gives a simplified overview according to sensory information and tasks on the basis of**
 158 **Land and Nilsson (2012) and (Nilsson, 2009). Supplement S1 lists examples of taxonomic occurrence and**
 159 **photosensory systems (non-exhaustive). Note that animals can have several photosensory systems.**

	Photoreceptor cells & eye spots	Simple eyes	Compound eyes	Camera-type eyes
Description of photosensory systems	Regions of concentrated or dispersed cells containing light sensitive pigments (including skin)	Eyespots with or without a simple lens or concave eye (pit or pigmented cup eyes)	Composed of independent ommatidia or functionally similar structures, can contain cornea and lens	Single organ, with a pinhole and/ or cornea and lens-systems
Information captured	Intensity, cycles	Intensity, cycles, direction, contrast	Intensity, cycles, direction, contrast, image, colour	Intensity, cycles, direction, contrast, image, colour
Biological responses	Phototaxis, chronobiology (e.g. synchronised reproduction, feeding rhythms, circadian activity), habitat selection, predator avoidance	Phototaxis, chronobiology, habitat selection, predator avoidance, navigation	Phototaxis, chronobiology, habitat selection, predator avoidance, navigation, mate selection, resource acquisition	Phototaxis, chronobiology, habitat selection, predator avoidance, navigation, mate selection, resource acquisition
Taxonomic occurrence	Annelida, Arthropoda, Bryozoa, Cephalochordata,	Annelida (Polychaeta), Arthropoda,	Arthropoda, Echinodermata	Chordata (Actinopterygii,

	Cnidaria, Chordata, Ctenophora, Echinodermata, Mollusca, Nematoda, Nemertea, Platyhelminthes, Porifera	Cnidaria (Hydrozoa), Hemichordata (Enteropneusta), Mollusca, Porifera	(Asteroidea, Echinoidea)	Agnatha, Aves, Chondrichthyes, Mammalia, Osteichthyes, Reptilia), Cnidaria (Cubozoa), Mollusca (Cephalopoda)
Optical sensor analogue	Planar hyperspectral irradiance	Spectral radiance	Hyperspectral irradiance/ imaging	Hyperspectral irradiance/ imaging

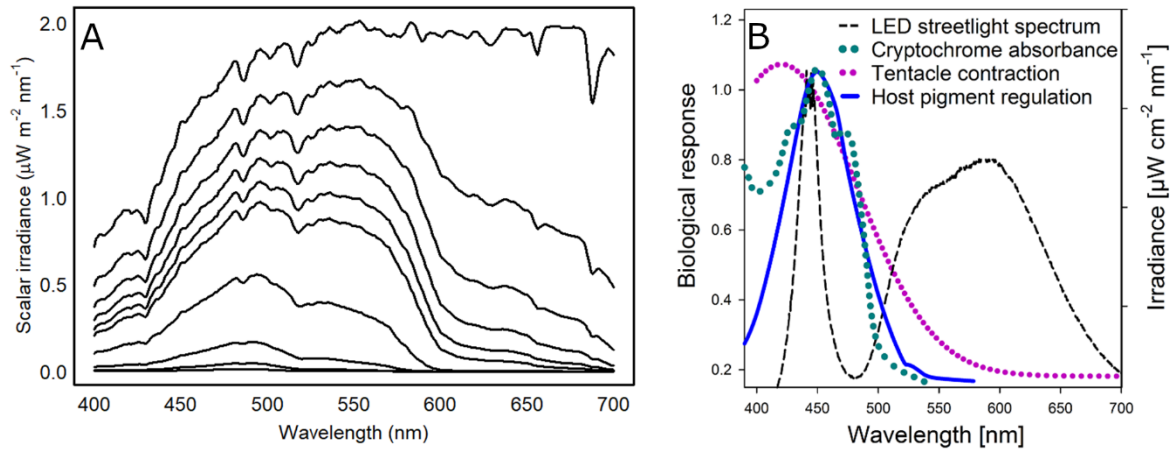
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161 An animal's photosensory system is closely linked to its photic environment (Land & Nilsson, 2012)
 162 down to the scale of variations in the (micro)habitat (Luehrmann et al., 2020), its ecology (e.g.
 163 coastal/ inter- or subtidal; sessile/ mobile; benthic/ demersal/ pelagic) and activity pattern (diurnal/
 164 crepuscular/ nocturnal/ cathemeral) (Schmitz & Wainwright, 2011). For instance, nocturnal fish
 165 show less divergent optical characteristics than diurnal species but have larger eye to body ratios
 166 (Schmitz & Wainwright, 2011). Diurnal fish populating bright microhabitats around single coral
 167 outcrops have a higher gene expression in opsins sensitive to short-wavelengths than fish in dimmer
 168 photic environments inside corals (Luehrmann et al., 2020).

169 Given the rhythmicity, stability and hence predictability of natural photoperiods over geological and
 170 evolutionary time, timing of behaviours and other biological processes is one of the taxonomically
 171 most prevalent adaptations to natural light. Diel activity patterns can vary between and within
 172 species depending on traits like life stage, age, size, sex, migratory phase, density, lunar phase,
 173 habitat, weather and timing of prey/ predator activity (reviewed by Gaston, 2019). For instance, fish
 174 show plastic diel rhythms of foraging and resting with ontogeny (Helfman et al., 1982) and between
 175 populations inhabiting adjacent microhabitats (Fox & Bellwood, 2011). Many crustaceans forage
 176 cathemerally but spawn during nocturnal high tides (Naylor, 2010). Particularly broadcast spawning
 177 organisms synchronise phenological life history events to light-dark cycles (Naylor, 2010; Righton et
 178 al., 2016), sometimes around few nights a year such the well-known mass spawning of reef building
 179 corals (Boch et al., 2011; Craggs et al., 2017). Sessile broadcast spawners can play an important role

180 in community ecology by creating habitats (Matsumura & Qian, 2014) or even ecosystems (Boch et
181 al., 2011). For mobile organisms successful reproduction can start with light-induced seasonal
182 migration over thousands of kilometres (Righton et al., 2016). Lunar and tidal cycles serve as
183 zeitgebers to entrain internal biological clocks that orchestrate large-scale synchronised responses
184 (reviewed in Andreatta & Tessmar-Raible, 2020; Naylor, 2010). Clock genes are crucial to an
185 organism's health (D'Angelo et al., 2008) and regulate key physiological processes such as cell cycles,
186 DNA repair, melatonin expression, stress responses and metabolism (see overview by Frøland
187 Steindal & Whitmore, 2019; Grubisic et al., 2019). Changes in light intensity, spectra and direction
188 make twilight a particularly reliable zeitgeber (Grubisic et al., 2019).

189 Remarkable light sensitivity characterises species adapted to dim light conditions including twilight
190 (Helfman et al., 1982; McGeady et al., 2019). Arctic zooplankton adjusts its diel vertical migrations to
191 the varying intensity of the lunar light cycle down to 200m depths thereby contributing to the
192 ocean's nutrient cycle (Berge et al., 2020; Cohen et al., 2020). The crustacean *Vargula annecohenae*
193 forages and reproduces only at critical dark thresholds (Gerrish et al., 2009). Light intensity and
194 spectra both act as cues. Coral spawning is synchronised to blue wavelengths (Boch et al., 2011;
195 Kaniewska et al., 2015). Physiological processes like phototrophic growth, calcification (Cohen et al.,
196 2016) and the expression of photoprotective pigments (D'Angelo et al., 2008) depend on specific
197 light spectra (Figure 3B). Spectral information facilitates various colour-guided behaviours. For
198 instance, larvae of sessile organisms base their once-in-a-life decision for suitable habitats based on
199 substrate spectra (Matsumura & Qian, 2014). Spectral contrasts and patterns enable intra- and
200 interspecific signalling during contests (Brown et al., 2012), mate selection (Detto, 2007) and
201 cleaner-client relationships (Cheney et al., 2009). Animals display visual and light-dependent signals
202 under dim light conditions and at night such as the giant cuttlefish *Sepia apama* which camouflages
203 at night (Warrant, 2007).



204

205 **Figure 3 The importance of moonlight for spectrally dependent biological processes and potential ALAN**
 206 **disruption. (A)** The attenuation of moonlight irradiance over 2m depth intervals (modelled assuming 0.3 mg
 207 m⁻³ chl-a typical non-bloom in open water as in Smyth et al. (2010)) showing the increasing importance of
 208 short wavelength moonlight with depth. **(B)** Absorbance spectrum of cryptochrome (involved in sensing
 209 moonlight for broadcast spawning; Kaniewska et al., 2015), peak spectral sensitivity of coral polyp retraction
 210 (Levy et al., 2003) and expression of blue photoprotective coral pigment genes (D'Angelo et al., 2008) are
 211 compared to the spectrum of cool white LED lighting (data Thorlabs, 2020).

212

213 **Quantifying the ALAN exposure of marine and coastal organisms**

214 The satellite-derived atlas of artificial night sky brightness (Falchi et al., 2016) is the only global
 215 assessment of the extent and intensity of ALAN. The atlas can be indicative of the ALAN exposure of
 216 coastal and intertidal organisms above the sea surface and help to identify ALAN pristine areas (1.7
 217 $\mu\text{cd}/\text{m}^2$ = up to 1% above natural light). However, those estimations cannot readily be translated into
 218 the distribution of ALAN underwater due to the properties of seawater (see 'Marine lightscapes'),
 219 temporal variations (it is a snapshot in time) and challenges in capturing different lighting spectra. A
 220 better understanding of the exposure of marine organisms to ALAN underwater (and in many cases
 221 to natural light) is required to quantify responses to ALAN that have real-world applications. The
 222 recognized detection limits of commercially available instruments (Cohen et al., 2020), i.e.
 223 submersible hyperspectral sensors, is one of the many reasons why quantifying natural and
 224 biologically relevant artificial light underwater is a challenging interdisciplinary endeavour often
 225 requiring customised and expensive approaches.

226 Before discussing how ALAN exposure of marine organisms can be measured and modelled, one
 227 needs to consider that light is quantified in a multitude of ways. Photometric units are common in
 228 ALAN studies, while radiometric units are often used in optical oceanography and visual ecology of
 229 non-human animals (for an excellent basic introduction on radiometry including conversions see
 230 Grubisic et al., 2019). Radiometric measurements quantify light in its physical form (its energy
 231 content either as numbers of photons or associated spectral power density) and can be spectrally
 232 resolved making them suitable for modelling organism exposure (Cohen et al., 2020; Mobley, 1994).
 233 Photometric units express the light sensitivity in the spectrum of a standardised human eye (Falchi
 234 et al., 2016; Mobley, 1994) and are the standard unit in the lighting industry which makes ALAN
 235 studies more easily translatable into policy. Table 2 summarises common photometric and
 236 radiometric measurements.

237 **Table 2 Photometric and Radiometric measurements of light as typically quantified in ALAN research (SI**
 238 **units given in brackets). *The units are analogous but not equivalent.* For conversions, see for instance**
 239 **Grubisic et al. (2019).**

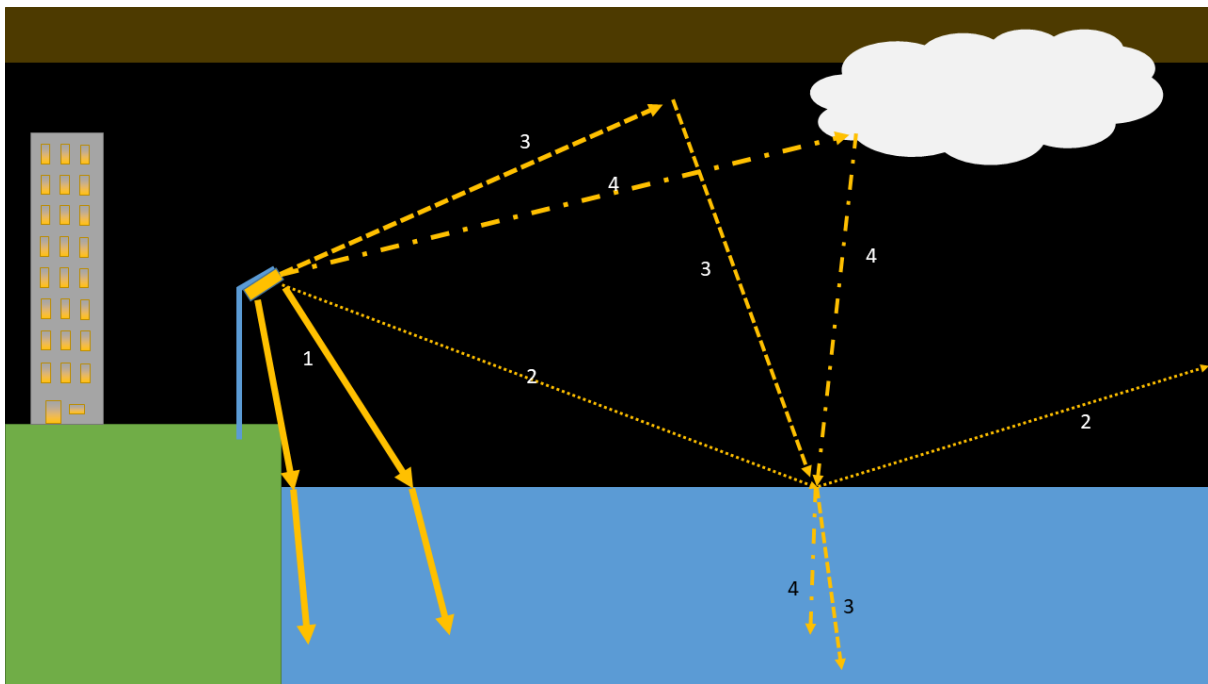
Description	Radiometric measurement	Photometric measurement
Light received from an object	Radiant Flux (W)	Luminous Flux (lm)
Light received per unit area	Irradiance (W m^{-2})	Illuminance (lux)
Light received per unit solid angle	Radiance ($\text{W m}^{-2} \text{sr}^{-1}$)	Luminous intensity (cd)

240

241 ***Measuring biologically relevant ALAN underwater***

242 Field measurements require careful planning around environmental conditions that alter light
 243 reflectance (Figure 4) and attenuation. To reduce the influence of natural light sources, sampling
 244 should be restricted to astronomical night (the moon is below the horizon and the sun is lower than
 245 -18° below the horizon). To correct for light from stars and the Milky Way one would have to
 246 measure light in ALAN naïve areas (Falchi et al., 2016). An alternative could be to measure spectra of
 247 specific ALAN sources to numerically establish their contribution to observed signals. To the best of
 248 our knowledge, this has not yet been attempted. Cloud cover, type, height and thickness are less

249 predictable but nonetheless significantly change ALAN exposure (Kyba et al., 2011) and thus need to
250 be recorded to represent local conditions.



251

252 **Figure 4 Fate of shore-based light following different optical paths. 1.** Light emitted close to the vertical and
253 directly incident upon the sea surface is largely transmitted into the water column. **2.** Light emitted close to
254 the horizontal will mainly be reflected at the sea surface. **3. & 4.** Light directed initially upwards may be
255 scattered downwards close to the vertical by **(3)** molecular or aerosol scattering, or **(4)** reflection from clouds
256 and transmitted into the water column.

257

258 Measuring biologically relevant ALAN distribution underwater should be guided by organisms'
259 photobiology considering: (i) species' threshold light sensitivity, (ii) species' spectral coverage and
260 resolution (both measured in radiometric units, Table 2), and (iii) the orientation and geometry of an
261 animal's photosensory system (Table 1). If light sensitivity thresholds and spectral sensitivities are
262 lacking, researchers might consider representative thresholds (Davies et al., 2020; Ludvigsen et al.,
263 2018). Currently commercially available sensors only partially address high sensitivity to low light
264 intensity, wide spectral range and high spectral discrimination to measure light underwater (Cohen
265 et al., 2020; Ludvigsen et al., 2018). Previous studies have used non-submersible terrestrial sensors
266 (e.g. Sky Quality Meter, SQM) designed to measure sunlight above the sea surface (Davies et al.,
267 2020; Ges et al., 2018). Alternatively, marine light sensors (e.g. photosynthetically active radiation

268 meter (PAR) or multispectral radiometers) can partially profile ALAN penetration into the water
269 column (Marchesan et al., 2005; Tamir et al., 2017). Both options enable progress in underwater
270 light fields at reasonably low light levels, but do not provide sufficient spectral resolution to easily
271 discriminate ALAN from natural ambient light signals. Spectral measurements captured by above
272 water sensors require additional information on spectrally dependent absorption and scattering by
273 seawater to support modelling of light penetration to depth (Mobley, 1994). Panchromatic sensors
274 (e.g. PAR, SQM) provide minimal spectral selection (100's of nm bandwidth) but offer high
275 radiometric sensitivity and dynamic range. Multispectral sensors like the Biospherical Instruments
276 PRR-800 (Tamir et al., 2017) offer improved, but limited spectral resolution (width and number of
277 channels). Optimised sensitivity settings for each multispectral channel enable capture of rapid
278 changes in distribution across the spectral range (ultraviolet-visible-near infrared, UV-VIS-NIR).
279 Oceanographic hyperspectral radiometers (e.g. Trios RAMSES or Satlantic HyperPro) provide high
280 spectral resolution (3-5 nm) over a wide spectral range (Berge et al., 2020; McGeady et al., 2019).
281 However, limited radiometric sensitivity associated with dispersing received illumination over the
282 spectrometer's diode array constrains sensor performance in low light conditions relevant for many
283 marine organisms. An ideal marine ALAN sensor would consist of submersible (maximum depth > 20
284 m) hyperspectral sensor covering the UV-VIS range (350 – 700 nm) with sufficient spectral resolution
285 to facilitate identification of ALAN signals above the natural light background and sufficient
286 sensitivity low intensity light to record light levels relevant for specified biological responses. This
287 might be achieved in future by combining longer integration times with cooled sensors for noise
288 suppression.

289 Finally, it is important to consider how any particular species will perceive the underwater light field
290 depending on the morphology, orientation and angle of light detection and vision. The optical sensor
291 should consider the collection optic (e.g. irradiance vs radiance), light sensitivity and spectral
292 resolution needed to simulate response functions of animals' eyes. Future sensors could be designed
293 to account for an animals' eye morphology as best as possible.

294 ***Modelling biologically relevant ALAN underwater***

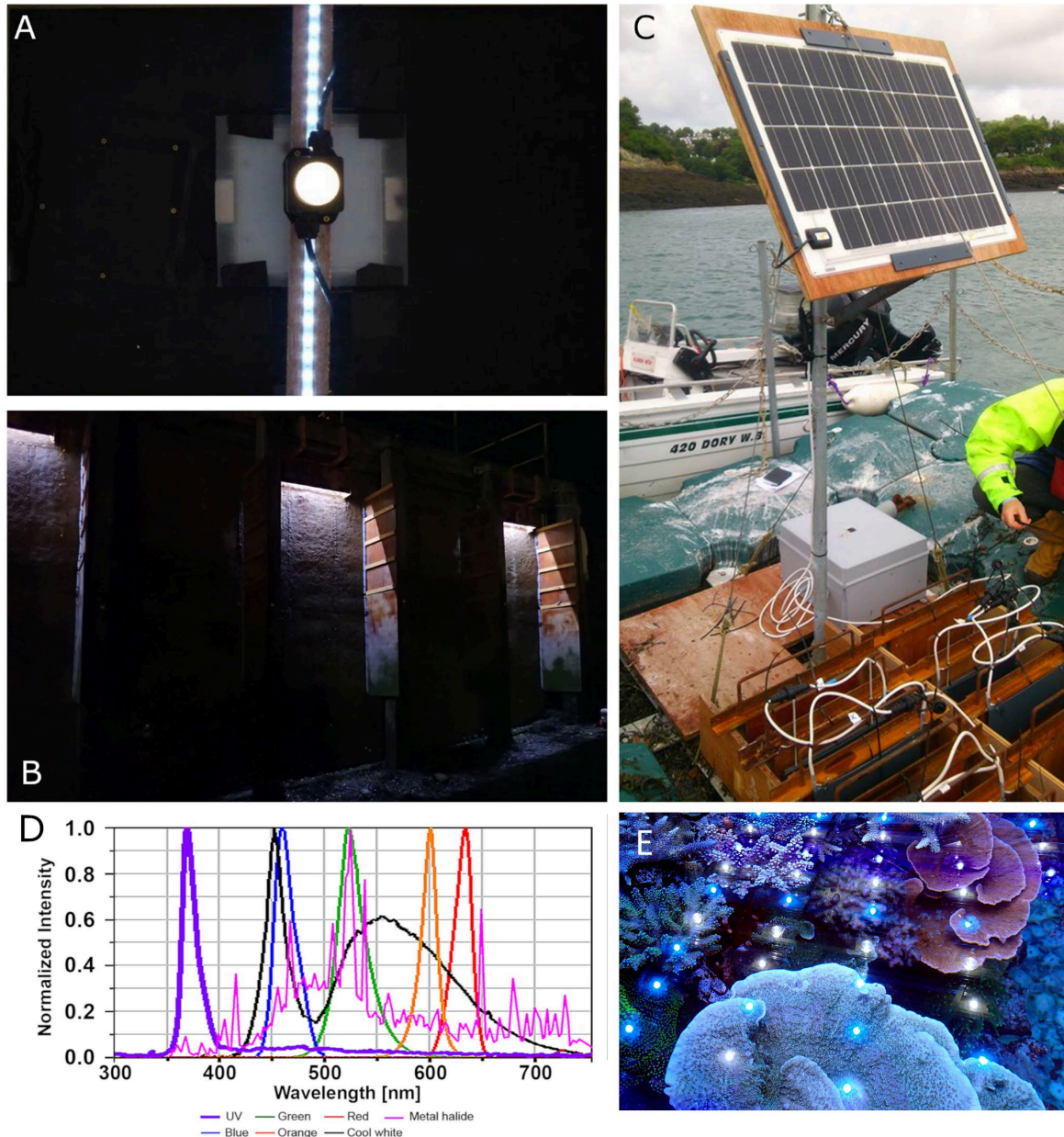
295 In the absence of global underwater ALAN measurements, modelling the distribution of ALAN
296 underwater holds great potential. Radiative transfer models (RTM) are well-established optical
297 oceanographic tools (Mobley, 1994). Resources on how to implement these are openly accessible
298 (<https://www.oceanopticsbook.info/>). RTMs such as HYDROLIGHT calculate spectral radiance
299 distributions and related quantities for the marine ecosystem of interest (Mobley & Sundman,
300 2013). Critical are two primary datasets to parameterise RTMs for the desired ecosystem: (i) light
301 measured above water and (ii) inherent optical properties (IOPs) that govern light penetration
302 through the water column (see 'Marine lightscapes'). The partitioning of IOPs into representative
303 components (absorption by phytoplankton (a_{ph}), coloured dissolved organic matter (CDOM; a_{dy});
304 backscatter due to particulates (b_{bp})) allows to account for spatiotemporal variations. Obtaining
305 these values *in situ* improves model accuracy (Werdell et al., 2018).

306 So far, there are only few studies assessing ALAN prevalence, spatial extent and intensities
307 encountered by marine organisms throughout the water column (Berge et al., 2020; Davies et al.,
308 2020; Ludvigsen et al., 2018). While there are currently no globally derived hyperspectral satellite
309 images of night-time lighting, spectrally explicit global predictions of sea surface radiometric
310 measurements can be derived from empirical relationships between locally measured sea surface
311 radiometry and the Falchi atlas (Falchi et al., 2016). The atlas is derived from the VIIRS Day-Night
312 Band (DNB) sensor on the Suomi National Polar-orbiting Partnership (S-NPP) satellite, has a spatial
313 resolution of 742 m and is sensitive to light in the range 0.5–0.9 μm . This upscaling requires that
314 spectral power distributions and relative contributions of different lighting technologies influencing
315 locally derived sea surface radiometry are quantified or constrained. Implicit in this upscaling is the
316 assumption that ALAN spectra are globally uniform and closely approximate the spectra of local
317 measurements. The second primary datasets, the IOPs, can either be measured locally or derived
318 from monthly global climatologies such as the ESA Ocean Colour Climate Change Initiative
319 (<http://www.esa-oceancolour-cci.org/>). These two primary datasets can then be used to parametrize

320 spectrally explicit RTMs of ALAN penetration with depth for the desired marine ecosystem using
321 Beer's Law (Berge et al., 2020; Davies et al., 2020). To improve output representativity, models can
322 account for tidal fluctuation (Roberts et al., 2018), and meteorological conditions influencing IOPs
323 (Hieronymi & Macke, 2012). Global scale modelling across multiple depths, wavelengths, latitudes
324 and longitudes is likely to be computationally expensive but can be solved reducing the spatial,
325 depth and spectral resolution of models (Davies et al., 2020). A biological approach to understanding
326 spectrally explicit ALAN exposure of marine organisms circumventing these challenges could lie in
327 vision modelling (Cheney et al., 2009; Thoen et al., 2014) which is yet to be applied for ALAN.

328 **Quantifying ALAN impacts on marine and coastal ecosystems**

329 With the outlined biological adaptations to lightscapes and demonstrated marine ALAN impacts in
330 mind (Figure 1, Table S1, Davies et al., 2014) this section discusses study design and technology to
331 quantify marine ALAN impacts in a variety of field and laboratory approaches (Figure 5).



332

333 **Figure 5 Marine ALAN experiments. (A)** Simulated moonlight (lit sphere), daylight (unlit square) and ALAN (lit
 334 bar). Lunar cycles are programed using modelled lunar sky brightness (Figure 2A-B). **(B)** Varnished plywood
 335 prevents light trespassing and animals moving between replicates. **(C)** IP68 rated waterproof enclosures and
 336 connections: a solar trickle charged battery on a pontoon, Menai Strait, UK (Davies et al., 2015). **(D)** Spectral
 337 power distributions of alternative lighting simulations including metal halide lamps (pink), broad spectrum
 338 LEDs (black), and narrow spectrum (coloured) LEDs (data Thorlabs, 2020). **(E)** Without diffusion or distancing,
 339 close proximity LEDs create uneven light fields (Photos: authors).

340

341 **ALAN experiments**

342 Existing technology allows experimental decoupling of discrete ALAN characteristics by installing

343 different lighting components. Setup complexity varies with research questions and design ranging

344 from ALAN presence/ absence, different intensities, photoperiod and spectra, to interference with
345 natural light cycles and timings. If conducted in the lab, the latter two setups need to simulate
346 natural light accurately, often over months (Fobert et al., 2019) and sometimes even years (Craggs et
347 al., 2017). Integrating environmental conditions that alter lightscapes and organisms' biology (e.g.
348 moon, tides, clouds) improve real-world settings but add complexity to design and technology.

349 The vast majority of marine ALAN studies have assessed the presence of direct, high intensity ALAN
350 (Davies et al., 2015; Fobert et al., 2019; O'Connor et al., 2019) which is the most straightforward to
351 simulate. Few studies have mimicked ALAN as low as artificial skyglow integrating dimmers or
352 dimming shields (a freshwater example Franke et al., 2013; the only marine experiment Torres et al.,
353 2020). Marine organisms' high sensitivity to dim light means to avoid ALAN adapted animals and
354 identify ALAN naïve locations (including artificial skyglow) by using the Falchi map (Falchi et al.,
355 2016) or by measuring ALAN *in situ*. Whilst sufficiently sensitive handheld lux meters present an
356 affordable tool to establish light naïve areas and gradients of ALAN intensity, they lack information
357 on spectrally relevant intensities and ALAN underwater. Experimenters need to avoid light trespass
358 (Figure 5B) between exposure and control treatments (Davies et al., 2015; Fobert et al., 2019).
359 Introducing light to record behavioural responses can compromise the control (dark) treatment.
360 (Infra-)Red lighting has proved useful (Ugolini et al., 2016); however, the assumption is that long
361 wavelengths are less detectable by marine organisms.

362 The widespread occurrence and importance of light-induced rhythmicity in marine ecosystems
363 highlights the potential of ALAN to influence processes on the molecular and cellular level. Analysing
364 rhythmic clock gene expression to infer clock function is well established in chronobiology and has
365 been described in a range of marine taxa (see below). Defining their expression over a natural light-
366 dark cycle and contrasting these under ALAN is a logical first step and has recently been
367 demonstrated in corals (Rosenberg et al., 2019a). Contrasting gene expression is now readily
368 achieved, even in non-model species, using modern molecular technologies such as transcriptomics

369 (Andreatta & Tessmar-Raible, 2020). Measurable phenotypes related to behaviour, reproduction,
370 and growth (for instance Diptera *Clunio marinus* Kaiser et al., 2016; Scleractinia *Acropora millepora*
371 Kaniewska et al., 2015; Amphipoda *Talitrus saltator* Ugolini et al., 2016; Phyllodocida *Platynereis*
372 *dumerilii* Zantke et al., 2013; Isopoda *Eurydice pulchra* Zhang et al., 2013) are essential to establish
373 the influence of the core oscillatory mechanism. Measuring rhythmic molecular and cellular
374 phenotypes, together with rhythmic behavioural outputs over appropriate temporal scales or at
375 carefully designed time points, represents a robust strategy to advance chronobiology and evaluate
376 ALAN impacts on clock-driven processes at the organismal and population level. A recent study
377 demonstrates marine ALAN affects gene expression related to cell cycle, cell proliferation, cell
378 growth and protein synthesis (Rosenberg et al., 2019b) making cellular biology a novel and
379 promising angle for future research.

380 Many photobiological responses are driven by distinct wavelengths making spectral sensitivity key to
381 understanding and mitigating ALAN effects (Table S3). LEDs come in a large range of emission
382 colours and narrow-banded spectra (Figure 5D; Boch et al., 2011) enabling to determine organisms'
383 responses to specific spectra. Alternatively, white light sources can be combined with band-pass
384 filters (D'Angelo et al., 2008; Marchesan et al., 2005). Commonly proposed ALAN mitigation
385 strategies include dimming lights, part-time lighting (e.g. only during high demand) and manipulating
386 wavelengths (Gaston et al., 2012). Readily available approaches combine customisable LEDs, narrow
387 band-pass filters and timed photocells. The described attenuation of long wavelengths in seawater
388 highlights the potential of spectral manipulation for mitigating ALAN impacts on marine ecosystems.
389 Manipulating and reporting ALAN spectral power distribution where possible will yield deeper
390 insights for individual studies and future meta-analyses.

391 ***Natural light simulations***

392 Natural light simulations become essential for studies interested in mechanistic understanding of
393 ALAN impacts (e.g. on diel activity patterns, chrono- and lunar-biology), which thereby can

394 contribute to advancing basic night-time ecology. Realistically simulating natural night-time light
395 conditions (occurrence, periodicity, timing, intensity and spectra) can be challenging, even more so
396 when experiments span more than one night (the most elaborate example of over a year is Craggs et
397 al., 2017). Natural daylight spectra are broad and evenly distributed. While metal halide (D'Angelo et
398 al., 2008) and fluorescent lamps (Rosenberg et al., 2019a) are commonly used for their broad
399 spectral distribution, they can show extreme spikes and peaks; modern white LEDs achieve more
400 even broadband emission spectra (Figure 5D; for comparisons of lighting and emission spectra see
401 Elvidge et al., 2010). Metal halide lamps can illuminate relatively large areas at high but immutable
402 intensity which can be reduced with neutral density filters (Kaniewska et al., 2015). The spectral
403 breadth in single types of LEDs is limited; even white LEDs lack essential short and long wavelengths
404 and often peak in the blue (Figure 5D). Broadband LED lamps that consist of arrays of individual LEDs
405 with different colours including the near-UV range (Craggs et al., 2017) are preferable (Figure 5D).
406 The colour contribution of each lamp can be adjusted in multi-channel systems enabling simulations
407 of complex light fields. Diffusion filter and distancing of individual LEDs avoid focussed beams with
408 colour and intensity patches (Figure 5E). Many smaller LEDs are superior to systems with few, more
409 powerful LEDs. As the photonflux of the illuminated area drops with distance to the lamp (Dick,
410 2020), an even light field will come at the expense of intensity.

411 Twilight is characterised by changes in light intensity ($\sim 0.1 \text{ lx}$), spectra, direction and timing
412 (Grubisic et al., 2019). Modern LEDs can be gradually dimmed and selected to mimic changes in
413 spectra (Boch et al., 2011). Off-the-shelf programmable daylight control systems (e.g. BioLumen,
414 Figure 5A) simulate day length (the timing of sunrise and sunset with latitude) but can replicate
415 neither twilight intensity at more extreme latitudes (long periods in summer, contraction in winter)
416 nor changing spectra. Lighting systems can be customised to simulate twilight timing and spectra
417 (Craggs et al., 2017). Results around ALAN impacts of twilight ecology obtained from off-the-shelf
418 daylight control systems should be interpreted carefully.

419 Assessing ALAN interference with moon-driven individual- and population-level processes in marine
420 organisms has presented a significant barrier to progress in (marine) ALAN research. Studies on
421 biological adaptations to dim natural light (e.g. melatonin) often suffer from controls which are too
422 dark (Grubisic et al., 2019). No current off-the-shelf lighting system accurately simulates moon-
423 driven light-dark cycles. Whereas constant dim light to simulate the moon is already available in
424 certain commercial lamps, accurate systems require that intensity tracks the moons altitude
425 throughout the night, varying between months and years (Figures 2, 5A; Craggs et al., 2017).
426 Simulations that do not account for the moon's altitude omit potentially critical signals likely to
427 impact precise and accurate timings of lunar informed phenological events (Cohen et al., 2020). One
428 of the most challenging environmental conditions to simulate in marine ALAN research is the
429 combined effect of lunar and tidal cycles. Where possible, both should be simulated in the
430 laboratory, for instance based on modelling tidal modulation of natural (Figure 2; Roberts et al.,
431 2018) and artificial light regimes.

432 ***ALAN field studies***

433 Where ALAN naïve areas are not accessible, treatments in manipulative field experiments (i.e. in
434 which ALAN is introduced) can be set above what is currently found at this particular location
435 (Bolton et al., 2017). Field experiments should control for, or better build-in, environmental factors
436 that influence natural light and hence organisms' activity in their design, first of all the lunar cycle
437 and clouds (Duarte et al., 2019; Torres et al., 2020). Experiments conducted away from electrical
438 sources require water- and weatherproofed power to maintain reliable treatments over time using
439 batteries (Navarro-Barranco & Hughes, 2015) or generators (Duarte et al., 2019). Solar power and
440 photocells can regulate ALAN timing and extend battery longevity (Figure 5C, Davies et al., 2015).
441 Bioacoustics equipment such as acoustic profilers circumvent introducing light to record behaviours
442 by listening to changes in activity (Berge et al., 2020; Bolton et al., 2017; Sameoto et al., 1985).
443 Indeed, there is untapped potential in a range of tools already commonly used in marine ecology for
444 both marine photobiology and marine ALAN field studies (e.g. light traps, tagging, telemetry).

445 Observational field studies (i.e. existing, 'real-world' ALAN) should measure natural and artificial light
446 to characterise ALAN exposure. Ecological patterns and behaviours can be sampled under ALAN
447 levels either derived from global satellite data (e.g. VIIRS DNB, Rodriguez et al., 2015) or measured
448 and mapped *in situ* (Garratt et al., 2019). As with any other field study, environmental conditions
449 causing collinearity or altering natural light need to be controlled for (Garratt et al., 2019).

450 Offshore surveys on marine ALAN impacts remain limited due to the technological constraints of
451 measuring ALAN underwater as well as general limitations in conducting offshore research. Studies
452 on offshore birds attracted by artificial lighting represent an exception (Merkel & Johansen, 2011).
453 Recently, bioacoustics, ALAN surface measurements and radiative transfer modelling of the
454 underwater light field have been successfully deployed to show that ALAN suppresses zooplankton's
455 diel vertical migration (Berge et al., 2020; Ludvigsen et al., 2018). This approach shows great promise
456 for quantifying ALAN exposure and impacts underwater but the technological costs might be
457 prohibitive for many researchers.

458 **Synthesis: Current challenges and future directions of marine ALAN** 459 **research**

460 Marine light pollution is an emerging research field. We have highlighted several challenges
461 regarding knowledge, design and technology that need to be considered when quantifying marine
462 ALAN exposure and impacts. In the absence of current comprehensive solutions to these challenges,
463 we have recommended best-practices. Unresolved are diverse measurement and reporting
464 approaches that are likely to hinder the consolidation of results for meta-analyses, ecosystem wide
465 assessments and eventually policy and management formulation.

466 Quantifying the distribution of ALAN (and natural light) underwater is technically challenging yet a
467 prerequisite to inform exposure experiments. Lab experiments need to tackle the realistic simulation
468 of natural light regimes focusing on twilight, moonlight, and where possible tides and spectrally
469 realistic light fields. Discretely manipulating ALAN characteristics that drive observed changes

470 facilitates better mechanistic understanding and provides empirical understanding for designing
471 mitigation strategies and technologies (Gaston et al., 2012). Contemporary molecular tools can be
472 used to quantify the impact of ALAN on light-influenced gene expression involved in clock regulation
473 (Frøland Steindal & Whitmore, 2019) and other fundamental molecular and cellular processes,
474 offering new avenues for exploring ALAN induced changes to organism phenology and health. As
475 research systems move offshore and into deeper water, marine ALAN research becomes technically
476 and financially more demanding, not least when it comes to quantifying ALAN exposure underwater
477 in space and time.

478 To scale-up marine ALAN research, predictive modelling that combines laboratory and field derived
479 responses to ALAN with global maps can help to identify future impacts, most susceptible species
480 and habitats (Davies et al., 2014) but is yet to be applied. Integrating data from ALAN distribution
481 and impacts could help to understand how ALAN affects populations, their biogeography and
482 eventually entire ecosystems now and in the future. Long-term observational and manipulated
483 marine ALAN studies are needed to expand from short-term, shock responses to assess the
484 consequences of chronic exposure (Dominoni et al., 2013). Few studies have mapped ALAN exposure
485 of global shallow coral reefs (Ayalon et al., 2020), bird and turtle colonies and linked these with field
486 data of offspring mortality and recruitment across populations and years (Kamrowski et al., 2014
487 covering Australia; Rodriguez et al., 2015 across Tenerife island). Scope to scale-up ALAN responses
488 of inter- and subtidal taxa could lie in population dynamics modelling (Le Corre et al., 2002).
489 Essential will be the quantification of ALAN underwater to identify ALAN hotspots and its co-
490 occurrence with other global change stressors in marine and coastal ecosystems thereby integrating
491 ALAN into the multi-stressor context. Advancing marine ALAN research will ultimately yield insights
492 into underpinning fundamental marine photobiology, chronobiology and night-time ecology.

493 **Authors' Contributions**

494 ST, TS, DMK, JW, SRJ, SW, AMQ, TWD conceived the idea for the manuscript. ST, TS, DMK, CDA, AJM,
495 AW, TWD contributed to data collection for figures and supplements. ST and TWD led the writing of
496 the manuscript. All authors contributed critically to the drafts and gave final approval for
497 submission.

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