



Coastal urban lighting has ecological consequences for multiple trophic levels under the sea



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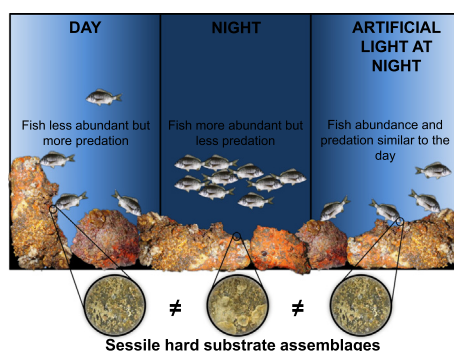
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HIGHLIGHTS

- Artificial light at night (ALAN) influences marine trophic interactions.
- We tested the effect of ALAN on fish behaviour and predation.
- ALAN resulted in higher predation but lower fish abundances than unlit nights.
- Prey assemblages changed accordingly among the experimental lighting treatments.
- Ecological processes in urban marine environments can be altered by ALAN.

GRAPHICAL ABSTRACT



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ABSTRACT

Urban land and seascapes are increasingly exposed to artificial lighting at night (ALAN), which is a significant source of light pollution. A broad range of ecological effects are associated with ALAN, but the changes to ecological processes remain largely unstudied. Predation is a key ecological process that structures assemblages and responds to natural cycles of light and dark. We investigated the effect of ALAN on fish predatory behaviour, and sessile invertebrate prey assemblages. Over 21 days fish and sessile assemblages were exposed to 3 light treatments (Day, Night and ALAN). An array of LED spotlights was installed under a wharf to create the ALAN treatments. We used GoPro cameras to film during the day and ALAN treatments, and a Dual frequency Identification SONar (DIDSON) to film during the night treatments. Fish were most abundant during unlit nights, but were also relatively sedentary. Predatory behaviour was greatest during the day and under ALAN than at night, suggesting that fish are using structures for non-feeding purposes (e.g. shelter) at night, but artificial light dramatically increases their predatory behaviour. Altered predator behaviour corresponded with structural changes to sessile prey assemblages among the experimental lighting treatments. We demonstrate the direct effects of artificial lighting on fish behaviour and the concomitant indirect effects on sessile assemblage structure. Current and future projected use of artificial lights has the potential to significantly affect predator-prey interactions in marine systems by altering habitat use for both predators and prey. However, developments in lighting technology are a promising avenue for mitigation. This is among the first empirical evidence from the marine system on how ALAN can directly alter predation, a fundamental ecosystem process, and have indirect trophic consequences.

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1. Introduction

Daily and seasonal cycles of light and dark are among the most important drivers of ecological processes and interactions (Bradshaw and Holzapfel, 2010; Gaston et al., 2013; Gaston and Bennie, 2014). The introduction of artificial lighting at night (ALAN) is altering these natural cycles, with significant global consequences. The scale of ALAN impacts range from the molecular to entire ecosystems; modifying the behaviour, distribution, and abundance of species (Rich and Longcore, 2006; Gaston et al., 2013; Gaston and Bennie, 2014; Gaston et al., 2014). Moreover, the spatial extent of ALAN has nearly doubled in the last two decades, and this rate is predicted to increase (Minnaar et al., 2015). Although concerns about ALAN are not new (Holden, 1992), the potential for ecological impacts is outpacing related research (Davies et al., 2012). Furthermore, the implications of ALAN for many ecological systems, such as subtidal marine systems, are largely overlooked by researchers and managers alike (Davies et al., 2014). To gain a more holistic understanding of the ecological impacts stemming from ALAN, we need a range of detailed studies including experimental field-based manipulations that can substantiate observations and lab-based experiments.

ALAN can affect ecological processes such as predation, competition and habitat use, by altering the time organisms spend on activities such as foraging, hiding, and resting (Kronfeld-Schor and Dayan, 2003; Gutman and Dayan, 2005; Bennie et al., 2014). As ALAN changes the time available for such activities, evolutionary relationships between predators and prey may be affected (Minnaar et al., 2015). For many nocturnal species, darkness is critical for access to food and mates under reduced levels of competition and predation, but ALAN decreases this resource (Duffy et al., 2015). Furthermore, the reduction of naturally dark space may mean a loss of refuge for species that use this resource to rest and recover (Vollnes et al., 2009; Bradshaw and Holzapfel, 2010; Gaston et al., 2013).

With the expansion of urban centres, lit infrastructure, and advances in lighting technology the impacts of ALAN are extensive, potentially ranging from the source for up to hundreds of kilometres (Gaston et al., 2014; Luginbuhl et al., 2014). Night sky brightness in Hong Kong (an urban coastal area), for instance, has been recorded above 500 times brighter than rural equivalents (Pun and So, 2012). These findings suggest that light scenarios far beyond what are common to urban coasts are not only possible, but are currently reached and may be exceeded in the future. In a recent global study, Duffy et al. (2015) found that the majority of terrestrial mammalian species, most of which are nocturnal, are increasingly affected by higher than normal light intensities. Nocturnal mice (Rotics et al., 2011) and small rainforest mammals (Bengsen et al., 2010) have been shown to forage less in the presence of ALAN, which is attributed to a perceived increase in predation risk. Conversely, diurnal and crepuscular species can extend foraging times with ALAN, particularly insectivores that feed on insects attracted to lights (Lacoeuilhe et al., 2014; Minnaar et al., 2015; Russ et al., 2015). Impacts to terrestrial systems are immediately apparent due to their proximity of light sources (Gaston et al., 2014), but marine ecosystems are not immune.

Sixty percent of the world's largest cities are within 100 km of the coast (Tibbetts, 2002; Small and Nicholls, 2003) and >20% of the world's coastlines experience ALAN above normal levels (Davies et al., 2014) - a rate predicted to increase by 6% per year (Hölker et al., 2010). Industrial port facilities are among the brightest lit coastal infrastructures, often lit 24 h for safety reasons, with some areas reaching 210 lx - 4 times over the Australian/New Zealand Standard (AS/NZS 1680.2.4) (1997) recommendation (GHD, 2012). Advances in lighting technology are also contributing to the growing impact of ALAN. The implementation of more efficient lighting is rising as pressure is applied to municipalities to reduce carbon footprints. Although light emitting diodes (LEDs) are more cost effective than traditional lighting, their ecological impacts are considered greater (Gaston et al., 2012; Dick, 2013). LEDs emit a

broader spectrum (white) light with peaks in the blue and green wavelengths (Elvidge et al., 2010), which are attenuated at greater depths. In the marine environment, urban lighting has been shown to increase predator access to nocturnally foraging prey, as their ability to detect prey is enhanced (Mazur and Beauchamp, 2006). Since even subtle changes to variation in natural light (e.g. the difference between a full and new moon) can affect marine organisms (Luecke and Wurtsbaugh, 1993), it is reasonable to expect significant impacts of ALAN on these systems.

ALAN can increase predation both by improving the vision of predators, and increasing the attraction of prey to light (Davies et al., 2014; Gaston et al., 2014). Similar to the attraction of insects to street lights (Perkin et al., 2014), small schooling bait fish can be attracted to ALAN, leading to increased local abundances of large piscivorous fish (Becker et al., 2013). Thus, the influence of ALAN on both predator and prey behaviour makes it difficult to estimate how impacted food webs may be altered (Gaston et al., 2014). Sessile invertebrates are a major component of nearshore food webs, contributing important ecological services such as water filtration and food resources (Barbier et al., 2011). While some mobile prey can actively avoid lit areas, the effects of ALAN on sessile assemblages are relatively unknown. A number of fish species consume sessile invertebrates (Keough, 1984; Connell and Anderson, 1999) and are visual predators (Guthrie, 1986), but experimental manipulations of ALAN are needed to understand the direct and indirect consequences of ALAN for different trophic levels.

While awareness of the potential ecological impacts from ALAN is growing, there remains a lack of empirical information on its effects within the marine environment, and particularly to ecological processes. Although, it is difficult to observe animal behaviour at night without introducing artefacts, particularly in aquatic environments, new technology has come a long way towards overcoming these limitations. Equipment such as acoustic cameras now allow near video quality footage based on sound to be captured in zero light environments (Becker et al., 2013).

Here we experimentally tested the effect of ALAN on fish behaviour and predation using acoustic cameras and underwater video, and concurrently tested for changes to sessile invertebrate prey assemblages when exposed to fish predators. We hypothesised that the addition of ALAN would increase fish activity at night, specifically predatory behaviour, and would consequently reduce cover of sessile invertebrates and alter assemblage structure. This is the first empirical evidence from the marine system on how ALAN can directly alter fish behaviour and have indirect trophic consequences through predation.

2. Materials and methods

2.1. Study design

To test for direct effects of ALAN on fish behaviour, and how this might affect sessile invertebrate assemblages, we manipulated light environments under a wharf in Sydney Harbour (33°50'22"S, 151°15'17"E). Light environment treatments were 'Day', 'Night', and 'ALAN'. Artificial lighting was provided by ten 4050 lm, warm light, LED spotlights, installed under the wharf and angled 45° below horizontal. This level of artificial light, while not currently found at this particular location, is similar or lower than ALAN recorded in other urban coastal cities and port facilities (Pun and So, 2012; GHD, 2012). LEDs produce efficient near-white light, and are increasingly popular for commercial and street lighting. Spotlights were mounted on the bearers supporting the joists and wharf decking, positioned at least 1 m above the high-water mark (see Fig. S1, Supporting information). Light intensities were measured for each light treatment using a Skye SpectroSense 2 light meter, positioned at the same depth as the sessile invertebrate communities.

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