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

D. Bolton [a], M. Mayer-Pinto [a,b,*], G.F. Clark [a], K.A. Dafforn [a,b], W.A. Brassil [a], A. Becker [c], E.L. Johnston [a,b]

[a] Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia
[b] Sydney Institute of Marine Sciences, Mosman, NSW 2088, Australia
[c] NSW Department of Primary Industries, Port Stephens Fisheries Institute, Taylors Beach, NSW, Australia

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
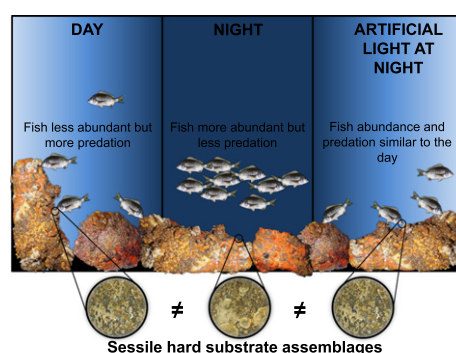
ARTICLE INFO

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.

---

* Corresponding author at: Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia.
E-mail address: m.mayerpinto@unsw.edu.au (M. Mayer-Pinto).

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 (Vollsnes 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 SpectroSence 2 light meter, positioned at the same depth as the sessile invertebrate communities.

The LED spotlights produced a Lux significantly greater than levels measured from unlit nights (i.e. sky glow only) and over half as much of a day (Day > Light > Night; Table 1).

2.2. Fish behavioural changes in response to ALAN

We used a Dual frequency IDentification SONar (DIDSON 300) unit to observe fish abundance and behaviour in the absence of light. The DIDSON uses multi-beam sonar to create video-like footage of objects in low visibility water. The DIDSON was attached to a bottom-weighted vertical metal stand, and positioned on the seabed 5–8 m away from the sessile invertebrate assemblages. The sonar beams were angled slightly below horizontal, aimed at the sessile invertebrate assemblages while avoiding digging them into the substrate (Maxwell and Smith, 2007). The DIDSON was run for 21 days in high-frequency mode (1.8 MHz) with a window length of 10 m, collecting two replicates for each light treatment.

DIDSON footage was manually processed using the Soundmetrics DIDSON software V5.25.24. Each 11.5 h filming period was further divided into blocks of 15 min, and the relative abundance of fish was calculated using the MaxN method (Cappo et al., 2004). Using 15 min blocks to capture the change in relative abundance over a long time period avoids misleading data, where the area captured on film may be devoid of fish except for a single passage of a large school of fish (Becker et al., 2013). DIDSON footage did not allow counting of fish bites (mouth contact with settlement plate), as the acoustic shadows of the fish blended with the acoustic shadows of the units. DIDSON data was therefore used only to assess fish abundance and observe general behaviour.

The DIDSON software includes a tool to measure total length (TL) of individual fish, allowing MaxN to be recorded for three size classes of fish: small (<20 cm TL), medium (20–40 cm TL), and large (>40 cm TL). During the first day treatment, a GoPro camera was attached to the DIDSON to simultaneously observe fish on video and the DIDSON. We chose size classes based on the most common fish species observed. Fish in the small size class were most commonly Yellowtail Scad (*Trachurus novaezelandiae*), which are a planktivorous species. The medium size class was dominated by leatherjackets (Monocanthidae spp.) and Yellowfin Bream (*Acanthopagrus australis*); two species observed feeding on sessile invertebrate communities. Also included in the medium size class were; Luderick (*Girella tricuspidata*), Red Morwong (*Cheilodactylus fuscus*), and Wrasses (Labridae spp.). Fish in the over 40 cm size class were most commonly Flutemouth (*Fistularia petimba*), which feed almost exclusively on small fish (<5 cm TL), or Silver trevally (*Pseudocaranx georgianus*), which feed on benthic invertebrates and crustaceans. Fish under 5 cm were excluded as they could not be accurately observed.

2.3. Fish predation on sessile invertebrates under ALAN

To investigate changes in fish predation in response to ALAN, we exposed sessile invertebrate assemblages to predation during different light environment treatments, and quantified bite rates and fish

Table 1
The variation in Lux measured for each of the lighting treatments using a Skye SpectroSence 2 light meter. Light measurements were taken at the same depth as the experimental assemblages under Chowder Bay wharf.

Lighting treatment	Lux	Paired *t*-tests
Day (D)	256 ± 6.73	D > N; P < 0.001
Night (N)	0.137 ± 0.016	L > N; P = 0.003
ALAN (L)	158.9 ± 13.18	D > L; P = 0.002
Port loading conveyor at night[a]	210	
Urban sky glow[b] (clear - overcast)	0.015–0.15	
Clear night sky[b] (full moon)	0.1–0.3	
Clear to overcast night sky[b] (new moon)	0.001–0.0001	

[a] Abbot Point Coal Terminal Environmental Impact Assessment (GHD, 2012).
[b] Comparative light measurements from Gaston et al. (2013).

identities with underwater cameras. Sessile assemblages were initially collected on 90 individual settlement plates (110 × 110 mm roughened black Perspex; hereafter 'plates') deployed at 5 m depth in Sydney Harbour. Plates were evenly distributed on vertically-oriented steel reinforcing mesh (100 × 100 mm grid) frames and deployed for 12 weeks from February to May 2014. During colonisation, plates were caged using 15 mm plastic mesh to prevent fish predation. Cages were cleaned every 4 weeks to maintain flow (Connell, 1997). After 12 weeks, the plates were transferred to steel reinforcing mesh (100 × 100 mm grid) units (800 × 800 mm; hereafter 'units') suspended at 2 m depth (at mean low tide) underneath the wharf.

Plates were randomly assigned to light environment (day, night or with ALAN) and predation (caged or uncaged) treatments. Half the plates remained caged throughout the experiment (to control for the effects of predation) and the other half were exposed to predation (uncaged) during allocated light environment treatments, but were caged during other periods. Specifically, each predation exposure consisted of two 11.5 h periods of uncaging. Day treatments exposed to predation were uncaged after sunrise and re-caged before sunset, while night and ALAN treatments exposed to predation were uncaged after sunset and re-caged before sunrise. Three exposures per light environment treatment of 7 replicate predation treatments were randomly allocated over 21 days with at least 12 h between consecutive exposures. An additional six plates were deployed on the third day of predation exposure, and were partially caged to test for caging artefacts (procedural cage controls) (Connell, 1997).

Plates were photographed before and after each treatment and then preserved in 10% formaldehyde, buffered in seawater. Caged plates were returned to the water after being photographed. Sessile assemblage data were recorded using Coral Point Count (CPCe) software under a fixed 100-point grid overlaying the plate. Taxa occurring under each point were identified to the lowest possible taxonomic level, given a count of 1% and clustered as taxonomic groups for further analysis. If photo quality prevented classification, plates were examined under a dissecting microscope.

A GoPro® camera (Hero 3 + Black) with a battery backpack was attached to each unit on a PVC pipe (500 mm length of 20 mm PVC) and angled towards the settlement plates (see Sup. 1). GoPro cameras were used to film fish during the day and the ALAN treatments from the beginning of exposure until the batteries ran out (approx. 3 h). From this footage, fish species and number of bites were recorded across 3 replicate day exposures (126 h).

2.4. Data analysis

2.4.1. Fish abundance

General additive mixed models (GAMMs) were used to analyse fish abundance in light environment treatments over time. GAMMs are useful for modelling non-linear data using non-parametric smoothers over temporal or spatial measures (Mackenzie and Schiedek, 2007). Cubic spline smoothers were applied to time, and Gaussian distribution was used (rather than a count distribution like Poisson) as it was a better model for the mean variance relationship based on residual analysis. We fitted GAMMs and calculated likelihood ratio tests and, after allowing for trends within day and night, tested for an effect of the light environment treatments.

2.4.2. Fish predation on sessile invertebrates

The loss (or gain) in percentage cover of sessile invertebrates was calculated by subtracting the cover of each taxon before exposure to predation from counts after exposure. Total predation was calculated by adding the percent change for each taxonomic group in each plate from each treatment.

Six randomly selected uncaged plates were compared against 6 partially caged plates to test for caging artefacts. A single factor multivariate ANOVA was performed for the factor of predation (Fixed with 2 levels;

Table 2
Mean estimates and significance values for pair-wise comparisons of fish abundance in response to light environment treatments.

Contrasts	Overall fish abundance		Small fish (<20 cm TL)		Medium fish (20–40 cm TL)		Large fish (>40 cm TL)	
	Est.	P	Est.	P	Est.	P	Est.	P
ALAN – day	−15.287	P < 0.001	−3.575	P < 0.001	−12.266	P < 0.001	0.532	P = 0.095
Night – day	16.585	P < 0.001	−14.447	P < 0.001	33.468	P < 0.001	−2.330	P < 0.001
ALAN – night	−31.872	P < 0.001	10.872	P < 0.001	−45.734	P < 0.001	2.862	P < 0.001

uncaged and partial cage). There were no significant artefact effects, so further analyses to identify light environment effects on predation were done using only the caged and uncaged treatments.

A univariate ANOVA was done to examine the effects of light environment (Fixed with 3 levels; day, night and ALAN), predation (Fixed with 2 levels; uncaged and caged) and time (Random, nested in lighting with 3 levels; replicate 1, 2 and 3) on total predation. Data were untransformed and Euclidean distance was used to construct similarity matrices. Interaction terms in the ANOVA were pooled when non-significant (P > 0.25) to increase the power of analyses (Underwood, 1981).

Multivariate analyses were done on square-root transformed data and Bray-Curtis dissimilarity matrices to calculate differences in the final assemblage structure (i.e. after predation) among light environment treatments (Anderson et al., 2008).

Post-hoc pairwise comparisons were run on all pairs of light environment treatment levels for uncaged plates for total predation and total assemblage. A canonical analysis of principal coordinates (CAP) was used to visualise the changes in assemblage structure with the data constrained to the main effects. Variance heterogeneity was examined using PERMDISP (Anderson et al., 2008). All statistical analyses on sessile assemblage data were done using Primer v.6 and PERMANOVA plus v.1 software.

3. Results

3.1. Fish abundance

Light environment treatments had a significant effect on fish abundance patterns with the exception of large fish which were equally abundant during day and ALAN treatments (Table 2; Fig. 1).

These abundance patterns suggest significant changes in fish behaviour in response to ALAN. In night treatments, relative abundances of fish increased after sunset, from one or two fish to approximately 60 to 90 individuals by midnight, decreasing again from 3 am (Fig. 1). Changes in fish abundances at night were mainly explained by patterns for medium sized fish (Fig. 2B). However, these fish were more sedentary at night than during the day or ALAN treatments (per. obs.). In contrast, fish swam more rapidly during the day and when exposed to the ALAN treatments (Pers. obs.), similar to behaviour observed by Becker et al. (2013). Patterns of fish abundance during night treatments differed from those in the ALAN treatments. During ALAN, abundances of all fish remained similar to daytime levels during most of the night, though there was an apparent increase in activity under the wharf (from 4 am) before sunrise (Fig. 1). The increased activity at 4 am in the ALAN treatments can be mainly attributed to small fish (Fig. 2A). Large fish were found in low abundances under all light environment treatments (Fig. 2C).

3.2. Fish predation and trophic changes in response to ALAN

Sessile assemblages that were uncaged during the day and those uncaged at night and exposed to artificial light showed a significant reduction in total cover of organisms when compared to the uncaged assemblages from the night treatments and the caged assemblages (Fig. 3A; Table 3A). Uncaged assemblages from the night treatment had very little predation (<10% reduction in cover), and remained similar to caged assemblages from all light environment treatments (Fig. 3A; Table 3A).
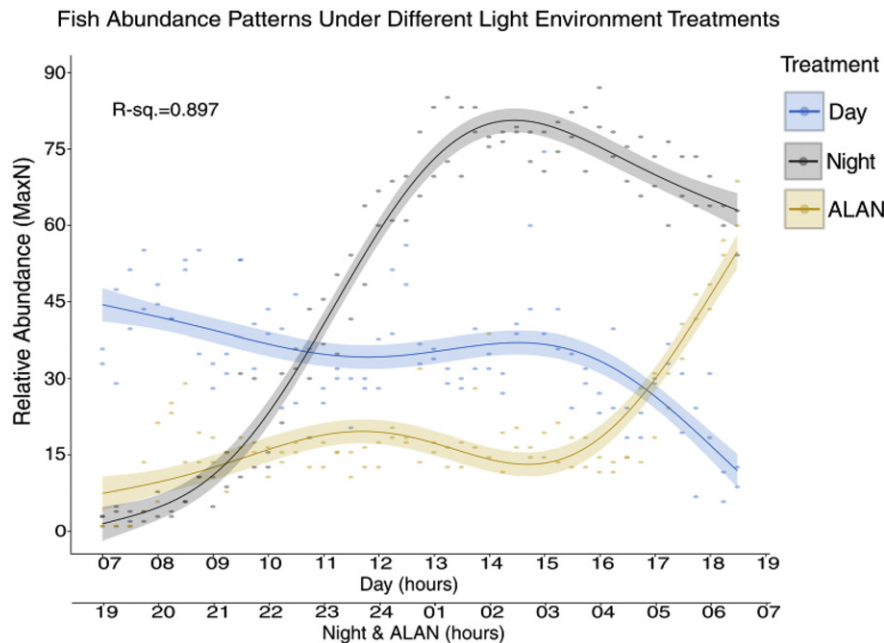
Fig. 1. Observed fish abundances (MaxN) per 15 min block with fitted GAMM models over an 11.5 h period between light environment treatments (from 7 am to 6:30 pm for day treatments and from 7 pm to 6:30 am for the night and ALAN treatments).
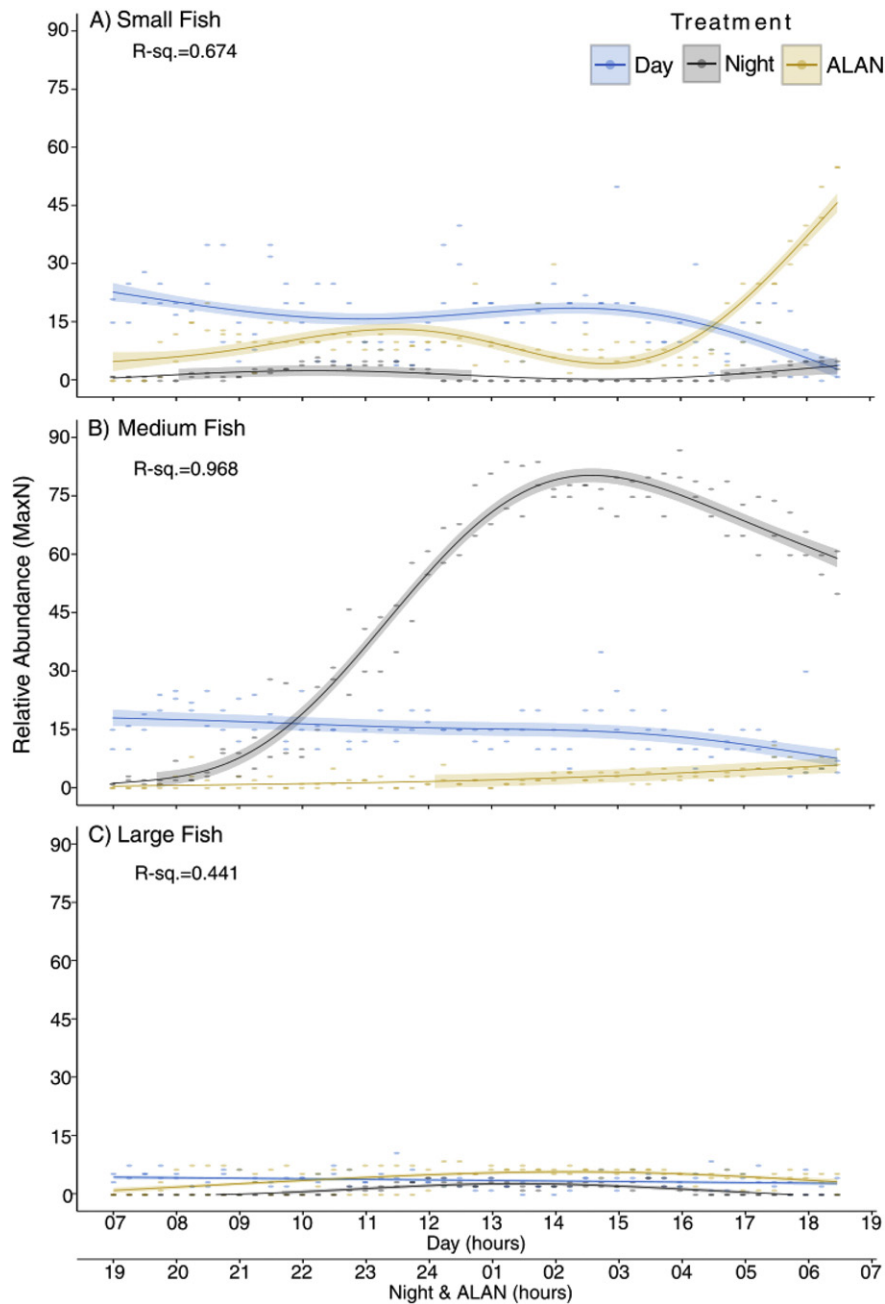
Fig. 2. Observed fish abundances (MaxN) per 15 min block with fitted GAMM models over an 11.5 h period (from 7 am to 6:30 pm for day and from 7 pm to 6:30 am for night and ALAN treatments) for A) small fish; B) medium fish; and C) large fish.

Fish predation also resulted in structurally different sessile assemblages between the light environment treatments (Fig. 3B; Table 3B). Sessile assemblages from day and ALAN treatments exposed to predation (uncaged) were similar to each other and significantly different from the caged assemblages. Sessile assemblages from night treatments (no artificial light), however, did not differ between predation exposure (i.e. caged vs uncaged plates).

Most predation on sessile invertebrate communities was observed during day treatments (Fig. 4). Medium sized fish (20–40 cm TL), including leatherjackets (Monocanthidae spp.) and Yellowfin Bream (*Acanthopagrus australis*) were observed to be the main predators of sessile invertebrates. These two families have been observed foraging on sessile invertebrates in previous studies (Fig. 1; Bolton et al., unpublished data). Less predation was captured on the GoPro video footage from the ALAN treatment, but a small number of Yellowfin Bream (n = 2) were recorded foraging. In addition, squid

(Cephalopoda) were only observed under the wharf during the ALAN treatment and not in the day or night treatments. Squid presence may influence fish abundances and behaviour.

4. Discussion

To our knowledge, this study is the first to empirically demonstrate that ALAN affects fish behaviour and predation, with significant consequences for sessile marine assemblages. We showed that predation during artificially lit nights is greater than on dark nights, and resembles the levels of daytime predation. The addition of artificial light at night also changed fish abundance and habitat use. Fish were more abundant during natural dark nights than in other treatments. These results have significant implications for the structuring of trophic webs in urban marine systems, potentially leading to altered functioning and consequences for ecosystem services.
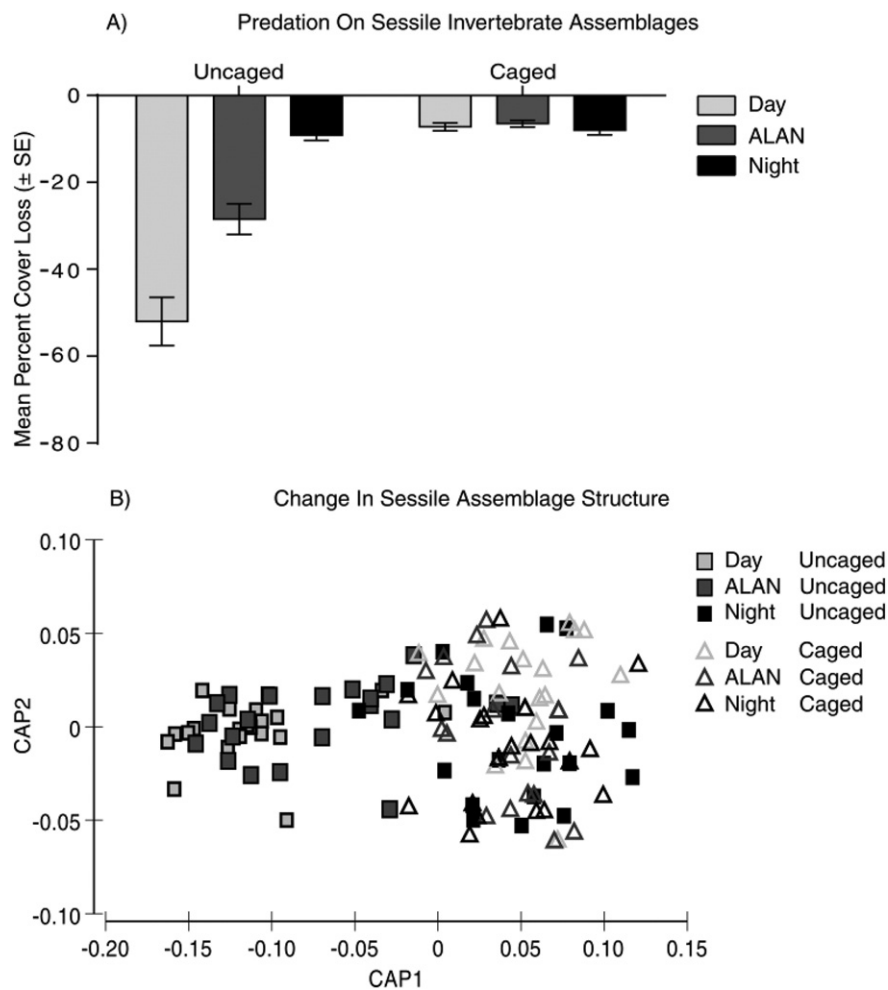
Fig. 3. A) The mean change of total percentage cover (±SE) of all taxa from uncaged and caged light environment treatments. B) Canonical analysis of principle coordinates (CAP) showing the similarities between sessile assemblage structure from uncaged and caged light environment treatments.

4.1. Altered predation and habitat use

We observed more medium size predatory fish (e.g. Yellowfin Bream and Leatherjacks) under the wharf on natural dark nights, but this did not correspond with increased predation on the sessile invertebrate assemblages. Fish on dark nights were more sedentary than those during the day and under artificial light. These observations suggest that fish were using the structure provided by the wharf and our experiment as habitat (e.g. for shelter) during dark nights. They were using the wharf and the structures as feeding grounds during the day and on artificially lit nights. In a recent study, Taylor et al. (2013) found Yellowfin Bream activity was closely tied to diel cycles, being lowest during the

Table 3

A) Univariate analysis of variance of change in total percentage cover of organisms. Light environment (Li) and predation (Pr) are fixed with 3 and 2 levels respectively. Time (Ti) is random and nested within light environment. Pr x Ti (Li) was pooled (P > 0.25) to increase power of detecting main effects. B) Multivariate analysis of variance of the sessile assemblages among treatments. Same statistical design as the univariate analysis however using Bray-Curtis distance measures for dissimilarity matrix rather than Euclidean. Bold values represent P < 0.05. Posthoc pairwise tests were performed to identify the Li effect within uncaged sessile assemblages. Monte Carlo P-values P(MC) were used on the pairwise tests due to low number of unique permutations (Anderson et al., 2008).

A) Main test: total change in percentage cover					B) Main test: changes in assemblage structure		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Light environment	2	4687	6.078	**0.029**	8946	5.476	**0.011**
Predation	1	16,139	120.5	**<0.001**	21,119	9.131	**0.000**
Time (Li)	6	771	5.759	**<0.001**	1634	0.706	0.845
Li × Pr	2	5019	37.48	**<0.001**	6463	2.794	**0.004**
Pr × Ti (Li) pooled	114	134			2313		
Total	125						
Pair-wise test							

Li within uncaged		t	P(MC)			t	P(MC)
Day = ALAN		1.72	0.160			1.14	0.318
Day ≠ night		3.38	**0.027**			3.15	**0.001**
ALAN ≠ night		2.04	**0.020**			3.40	**0.027**
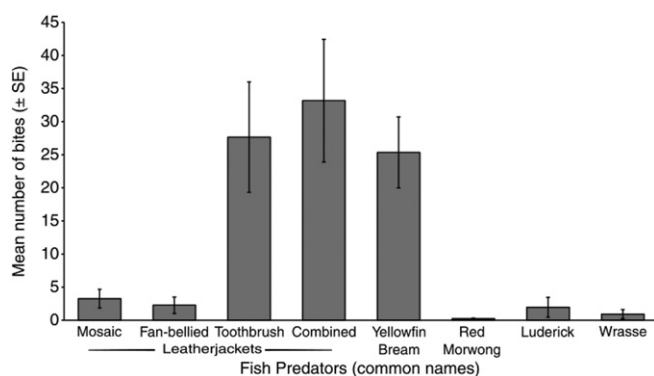
Fig. 4. The mean (± SE) number of bites on sessile invertebrate assemblages by all the fish species identified across 3 replicate day exposures.

night and highest during the day. Becker et al. (2013) also found that fish in this size class displayed an increase in 'slow meandering' behaviour during natural darkness. Increased illumination causes some fish to migrate to deeper habitats, or to seek dark space as a refuge from potential predators (Luecke and Wurtsbaugh, 1993; Rechencq et al., 2011). Here, the abundance of predators was markedly reduced under artificial lighting, suggesting that either artificial light makes this habitat unsuitable for standard night-time activities, and/or it makes the fish feel (Preisser et al., 2005) or actually be, more vulnerable to predation. Interestingly, there was significantly more evidence of fish predation on the sessile assemblages under artificial lighting than during the natural dark night. So, while the addition of light reduces the abundance of the potential predators identified in this study, sessile assemblages were *more* likely to be heavily preyed upon.

Squid were observed on the GoPro videos during the ALAN treatments, but were completely absent from day and night footage (pers. obs). Artificial light is often used to attract squid in commercial fisheries (Kiyofuji and Saitoh, 2004). Cephalopods are visual predators with the most advanced eye sight of all marine invertebrates (Smith, 2009), thus their predation success may be enhanced with the addition of light. Further, it is possible that squid preyed on the medium sized fish (20–40 cm), leading to the observed reduction of fish within this size class under ALAN. There was also a rapid increase in the abundance of small fish during the predawn crepuscular period under ALAN conditions, suggesting some benefit for these fish. This size class of fish includes species that feed primarily on plankton (*T. novaezelandiae*), thus these results might be directly related to changes in zooplankton densities caused by the artificial lights (Navarro-Barranco and Hughes, 2015).

4.2. Consequences of altered predator behaviour

Organisms partition time according to their biological and physiological needs, such as the need to balance energy consumption and use, maximise predation success, and to reduce predation risk (Bennie et al., 2014). Change in habitat use caused by the reduction of dark space suggests that fish might be switching their daily cycles (i.e. doing 'daytime activities') during artificially lit nights. This has been previously observed in snakes and lizards (Henderson and Powell, 2009); jumping spiders (Frank, 2009); and many bird species (Santos et al., 2010; Russ et al., 2015). DIDSON data suggests that predator abundance, when exposed to ALAN, is highest in the predawn crepuscular period (from 3:30 am onwards). This may indicate that fish are foraging earlier when there is ALAN, as fish were observed to start foraging from 7 am during the daytime. Urban blackbirds, which are normally diurnal, were seen to extend their foraging time into the night when ALAN was present (Russ et al., 2015). The increase in light resources for visual predators provides an obvious advantage to gain more food resources. However, extended foraging time carries a cost of foraging (predation

risk and energy expenditure) (Brown and Kotler, 2004). Often, time spent not actively feeding is used for other physiological needs, such as rest and recovery, and is thus vital to maintain body condition (Siegel, 2005). Therefore, the energy cost associated with actively foraging instead of resting and recovering may not be compensated by gaining extra food resources. Russ et al. (2015) found that increased foraging time did not correlate with increased body condition in urban blackbirds, suggesting their altered behaviour was triggered by their circadian clocks. If fish are extending their foraging time under ALAN, information on body condition would be useful to gauge the cost/benefit of this altered behaviour.

4.3. Influence on prey community structure

Changes in predator behaviour and habitat use by ALAN can indirectly affect prey assemblages. During day times, predation pressure on sessile invertebrates was high, with assemblage structure being significantly altered when exposed to predation. At night, predation pressure was markedly lower, with no differences between assemblages exposed to or protected from predation. The addition of ALAN caused an increase in predation pressure on sessile invertebrate assemblages, consequently altering their structure, so they became more similar to assemblages exposed to predation during day time than those exposed to predation at night. Natural darkness is an ecologically important time for sessile assemblages to perform essential activities, such as spawning, settlement and feeding, under reduced predation pressure (Brierley, 2014; Davies et al., 2015). Feeding can reduce an animals ability to remain undetected, thus making them more vulnerable to predation (Bednekoff, 2007). Sessile invertebrates by their very nature cannot move to avoid predation and so must undertake other strategies like actively settling in refuges to increase survival (Walters and Wethey, 1996). Since some filter feeders are conspicuous when they are feeding, because they emerge or extend part of their body, (Troscianko et al., 2009), predation risk by visual predators is lower during dark nights. Therefore, it is likely this is the period when many organisms, e.g. corals, feed (Sebens et al., 1996) or spawn (Babcock et al., 1986) to take advantage of reduced predation pressure. Thus, dark night-time may be a refuge for sessile prey assemblages to perform crucial activities much in the same way as it is for mobile prey.

4.4. The urban marine environment

The urban marine environment is subject to multiple stressors, that can in combination have severe implications for the functioning of these systems (Johnston et al., 2015). One of the most common stressors in urban areas is the modification of habitats, which includes the introduction of artificial structures (Dafforn et al., 2015). Since the use of ALAN is often associated with artificial structures, e.g. marinas, additive or synergistic effects are likely in urban coastal systems. Marine infrastructure such as pilings provides a unique habitat that supports different ecological assemblages from natural rocky shores or soft-sediments. These structures are usually characterized by reduced diversity and increased abundances of opportunistic and non-indigenous species (Glasby and Connell, 1999). Increased predation on sessile organisms due to ALAN could affect the invasibility of these structures, by either removing indigenous species and providing more space for NIS to establish or by removing NIS and increasing the biotic resistance to invasion (Clark and Johnston, 2009).

The use of LED lighting is likely to increase given the efficiency, low cost and versatility of this technology (Gaston et al., 2012). Even low levels of ALAN have been shown to influence ecological processes (Cohen et al., 2010; Rotics et al., 2011), and many studies recommend maintaining natural dark space as the best option for management (Gaston et al., 2012). Unfortunately, this course of action is likely to be problematic as it clashes with other social and economic objectives requiring ALAN (Gaston et al., 2012). Technological advances in LEDs

(Schubert and Kim, 2005), that would allow greater control over the light intensities and wavelengths emitted, may provide greater success in mitigating the ecological impacts of ALAN (Gaston et al., 2012). The use of wavelengths in the marine environment that attenuate quickly, such as in the red band, might be a way forward for nearshore lighting (Dick, 2013). This is especially pertinent given the high demand on coastal property for recreation, high profile housing and industry.

5. Conclusion

We have shown the addition of light to an otherwise dark system causes significant changes in fish behaviour and habitat use, with flow-on effects to lower trophic levels. The abundance of predatory fish was lower during the day and under ALAN, however their behaviour was more predatory than during dark nights. This behaviour corresponded with changes to prey assemblages among the experimental lighting treatments. Darkness during a natural night offers assemblages of sessile invertebrates protection from predation, but ALAN creates day-like foraging opportunities for predators. Current increases in ALAN could therefore lead to drastically altered ecosystems, as more areas of natural darkness become lit. Understanding the influence of ALAN on the ecology of marine organisms will enhance our capability for building protection measures into future developments, establish safe levels, as well as remediating current lighting strategies to minimise impacts.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.10.037.

References

1680.2.4, A. N. Australian/New Zealand Standard, 1997. AS/NZS 1680 Part 2.4: Interior Lighting - Industrial Tasks and Processes.
Anderson, M.J., Gorley, R.N., Clarke, R.K., 2008. Permanova+ for Primer: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.
Babcock, R.C., Bull, G.D., Harrison, P.L., Heyward, A.J., Oliver, J.K., Wallace, C.C., Willis, B.L., 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Mar. Biol. 90, 379–394.
Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81, 169–193.
Becker, A., Whitfield, A.K., Cowley, P.D., Järnegren, J., Næsje, T.F., 2013. Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. J. Appl. Ecol. 50, 43–50.
Bednekoff, P.A., 2007. Foraging in the face of danger. In: Stephens, D.W., Brown, J.S., Ydenberg, R.C. (Eds.), Foraging: Behavior and Ecology. University of Chicago Press, pp. 305–329.
Bengsen, A.J., Leung, L.K.P., Lapidge, S.J., Gordon, I.J., 2010. Artificial illumination reduces bait-take by small rainforest mammals. Appl. Anim. Behav. Sci. 127, 66–72.
Bennie, J.J., Duffy, J.P., Inger, R., Gaston, K.J., 2014. Biogeography of time partitioning in mammals. Proc. Natl. Acad. Sci. U. S. A. 111, 13727–13732.
Bolton, D. K., G. F. Clark, M. A. Coleman, and E. L. Johnston. Unpublished data. Caught between a rock and a hard place: fish predation and crevice width explain subtidal sessile community structure.
Bradshaw, W.E., Holzapfel, C.M., 2010. Light, time, and the physiology of biotic response to rapid climate change in animals. Annu. Rev. Physiol. 72, 147–166.
Brierley, A.S., 2014. Diel vertical migration. Curr. Biol. 24, R1074–R1076.
Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. Ecol. Lett. 7, 999–1014.
Cappo, M., Speare, P., De'ath, G., 2004. Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. J. Exp. Mar. Biol. Ecol. 302, 123–152.
Clark, G.F., Johnston, E.L., 2009. Propagule pressure and disturbance interact to overcome biotic resistance of marine invertebrate communities. Oikos 118, 1679–1686.
Cohen, R., Smale, L., Kronfeld-Schor, N., 2010. Masking and temporal niche switches in spiny mice. J. Biol. Rhythm. 25, 47–52.
Connell, S.D., 1997. Exclusion of predatory fish on a coral reef: the anticipation, preemption and evaluation of some caging artefacts. J. Exp. Mar. Biol. Ecol. 213, 181–198.

Connell, S.D., Anderson, M.J., 1999. Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. J. Exp. Mar. Biol. Ecol. 241, 15–29.
Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L., 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. Front. Ecol. Environ. 13, 82–90.
Davies, T.W., Bennie, J., Gaston, K.J., 2012. Street lighting changes the composition of invertebrate communities. Biol. Lett. 8 (5), 764–767.
Davies, T.W., Duffy, J.P., Bennie, J., Gaston, K.J., 2014. The nature, extent, and ecological implications of marine light pollution. Front. Ecol. Environ. 12, 347–355.
Davies, T.W., Coleman, M., Griffith, K.M., Jenkins, S.R., 2015. Night-time lighting alters the composition of marine epifaunal communities. Biol. Lett. 11.
Dick, R., 2013. Royal Astronomical Society of Canada: Guidelines for Outdoor Lighting in Nocturnal Preserves (RASC-NP-GOL).
Duffy, J.P., Bennie, J., Duran, A.P., Gaston, K.J., 2015. Mammalian ranges are experiencing erosion of natural darkness. Scientific Reports 5.
Elvidge, C.D., Keith, D.M., Tuttle, B.T., Baugh, K.E., 2010. Spectral identification of lighting type and character. Sensors 10, 3961–3988.
Frank, K.D., 2009. Exploitation of artificial light at night by a diurnal jumping spider. Peckhamia 78, 1–3.
Gaston, K.J., Bennie, J., 2014. Demographic effects of artificial nighttime lighting on animal populations. Environ. Rev. 22, 323–330.
Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. REVIEW: reducing the ecological consequences of night-time light pollution: options and developments. J. Appl. Ecol. 49, 1256–1266.
Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biol. Rev. 88, 912–927.
Gaston, K.J., Duffy, J.P., Gaston, S., Bennie, J., Davies, T.W., 2014. Human alteration of natural light cycles: causes and ecological consequences. Oecologia 176, 917–931.
GHD. 2012. Abbot Point Cumulative Impact Assessment (CIA) Technical Report: Lighting. Prepared for Abbot Point Working Group, October 2012.
Glasby, T.M., Connell, S.D., 1999. Urban structures as marine habitats. Ambio 28, 595–598.
Guthrie, D.M., 1986. Role of vision in fish behaviour. In: Pitcher, T.J. (Ed.), The Behaviour of Teleost Fishes. Croom Helm, pp. 75–113.
Gutman, R., Dayan, T., 2005. Temporal partitioning: an experiment with two species of spiny mice. Ecology 86, 164–173.
Henderson, R.W., Powell, R., 2009. Natural History of West Indian Reptiles and Amphibians. University Press of Florida.
Holden, A., 1992. Lighting the night: technology, urban life and the evolution of street lighting. Places 8 (2), 56–63.
Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C.C., Henckel, D., Hänel, A., Kappeler, P.M., Völker, S., Schwope, A., 2010. The dark side of light: a transdisciplinary research agenda for light pollution policy. Ecol. Soc. 15.
Johnston, E.L., Hedge, L.H., Mayer-Pinto, M., 2015. The urgent global need to understand port and harbour ecosystems. Marine and Freshwater Research 66, i–ii.
Keough, M.J., 1984. Dynamics of the epifauna of the bivalve *Pinna bicolor*: interactions among recruitment, predation, and competition. Ecology 65, 678–688.
Kiyofuji, H., Saitoh, S.-I., 2004. Use of nighttime visible images to detect Japanese common squid *Todarodes pacificus* fishing areas and potential migration routes in the Sea of Japan. Mar. Ecol. Prog. Ser. 276, 173–186.
Kronfeld-Schor, N., Dayan, T., 2003. Partitioning of time as an ecological resource. Annu. Rev. Ecol. Evol. Syst. 34, 153–181.
Lacoeuilhe, A., Machon, N., Jullen, J.F., Le Bocq, A., Kerbiriou, C., 2014. The influence of low intensities of light pollution on bat communities in a semi-natural context. PLoS One 9.
Luecke, C., Wurtsbaugh, W.A., 1993. Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. Trans. Am. Fish. Soc. 122, 112–120.
Luginbuhl, C.B., Boley, P.A., Davis, D.R., 2014. The impact of light source spectral power distribution on sky glow. J. Quant. Spectrosc. Radiat. Transf. 139, 21–26.
Mackenzie, B.R., Schiedek, D., 2007. Daily ocean monitoring since the 1860s shows record warming of northern European seas. Glob. Chang. Biol. 13, 1335–1347.
Maxwell, S.L., Smith, A.V., 2007. Generating River bottom profiles with a dual-frequency identification sonar (DIDSON). N. Am. J. Fish Manag. 27, 1294–1309.
Mazur, M.M., Beauchamp, D.A., 2006. Linking piscivory to spatial-temporal distributions of pelagic prey fishes with a visual foraging model. J. Fish Biol. 69, 151–175.
Minnaar, C., Boyles, J.G., Minnaar, I.A., Sole, C.L., McKechnie, A.E., 2015. Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. J. Appl. Ecol. 52, 522–531.
Navarro-Barranco, C., Hughes, L.E., 2015. Effects of light pollution on the emergent fauna of shallow marine ecosystems: amphipods as a case study. Mar. Pollut. Bull. 94, 235–240.
Perkin, E.K., Hölker, F., Tockner, K., 2014. The effects of artificial lighting on adult aquatic and terrestrial insects. Freshw. Biol. 59, 368–377.
Preisser, E.L., Bolnick, D.I., Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86, 501–509.
Pun, C.S.J., So, C.W., 2012. Night-sky brightness monitoring in Hong Kong. Environ. Monit. Assess. 184, 2537–2557.
Rechencq, M., Sosnovsky, A., Macchi, P.J., Alvear, P.A., Vigliano, P.H., 2011. Extensive diel fish migrations in a deep ultraoligotrophic lake of Patagonia Argentina. Hydrobiologia 658, 147–161.
Rich, C., Longcore, T., 2006. Ecological Consequences of Artificial Night Lighting. Island Press.
Rotics, S., Dayan, T., Kronfeld-Schor, N., 2011. Effect of artificial night lighting on temporally partitioned spiny mice. J. Mammal. 92, 159–168.
Russ, A., Ruger, A., Klenke, R., 2015. Seize the night: European Blackbirds (*Turdus merula*) extend their foraging activity under artificial illumination. J. Ornithol. 156, 123–131.
Santos, C.D., Miranda, A.C., Granadeiro, J.P., Lourenço, P.M., Saraiva, S., Palmeirim, J.M., 2010. Effects of artificial illumination on the nocturnal foraging of waders. Acta Oecol. 36, 166–172.

Schubert, E.F., Kim, J.K., 2005. Solid-state light sources getting smart. Science 308, 1274–1278.

Sebens, K.P., Vandersall, K.S., Savina, L.A., Graham, K.R., 1996. Zooplankton capture by two scleractinian corals, Madracis mirabilis and Montastrea cavernosa, in a field enclosure. Mar. Biol. 127, 303–317.

Siegel, J.M., 2005. Clues to the functions of mammalian sleep. Nature 437, 1264–1271.

Small, C., Nicholls, R.J., 2003. A global analysis of human settlement in coastal zones. J. Coast. Res. 19, 584–599.

Smith, C.U.M., 2009. Invertebrate Vision. Biology of Sensory Systems. John Wiley & Sons, Ltd, Chichester, UK, pp. 253–279.

Taylor, M.D., McPhan, L., van der Meulen, D.E., Gray, C.A., Payne, N.L., 2013. Interactive drivers of activity in a free-ranging estuarine predator. PLoS One 8, e80962.

Tibbetts, J., 2002. Coastal cities: living on the edge. Environ. Health Perspect. 110, A674–A681.

Troscianko, T., Benton, C.P., Lovell, P.G., Tolhurst, D.J., Pizlo, Z., 2009. Camouflage and visual perception. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364, 449–461.

Underwood, A.J., 1981. Techniques of Analysis of Variance in Experimental Marine Biology and Ecology.

Vollsnes, A.V., Eriksen, A.B., Otterholt, E., Kvaal, K., Oxaal, U., Futsaether, C.M., 2009. Visible foliar injury and infrared imaging show that daylength affects short-term recovery after ozone stress in Trifolium subterraneum. J. Exp. Bot. 60, 3677–3686.

Walters, L.J., Wethey, D.S., 1996. Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. Mar. Ecol. Prog. Ser. 137, 161–171.