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REVIEW

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Marine artificial light at night: An empirical and technical guide

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Abstract

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

KEYWORDS

Artificial light at night, coastal ecosystems, light pollution, marine ecology, night-time ecology, nocturnality, photobiology, underwater lightscapes

1 | INTRODUCTION

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

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

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

2 | MARINE LIGHTSCAPES

As in terrestrial ecosystems, the moon and the sun govern marine lightscapes in the photic zone (Warrant & Locket, 2004). The earth's rotation creates diurnal light–dark cycles (24 hr) including twilight (Kronfeld-Schor & Dayan, 2003). The earth's axis of rotation and orbital plain around the sun creates seasonal (365.24 days) variations in day–night length (Helm et al., 2013). The orbit of the moon around the earth, and changes in full moon altitude as the earth orbits the sun create 29.5 day and annual lunar cycles in natural night-time lighting (Kronfeld-Schor et al., 2013). Lunar light cycles create spatially discrete but temporally predictable mean nocturnal sea surface illuminances. Light intensities diverge considerably: Full moon (0.1–0.3 lux) is around six orders of magnitude dimmer than full sunlight (130,000 lux) but 1,000 times brighter than a clear starry night (0.0001 lux; for an overview see Dick, 2020). Light–dark cycles

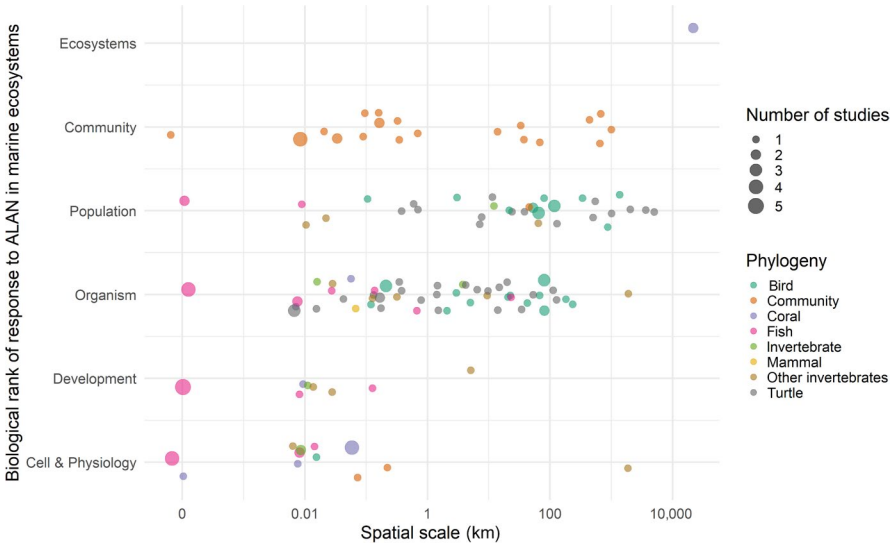

FIGURE 1 Spatial, biological and phylogenetic focus of marine artificial light at night (ALAN) research over the last 35 years (based on peer reviewed publications retrieved by Web of Science keyword search and complemented by references from ALAN reviews and papers). Note that some studies assessed responses to ALAN in more than one biological rank

vary with latitude exhibiting larger amplitude towards the poles (Hut et al., 2013). For instance, full moon altitude and night-time sky brightness at high latitudes peak annually during winter solstice (Figure 2a) and close to the equator biannually during equinoxes (Figure 2b).

The properties of seawater, together with numerous meteorological, geographical and geological factors, influence the spatio-temporal extent, intensity and spectra of natural and artificial light underwater (Figures 2c–f and 3). Underwater lightscapes in the open ocean are relatively well understood. Light in the wavelengths of 475 nm transmits best (Figure 3a; Mobley, 1994) and penetrates down to 1,000 m creating dim conditions similar to starlight (Warrant & Locket, 2004). The high concentrations of optically active constituents such as Chlorophyll a, inorganic sediment and coloured dissolved organic matter (CDOM) govern wavelength-dependent light absorption and scattering which makes measuring shallow coastal, estuarine and temperate underwater lightscapes more complex (Ackleson, 2003; Mobley, 1994).

Seasonally variable sea temperatures, sunlight, rainfall and nutrient availability change concentrations of optically active constituents (e.g. high during spring phytoplankton bloom). Local bathymetry and topography affect wave and tidal driven resuspension of sediments, algae and detritus and thus the optical properties in coastal waters. Light in the spectrum of around 450 nm is attenuated and suspended particles reflect wavelengths between 495–570 nm (green to human eyes) and 570–590 nm (yellow; Mobley, 1994). Benthic ecosystems (seagrass, kelp, corals) further modify shallow underwater lightscapes (Ackleson, 2003). Tidal cycles change the path length of natural (Roberts et al., 2018) and artificial (Davies et al., 2020) light on the seafloor and expose intertidal marine organisms up to twice daily to direct light (Figure 2c–f). Tidal amplitudes vary monthly (spring and neap tides) and annually (equinoctial tides) and can range from a few centimetres up to more than 15 m (Desplanque & Mossman, 2001).

3 | BIOLOGICAL ADAPTATIONS TO MARINE LIGHTSCAPES

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

Table 1 showcases common photosensory systems, the information captured, biological responses to light and taxonomic occurrence. Light sensing abilities range from the detection of light, shade or darkness via single photoreceptor cells and eye spots to monochromatic imaging and complex, high-resolution multi-colour vision via compound or camera-type eyes (Land & Nilsson, 2012). Photopigments and receptor cells are the fundamental structures to detect and convert a photon of light into an electrochemical signal (Nilsson, 2009). This process depends on the spectral absorbance of molecules such as opsins and cryptochromes (Figure 3b; Kaniewska et al., 2015; Luehrmann et al., 2020). In animals, non-visual photoreception relies either on cryptochromes or opsins but opsin photopigments are solely responsible for vision (Nilsson, 2009).

An animal's photosensitivity is described by its minimal light sensitivity (intensity) and spectral sensitivity (measured as peak sensitivity, λ-max). To perceive colour, organisms need at least two photoreceptor cells with different spectral sensitivities (Land & Nilsson, 2012). In most cases, more photoreceptors mean more colours can be discriminated (up to 12 in mantis shrimp; Thoen et al., 2014). However, as the generation and integration of electrical signals varies between species, the widespread colour-opponent coding system is not always applicable (Thoen et al., 2014). The visual biology of marine animals is a fast moving research field and essential to inform how ALAN can disrupt or mask natural cues and signals (Figure 3b). Tables S1 and S2 provide a non-exhaustive overview on taxa, sensitivity measurements and methods. Table 1 presents optical sensor analogues that best resemble organisms' visual system to quantify its photosensitivity.

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

Given the rhythmicity, stability and hence predictability of natural photoperiods over geological and evolutionary time, timing of behaviours and other biological processes is one of the taxonomically most prevalent adaptations to natural light. Diel activity patterns can vary between and within species depending on traits like life stage, age, size, sex, migratory phase, density, lunar phase, habitat, weather and timing of prey/predator activity (reviewed by Gaston, 2019). For instance, fish show plastic diel rhythms of foraging and resting with ontogeny (Helfman et al., 1982) and between populations inhabiting adjacent microhabitats (Fox & Bellwood, 2011). Many crustaceans forage cathemerally but spawn during nocturnal high tides (Naylor, 2010). Particularly broadcast spawning organisms synchronise phenological life-history events to light–dark cycles (Naylor, 2010; Righton et al., 2016), sometimes around few nights a year such the well-known mass spawning of reef building corals (Boch et al., 2011; Craggs et al., 2017). Sessile broadcast spawners can play an important role in community ecology by creating habitats (Matsumura & Qian, 2014) or even ecosystems (Boch et al., 2011). For mobile organisms successful reproduction can start with light-induced seasonal migration over thousands of kilometres (Righton et al., 2016). Lunar and tidal cycles

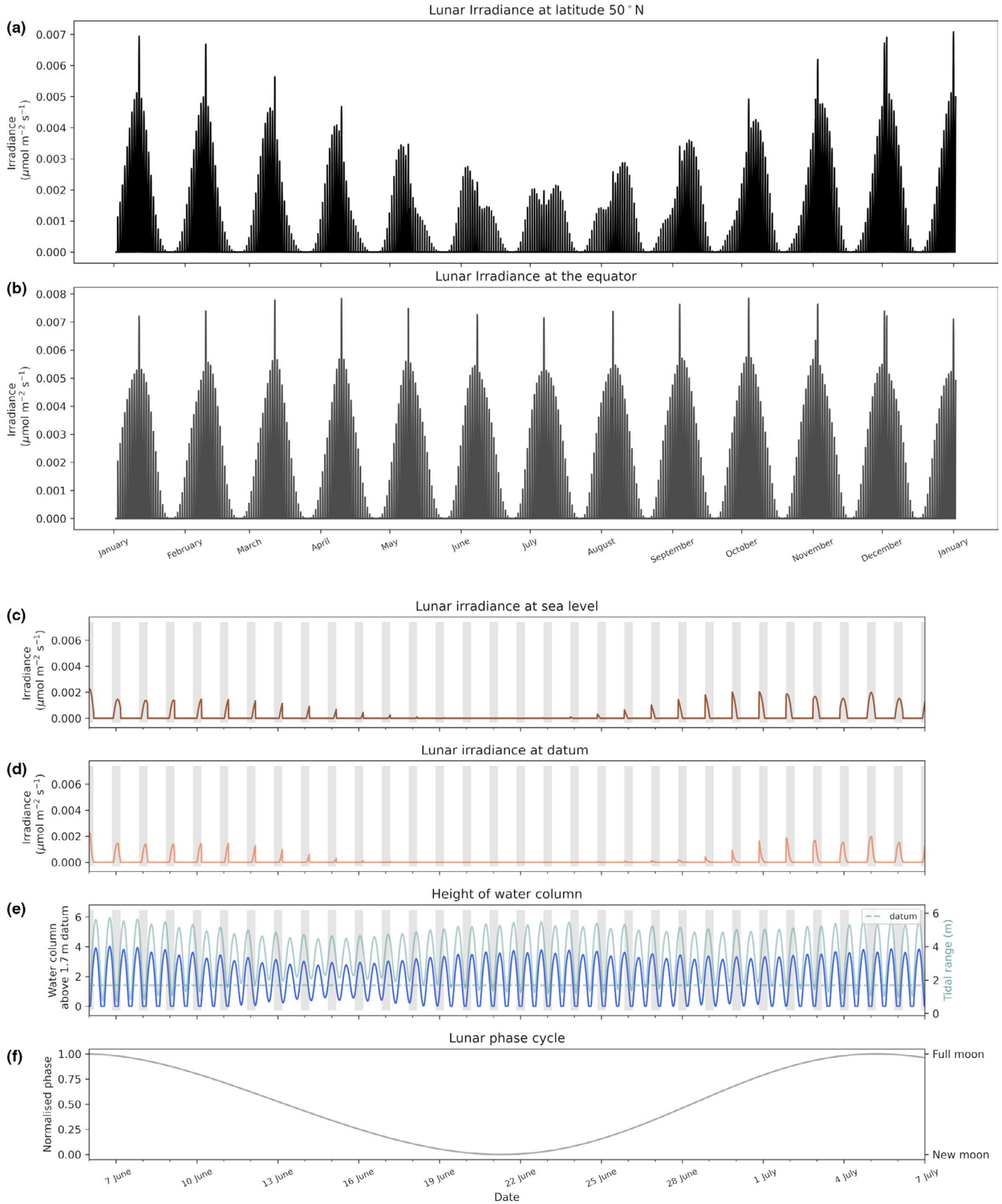

FIGURE 2 Moonlight cycles in and out of the sea. The 2020 lunar calendar in zenith sky brightness detectable at the sea surface at (a) 50° latitude and (b) the equator. (c–f) Modelled seabed (datum 1.7 m) moonlight irradiance in the intertidal through a synodic month accounting for the impact of the moon's phase angle (f) on sea surface irradiance (d), and tidal height above datum 1.7 m (e) on the attenuation of sea surface moonlight (c) for Plymouth, UK (~50° latitude). Light–tidal interaction model based on Roberts et al. (2018) and extended to include lunar components

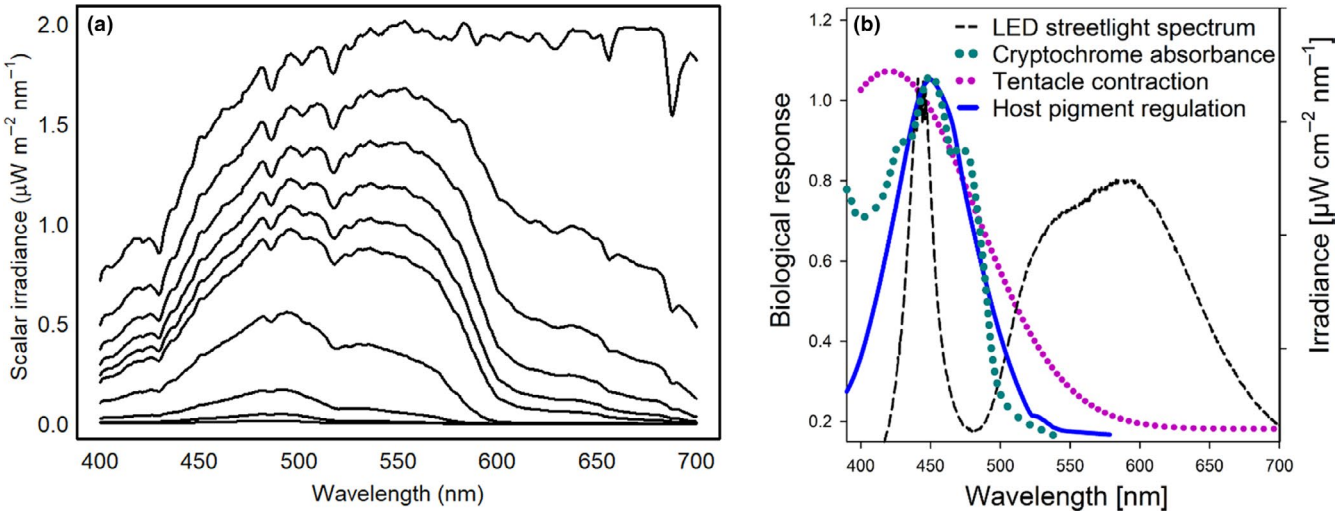

FIGURE 3 The importance of moonlight for spectrally dependent biological processes and potential artificial light at night disruption. (a) The attenuation of moonlight irradiance over 2 m depth intervals (modelled assuming 0.3 mg/m^3 chl-a typical non-bloom in open water as in Smyth et al. (2010)) showing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

serve as zeitgebers to entrain internal biological clocks that orchestrate large-scale synchronised responses (reviewed in Andreatta & Tessmar-Raible, 2020; Naylor, 2010). Clock genes are crucial to an organism's health (D'Angelo et al., 2008) and regulate key physiological processes such as cell cycles, DNA repair, melatonin expression, stress responses and metabolism (see overview by Frøland Steindal & Whitmore, 2019; Grubisic et al., 2019). Changes in light intensity, spectra and direction make twilight a particularly reliable zeitgeber (Grubisic et al., 2019).

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

4 | QUANTIFYING THE ALAN EXPOSURE OF MARINE AND COASTAL ORGANISMS

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

Before discussing how ALAN exposure of marine organisms can be measured and modelled, one needs to consider that light is quantified in a multitude of ways. Photometric units are common in ALAN studies, while radiometric units are often used in optical oceanography and visual ecology of non-human animals (for an excellent basic introduction on radiometry including conversions see Grubisic et al., 2019). Radiometric measurements quantify light in its physical form (its energy content either as numbers of photons or associated spectral power density) and can be spectrally resolved making them suitable for modelling organism exposure (Cohen et al., 2020; Mobley, 1994). Photometric units express the

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

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

light sensitivity in the spectrum of a standardised human eye (Falchi et al., 2016; Mobley, 1994) and are the standard unit in the lighting industry which makes ALAN studies more easily translatable into policy. Table 2 summarises common photometric and radiometric measurements.

4.1 | Measuring biologically relevant ALAN underwater

Field measurements require careful planning around environmental conditions that alter light reflectance (Figure 4) and attenuation. To reduce the influence of natural light sources, sampling should be restricted to astronomical night (the moon is below the horizon and the sun is lower than. -18° below the horizon). To correct for light from stars and the Milky Way one would have to measure light in ALAN naïve areas (Falchi et al., 2016). An alternative could be to measure the spectra of specific ALAN sources to numerically establish their contribution to observed signals. To the best of our knowledge, this has not yet been attempted. Cloud cover, type, height and thickness are less predictable but nonetheless significantly change ALAN exposure (Kyba et al., 2011) and thus need to be recorded to represent local conditions.

Measuring biologically relevant ALAN distribution underwater should be guided by organisms' photobiology considering: (a) species' threshold light sensitivity, (b) species' spectral coverage and resolution (both measured in radiometric units, Table 2) and (c) the orientation and geometry of an animal's photosensory system (Table 1). If light sensitivity thresholds and spectral sensitivities are lacking, researchers might consider representative thresholds (Davies et al., 2020; Ludvigsen et al., 2018). Currently commercially available sensors only partially address high sensitivity to low light intensity, wide spectral range and high spectral discrimination to measure light underwater (Cohen et al., 2020; Ludvigsen et al., 2018). Previous studies have used non-submersible terrestrial sensors (e.g. Sky Quality Meter, SQM) designed to measure sunlight above the sea surface (Davies et al., 2020; Ges et al., 2018). Alternatively, marine light sensors (e.g. photosynthetically active radiation meter [PAR] or multispectral radiometers) can partially profile ALAN penetration into the water column (Marchesan et al., 2005; Tamir et al., 2017). Both options enable progress in underwater light fields at reasonably low light levels, but do not provide sufficient spectral resolution to easily discriminate ALAN from natural ambient light signals. Spectral measurements captured by above water sensors require additional information on spectrally dependent absorption and scattering by seawater to support modelling of light penetration to depth (Mobley, 1994). Panchromatic sensors (e.g. PAR, SQM) provide minimal spectral selection (100's of nm bandwidth) but offer high radiometric sensitivity and dynamic range. Multispectral sensors like the Biospherical Instruments PRR-800 (Tamir et al., 2017) offer improved, but limited spectral resolution (width and number of channels). Optimised sensitivity settings for each multispectral channel enable capture of rapid changes in distribution across the spectral range (ultraviolet–visible–near infrared, UV–VIS–NIR). Oceanographic hyperspectral radiometers (e.g. Trios RAMSES or Satlantic HyperPro) provide high spectral resolution (3–5 nm) over a wide spectral range (Berge et al., 2020; McGeady et al., 2019). However, limited radiometric sensitivity associated with dispersing received illumination over the spectrometer's diode array constrains sensor performance in low light conditions relevant for many marine organisms. An ideal marine ALAN sensor would consist of submersible (maximum depth >20 m) hyperspectral sensor covering the UV–VIS range (350–700 nm) with sufficient spectral resolution to facilitate identification of ALAN signals above the natural light background and sufficient sensitivity low intensity light to record light levels relevant for specified biological responses. This might be achieved in future by combining longer integration times with cooled sensors for noise suppression.

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

4.2 | Modelling biologically relevant ALAN underwater

In the absence of global underwater ALAN measurements, modelling the distribution of ALAN underwater holds great potential. Radiative transfer models (RTM) are well-established optical oceanographic tools (Mobley, 1994). Resources on how to implement these are openly accessible (https://www.oceanopticsbook.info/). RTMs such as HYDROLIGHT calculate spectral radiance distributions and related quantities for the marine ecosystem of interest (Mobley & Sundman., 2013). Critical are two primary datasets to parameterise RTMs for the desired ecosystem: (a) light measured above water and (b) inherent optical properties (IOPs) that govern light penetration through the water column (see Section 2). The partitioning of IOPs

TABLE 2 Photometric and radiometric measurements of light as typically quantified in artificial light at night research (SI units given in brackets). *The units are analogous but not equivalent*. For conversions, see for instance 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 area and solid angle	Radiance ($W\ m^{-2}\ sr^{-1}$)	Luminance (cd/m^2)

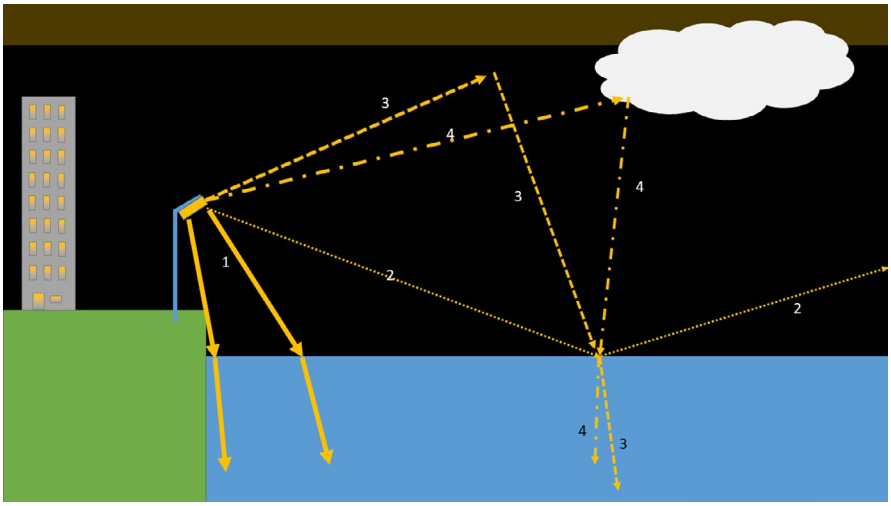

FIGURE 4 Fate of shore-based light following different optical paths. 1. Light emitted close to the vertical and directly incident upon the sea surface is largely transmitted into the water column. 2. Light emitted close to the horizontal will mainly be reflected at the sea surface. 3. and 4. Light directed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

into representative components (absorption by phytoplankton (a_{ph}), coloured dissolved organic matter (CDOM; a_{dy}); backscatter due to particulates (b_{bp})) allows to account for spatiotemporal variations. Obtaining these values in situ improves model accuracy (Werdell et al., 2018).

So far, there are only few studies assessing ALAN prevalence, spatial extent and intensities encountered by marine organisms throughout the water column (Berge et al., 2020; Davies et al., 2020; Ludvigsen et al., 2018). While there are currently no globally derived hyperspectral satellite images of night-time lighting, spectrally explicit global predictions of sea surface radiometric measurements can be derived from empirical relationships between locally measured sea surface radiometry and the Falchi atlas (Falchi et al., 2016). The atlas is derived from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day–Night Band (DNB) sensor on the Suomi National Polar-orbiting Partnership (S-NPP) satellite, has a spatial resolution of 742 m and is sensitive to light in the range 0.5–0.9 μm. This upscaling requires that spectral power distributions and relative contributions of different lighting technologies influencing locally derived sea surface radiometry are quantified or constrained. Implicit in this upscaling is the assumption that ALAN spectra are globally uniform and closely approximate the spectra of local measurements. The second primary datasets, the IOPs, can either be measured locally or derived from monthly global climatologies such as the ESA Ocean Colour Climate Change Initiative (http://www.esa-oceancolour-cci.org/). These two primary datasets can then be used to parametrise spectrally explicit RTMs of ALAN penetration with depth for the desired marine ecosystem using Beer's law (Berge et al., 2020; Davies et al., 2020). To improve output representativity, models can account for tidal fluctuation (Roberts et al., 2018), and meteorological conditions influencing IOPs (Hieronymi & Macke, 2012). Global scale modelling across multiple depths, wavelengths, latitudes and longitudes is likely to be computationally expensive but can be solved reducing the spatial, depth and spectral resolution of models (Davies et al., 2020). A biological approach to understanding spectrally explicit ALAN exposure of marine organisms circumventing these challenges could lie in vision modelling (Cheney et al., 2009; Thoen et al., 2014) which is yet to be applied to ALAN research.

5 | QUANTIFYING ALAN IMPACTS ON MARINE AND COASTAL ECOSYSTEMS

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

5.1 | ALAN experiments

Existing technology allows experimental decoupling of discrete ALAN characteristics by installing different lighting components. Setup complexity varies with research questions and design ranging from ALAN presence/absence, different intensities, photoperiod and spectra, to interference with natural light cycles and timings. If conducted in the laboratory, the latter two setups need to simulate natural light accurately, often over months (Fobert et al., 2019) and sometimes even years (Craggs et al., 2017). Integrating environmental conditions that alter lightscapes and organisms' biology (e.g. moon, tides, clouds) improve real-world settings but add complexity to design and technology.

The vast majority of marine ALAN studies have assessed the presence of direct, high intensity ALAN (Davies et al., 2015; Fobert et al., 2019; O'Connor et al., 2019) which is the most straightforward to simulate. Few studies have mimicked ALAN as low as artificial skyglow integrating dimmers or dimming shields (a freshwater example Franke et al., 2013; the only marine experiment, Torres et al., 2020). Marine organisms' high sensitivity to dim light means to avoid ALAN adapted animals and identify ALAN naïve locations (including artificial skyglow) by using the Falchi map (Falchi et al., 2016) or by

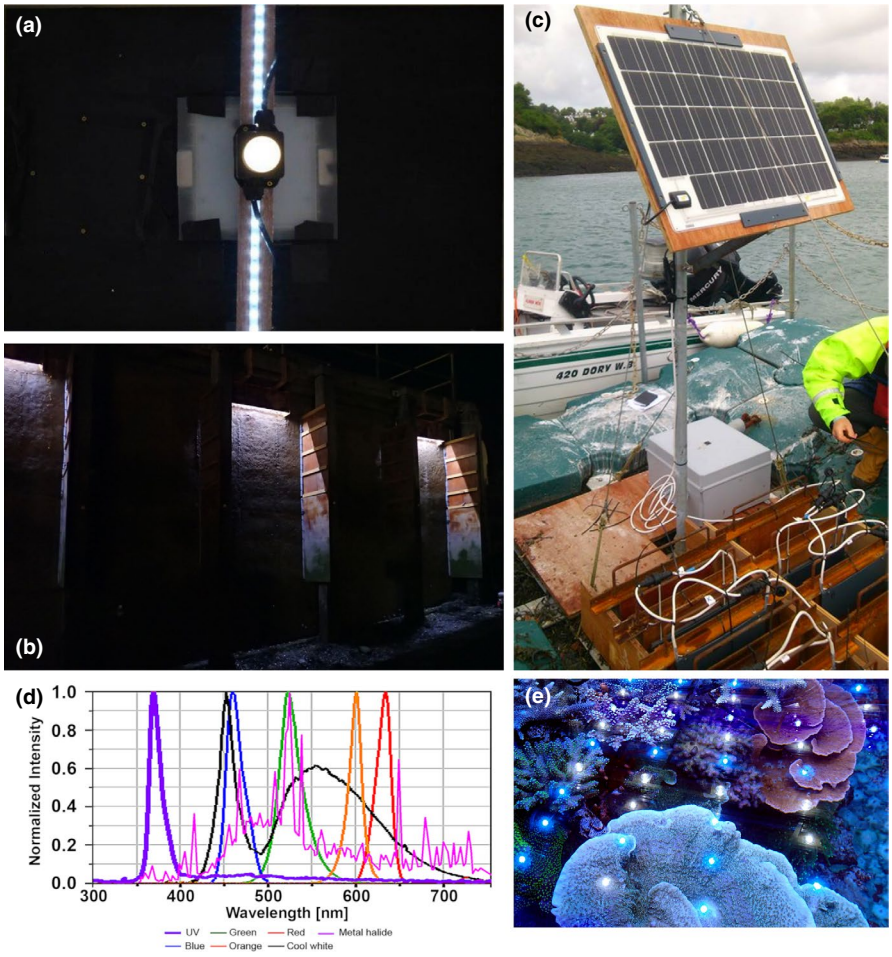

FIGURE 5 Marine artificial light at night (ALAN) experiments. (a) Simulated moonlight (lit sphere), daylight (unlit square) and ALAN (lit bar). Lunar cycles are programed using modelled lunar sky brightness (Figure 2a,b). (b) Varnished plywood prevents light trespassing and animals moving between replicates. (c) IP68 rated waterproof enclosures and connections: a solar trickle charged battery on a pontoon, Menai Strait, UK (Davies et al., 2015). (d) Spectral power distributions of alternative lighting simulations including metal halide lamps (pink), broad spectrum light-emitting diodes (LEDs; black), and narrow spectrum (coloured) LEDs (data Thorlabs, 2020). (e) Without diffusion or distancing, close proximity LEDs create uneven light fields (Photos: authors)

measuring ALAN in situ. While sufficiently sensitive handheld lux metres present an affordable tool to establish light naïve areas and gradients of ALAN intensity, they lack information on spectrally relevant intensities and ALAN underwater. Experimenters need to avoid light trespass (Figure 5b) between exposure and control treatments (Davies et al., 2015; Fobert et al., 2019). Introducing light to record behavioural responses can compromise the control (dark) treatment. (Infra-)Red lighting has proved useful (Ugolini et al., 2016); however, the assumption is that long wavelengths are less detectable by marine organisms.

The widespread occurrence and importance of light-induced rhythmicity in marine ecosystems highlights the potential of ALAN to influence processes on the molecular and cellular level. Analysing rhythmic clock gene expression to infer clock function is well-established in chronobiology and has been described in a range of marine taxa (see below). Defining their expression over a natural light–dark cycle and contrasting these under ALAN is a logical first step and has recently been demonstrated in corals (Rosenberg, Doniger, Harii, et al., 2019). Contrasting gene expression is now readily achieved, even in non-model species, using modern molecular technologies such as transcriptomics (Andreatta & Tessmar-Raible, 2020). Measurable phenotypes related to behaviour, reproduction and growth (for instance Diptera *Clunio marinus* Kaiser et al., 2016; Scleractinia *Acropora millepora* Kaniewska et al., 2015; Amphipoda *Talitrus saltator* Ugolini et al., 2016; Phyllodocida *Platynereis dumerilii* Zantke et al., 2013; Isopoda *Eurydice pulchra* Zhang et al., 2013) are essential to establish the influence of the core oscillatory mechanism. Measuring rhythmic molecular and cellular phenotypes, together with rhythmic behavioural outputs over appropriate temporal scales or at carefully designed time points, represents a robust strategy to advance chronobiology and evaluate ALAN impacts on clock-driven processes at the organismal and population level. A recent study demonstrates marine ALAN affects gene expression related to cell cycle, cell proliferation, cell growth and protein synthesis (Rosenberg, Doniger, Levy, 2019) making cellular biology a novel and promising angle for future research.

Many photobiological responses are driven by distinct wavelengths making spectral sensitivity key to understanding and mitigating ALAN effects (Table S2). LEDs come in a large range of emission colours and narrow-banded spectra (Figure 5d; Boch et al., 2011) enabling to determine organisms' responses to specific spectra. Alternatively, white light sources can be combined with band-pass filters (D'Angelo et al., 2008; Marchesan et al., 2005). Commonly proposed ALAN mitigation strategies include dimming lights, part-time lighting (e.g. only during high demand) and manipulating wavelengths (Gaston et al., 2012). Readily available approaches combine customisable LEDs, narrow band-pass filters and timed photocells. The described attenuation of long wavelengths in seawater

highlights the potential of spectral manipulation for mitigating ALAN impacts on marine ecosystems. Manipulating and reporting ALAN spectral power distribution where possible will yield deeper insights for individual studies and future meta-analyses.

5.2 | Natural light simulations

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

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

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

5.3 | ALAN field studies

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

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

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

6 | SYNTHESIS: CURRENT CHALLENGES AND FUTURE DIRECTIONS OF MARINE ALAN RESEARCH

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

Quantifying the distribution of ALAN (and natural light) underwater is technically challenging yet a prerequisite to inform exposure experiments. Laboratory experiments need to tackle the realistic simulation of natural light regimes focusing on twilight, moonlight and where possible tides and spectrally realistic light fields. Discretely manipulating ALAN characteristics that drive observed changes facilitates better mechanistic understanding and provides empirical understanding for designing mitigation strategies and technologies (Gaston et al., 2012). Contemporary molecular tools can be used to quantify the impact of ALAN on light-influenced gene expression involved in clock regulation (Frøland Steindal & Whitmore, 2019) and other fundamental molecular and cellular processes, offering new avenues for exploring ALAN-induced changes to organism phenology and health. As research systems move offshore and into deeper water, marine ALAN research becomes technically and financially more demanding, not least when it comes to quantifying ALAN exposure underwater in space and time.

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

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AUTHORS' CONTRIBUTIONS

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DATA AVAILABILITY STATEMENT

This manuscript does not contain original data. Data sources for Figure 1 are listed in the supplementary file Fig1_Marine_ALAN_studies.csv.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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