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Light pollution reduces activity, food consumption and growth rates in a sandy beach invertebrate☆

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ABSTRACT

The continued growth of human activity and infrastructure has translated into a widespread increase in light pollution. Natural daylight and moonlight cycles play a fundamental role for many organisms and ecological processes, so an increase in light pollution may have profound effects on communities and ecosystem services. Studies assessing ecological light pollution (ELP) effects on sandy beach organisms have lagged behind the study of other sources of disturbance. Hence, we assessed the influence of this stressor on locomotor activity, foraging behavior, absorption efficiency and growth rate of adults of the talitrid amphipod *Orchestoidea tuberculata*. In the field, an artificial light system was assembled to assess the local influence of artificial light conditions on the amphipod's locomotor activity and use of food patches in comparison to natural (ambient) conditions. Meanwhile in the laboratory, two experimental chambers were set to assess amphipod locomotor activity, consumption rates, absorption efficiency and growth under artificial light in comparison to natural light-dark cycles. Our results indicate that artificial light have significantly adverse effects on the activity patterns and foraging behavior of the amphipods, resulting on reduced consumption and growth rates. Given the steady increase in artificial light pollution here and elsewhere, sandy beach communities could be negatively affected, with unexpected consequences for the whole ecosystem.

1. Introduction

Natural light sources (sunlight and moonlight) play a fundamental role on an array of organisms and ecological processes (Gaston et al., 2012). For example, the light of stars provides essential signals for long distance migration of birds (Åkesson et al., 2001) as well as direction to nocturnal insects (Verheijen, 1985). Sunlight and moonlight are also key drivers of circadian rhythms (Scapini et al., 1997), nocturnal migrations of pelagic organisms (Ringelberg, 1999) and modulators of predator-prey interactions (e.g., Clarke, 1983; Kotler et al., 1991), among many other processes. In this context, human alteration of natural light cycles is likely to lead to important effects on biological processes and diversity. A 6% annual increase in worldwide artificial lighting due to the rise of human infrastructure and activity (Hölker et al., 2010), has triggered concerns about the potential impact of this stressor on a variety of organisms and communities (Longcore and Rich, 2004; Hölker et al., 2010; Gaston et al., 2012).

Ecological light pollution (hereafter ELP) is the “artificial light that alters the natural patterns of light and dark in ecosystems” (Longcore and Rich, 2004). Among the best understood effects of ELP are those documented for sea turtle orientation (Peters and Verhoeven, 1994), facilitated detection of prey by predators (Eisenbeis and Hassel, 2000; Kolligs, 2000; Rydell, 1992; Frank, 2006), visual interference (Le Corre et al., 2002), and alteration of feeding behaviors (Bird et al., 2004). As of 2010, over 20% of the

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world coastlines (excluding Antarctica) were exposed to some level of artificial lightning (Davies et al., 2014). In these systems, sandy beaches represent over 80% of the ice-free coastline (Short, 1999; Bascom, 1980), and yet, the potential effects of ELP on these habitats remain virtually unknown (Schlacher et al., 2016). Sea turtles are, again, an exception (Witherington and Martin, 2000): we know for example that artificial light networks inhibit turtle nesting in sandy beaches and disorient their hatchlings (Peters and Verhoeven, 1994).

Crustacean amphipods of the family Talitridae are, in terms of biomass and abundance, among the dominant organisms in the upper levels of temperate sandy beaches (e.g., Dahl, 1952; Scapini et al., 1997; Jaramillo et al., 2002). These amphipods play an important community role and accelerate the decomposition of stranded macroalgae wracks (Lastra et al., 2008; Olabarria et al., 2009; Duarte et al., 2010; MacMillan and Quijón, 2012). Most amphipods display distinctive circadian rythms entailing the active search for food during the night hours and the burying in the upper and mid intertidal sediments during daylight (Jaramillo et al., 2003; Dugan et al., 2004; Duarte et al., 2009, 2014). Among other cues, Talitrid amphipods rely on visual stimuli like the sun and the moon for their orientation and circadian rythms (Mezzetti et al., 2010; Scapini, 2006; Nardi et al., 2000; Scapini et al., 1997). Hence, it is reasonable to think that the widespread growth of artificial lightning would likely alter their activity patterns as well as their feeding behavior.

The Talitrid amphipod *Orchestoidea tuberculata* is among the numerically dominant species in the upper intertidal zone of exposed sandy beaches of central and southern Chile in the southeastern Pacific (Varela, 1983; Jaramillo et al., 2000, 2003). Activity patterns in this species change along the life cycle: while juveniles are active along the 24 h cycle (Jaramillo et al., 1980), subadults are more active at dusk and night, and adults are strictly nocturnal. Hence, based on their abundance and well known activity patterns, adult *O. tuberculata* represent ideal models for the study of the ELP in the central Chile coastline. Surprisingly though, little has been done about it with the exception of a survey conducted by Giaconni (2006). This author found abundant populations of this species in all but one sandy beach system which, coincidentally, was the only one exposed to ELP. However, no experimental studies to date have tested the relationship between ELP and any relevant aspects of the ecology of this species. Our study aims to fulfill that knowledge gap by experimentally assessing the influence of ELP on the locomotor activity and feeding ecology of adult *O. tuberculata*.

2. Materials and methods

2.1. Field experiments

We conducted field experiments in Las Docas (33°08′19.5″S; 71°42′21.2″W) and Quintay (33°11′00″S; 71°41′10″W) sandy beaches, in central Chile (Fig 1). We chose these sites because they are far enough from large urban centers as to provide full dark conditions and support large populations of *O. tuberculata* (Duarte unpublished). In December 2013, we deployed two experimental arrays in Las Docas (Fig. 1). Each array included three rows of 3 containers each holding 20 g of fresh pieces of the alga *Durvillaea antarctica*, a common alga in the area and a preferred food item for the amphipods (Duarte et al., 2010). Rows were 3 m apart and containers within lines were separated by 2 m. One of the arrays was associated to an artificial light system that include an halogen light set (with standard 665–950 nm wavelength) at the top of a 3 m height post connected to a distant 5000 W power source. The artificial light system was set 3 m away from the first line of the array and provided an average ground-level light intensity of approximately 60 lux. Such light intensity gradually decreased from the place where the light was placed towards the periphery and was measured with a TENMARS TM-202 lux meter. 60 lux also reflects the light intensity measured in Northern Chile sites exposed to ELP (Duarte unpublished data). This system was part of the “artificial light” treatment which was paired with the array kept in natural dark/light conditions (“ambient” treatment; see Fig. 1).

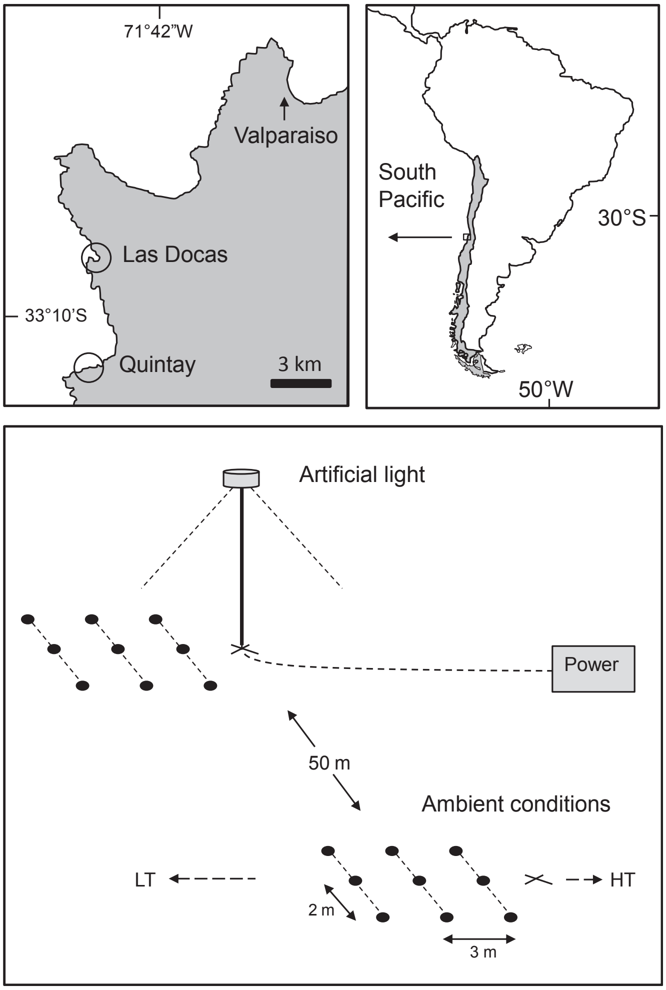

Fig. 1. Map of the study area, identifying the approximate location of Las Docas and Quintay beaches (insert). The bottom plot illustrates the experimental arrays set in both locations for the exposure of algal containers (filled circles) to ambient conditions or artificial light exposure. Rows of algal containers increased to 5 during the 2014 trials.

During three consecutive nights, we alternated the use of the artificial light system in two different sites of Las Docas to ensure that measurements of activity under ELP where not site-specific. The array maintained in ambient conditions remained in the same place.

To assess the influence of ELP on amphipod activity, each container with algae was checked once per hour, during three hours starting with the beginning of the activity of the adults (approximately 9 p.m.). If adult amphipods were detected at least once during a night, patches were classified as showing activity (coded as 1), otherwise they were considered inactive (coded as 0). Containers with algae were renewed every night. If ELP has a negative effect on foraging activity, our expectation was that activity on containers exposed to ELP would be lower than in those at ambient conditions (without ELP).

In July 2014, we repeated our experiment in two beaches, Las Docas and Quintay, to assess the generality of the findings gathered at Las Docas during 2013. The approach used was similar, but this time the arrays at each beach included 5 rows of algal containers instead of 3. Experiments in both locations were conducted during one night only.

2.2. Laboratory manipulations

To contrast our results in the field, we conducted experiments under controlled laboratory conditions and similar light intensity exposure (60 lux). For this purpose, we manually collected adult amphipods from Las Docas beach during the 2014 austral summer and transported them in plastic containers with wet sand to the laboratory in Centro de Investigaciones Marinas de Quintay (CIMARQ). The containers had perforated lids to facilitate air exchange and served as storage units for a standard 24 h starvation/acclimation period in the laboratory (see Duarte et al., 2014). We collected blades of *D. antarctica* from a rocky shore in the vicinity of Las Docas, immediately before their use in the experiments.

30 amphipods (approximately 15–20 mg in weight) were set individually in 1 L plastic containers with perforated lids. Each container was supplied with a fragment of *D. antarctica* of a standard size and a 5 cm layer of wet sand. Half of the amphipods ($n = 15$) were exposed to ELP from dusk to dawn, whereas the other half was exposed to ambient (dark) conditions. Experiments lasted 12 d and algal fragments were replaced with fresh fragments every morning.

2.3. Activity

To determine whether ELP influenced activity, every morning, during 9 days, we checked whether activity had taken place during the previous night. This was determined by visually assessing the presence of characteristic burrow holes in the surface of the sand (Jaramillo et al., 2003). For each of the amphipods, we summarize the information as the proportion of nights in which the individual was active. This approach was considered to be integrative of the activity occurred along the whole night.

2.4. Rates of growth and consumption

If ELP decreases activity, then food consumption and growth rates are also expected to decrease. To determine rates of growth, we weighted the amphipods before and after the 12 days experiment. Growth rates were expressed as weight gain amphipod^{-1} d^{-1}.

We measured amphipod consumption rates in ELP and ambient (dark) treatments over the course of three days, by measuring the daily loss in weight of the algal fragments used in the growth experiments. These measurements were paired with reference containers in which the change in weight of similar algal fragments was measured in the absence of amphipods. These reference containers provided an estimate of weight changes unrelated to grazing (cf. Roa, 1992) and provided a normalizing factor. Rates of consumption (RC) were estimated as follows:

$$\mathrm{RC} = \left(\mathrm{E_{initial}} - \mathrm{E_{final}}\right) - \left(\mathrm{R_{initial}} - \mathrm{R_{final}}\right)$$

where E and R correspond to experimental and reference algae, respectively. Rates of consumption were estimated as g individual^{-1} d^{-1}.

In order to determine whether ELP influences absorption efficiency, we followed the methodology of Conover (1966) that relies on the ratio of organic and inorganic fractions on both ingested food and fecal material. This methodology assumes that the absorption process affects the organic fraction only and, therefore, absorption efficiency (AE) can be estimated as a percentage as follows:

$$\mathrm{AE} = [(\mathrm{F}' - \mathrm{E}')/(1 - \mathrm{E}')\mathrm{F}'] \times 100$$

where F′ corresponds to the organic fraction in the food and E′ corresponds to the organic fraction in the feces. In order to apply this methodology, 3 amphipods were kept during 4 days in plastic containers with *D. antarctica* fragments in the conditions described above for the consumption experiments. From amphipods exposed to ELP and ambient (dark) conditions, feces were carefully collected and immediately frozen while algal fragments were replaced with fresh fragments. Feces were then dried at 60 °C for 48 h, weighted and subsequently incinerated at 500 °C during 4 h and weighted again. A similar methodology was used for the algal fragments.

2.5. Data analysis

Field data were analyzed in software R (R Core Team, 2016) using generalized linear mixed models (GLMM) with error distribution and logit link function (see Bolker et al., 2009). For the first experiment, the full model included treatment and distance from the light source as fixed effects, and plot (each array) and patch, nested within plot, as random effects. We could not test the interaction between distance and treatment due to lack of replicates, however we fitted alternative exploratory models treating distance classes as a random effect. These analyses showed no difference in the slope of the treatment of interest among distance groups, thus suggesting that no significant interaction exists between both factors. For the second experiment, the full model included treatment, distance and their interaction as fixed effects, and beach and plot (each array) nested within beach, as random effects. Model selection, among the models resulting from the combination of random and fixed effects, was based on the Akaike information criterion corrected for small sample size (AICc, Burnham and Anderson, 2003). Models were fit using the function glmer from package lme4 (Bates et al., 2015). In case of convergence problems, we used the function allFit() in package afex (Singmann et al., 2016), to assess whether the estimates were consistent when using different optimization algorithms. For the selected model we calculated the marginal (i.e., only fixed effects) and conditional (i.e., fixed and random effects) pseudo-R^2 following Nakagawa and Schielzeth (2013), and using the function sem.model.fits() in package piecewiseSEM (Lefcheck, 2016). Statistical analyses were conducted R programming environment.

For the laboratory data, the effects of treatment (i.e. ELP versus ambient) on the rates of growth, consumption and absorption efficiency were assessed using one-way ANOVAs (Zar, 1999). A Kruskall Wallis test was also used to compare the proportion of nights in which the amphipods were active in each of the treatments (ELP and ambient). Given that anomalies were detected in the circadian rhythm of the amphipods (locomotor activity was detected in the morning), a Fisher's exact test was also used to compare between treatments. Laboratory statistical analyses were conducted using Statistica 8.0.

3. Results

3.1. Field experiments

In the first experiment (2013; alternating light-darkness), we found amphipod activity at least once in all patches in ambient conditions (not exposed to artificial light). In contrast, none of the patches located at 3 m and only half of those located at 6 m from the light source presented *O. tuberculata* activity when exposed to light. The best AICc model included additive effects of treatment and distance (Table 1, Table S1). In the second field experiment (2014), the effect of artificial light exposure was more evident in both beaches. In Quintay, all patches set under ambient (dark) conditions had activity, whereas this was true for 53.3% of those exposed to artificial light. In the case of Las Docas, 86.7% of the patches in ambient conditions had activity whereas only 6.7% of those exposed to artificial light showed such activity. The best AICc model included only treatment as a fixed effect, providing support for the light but not for the distance effect (Table S2). Both experiments showed that light decreased adult amphipod activity, whereas the evidence for distance-to-light-source effects was limited (Table 1). None of the models included differences in slopes as random effects (i.e., the effect of treatment and distance did not change between plots, beaches or algae patches depending on the experiment). In both cases the random effects explained a small fraction of the total variance, thus explaining the scarce difference between marginal and conditional pseudo-R2, which indicated that in both experiments most of the variance in the response variable was explained by the selected model (Table 1).

3.2. *Laboratory experiments*

In the absence of ELP (ambient conditions), amphipods were active a higher proportion of nights (Kruskal-wallis $p = 0.00$; Fig. 2). Furthermore, starting at day 7, amphipods exposed to ELP exhibited anomalous circadian rhythm activity, showing signs of switching from night to day-light activity patterns (Fisher's exact test, $p = 0.04$).

Growth rates in amphipods exposed to ambient conditions (darkness) was nearly 3 times higher than those exposed to ELP (one-way ANOVA $F_{(1.27)} = 16.42$; $p = 0.00$; Fig. 3). Similarly, under ambient conditions consumption rates were nearly 2 times higher than under ELP exposure (one-way ANOVA $F_{(1.36)} = 5.46$; $p = 0.02$; Fig. 4). In contrast, we did not find differences in absorption efficiency between treatments (one-way ANOVA $F_{(1.5)} = 2.58$; $P = 0.17$; Fig. 5).

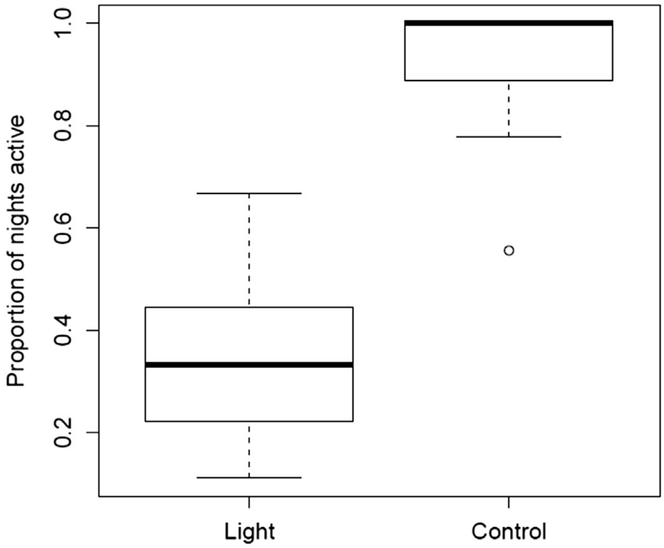

Fig. 2. Boxplots depicting the differences in amphipod activity in sediments exposed to artificial light and those kept at control conditions.

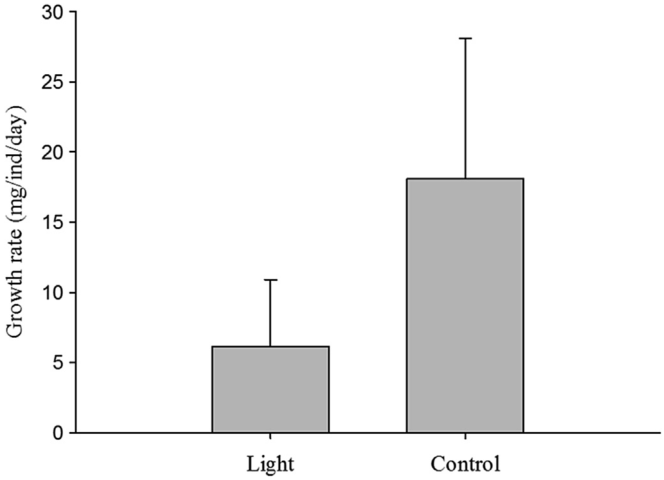

Fig. 3. Mean (+S.D.) amphipod growth rates in sediments exposed to artificial light and those kept in control conditions.

Table 1
Estimates of relevant parameters and derived quantities (pseudo-R^2) obtained after fitting the best GLMM models for the two field experiments. Marginal (i.e. fixed effects only) and conditional (i.e. fixed and random effects) pseudo-R^2 values obtained according to Nakagawa and Schielzeth 2013. Random effects in the models were included as nuisance (i.e. to account for confounding factors due to experimental design), and thus they do not constitute effects of interest to be evaluated. Accordingly, their significance was not assessed, and they were conserved as a means structure in all models irrespective their overall contribution to the response variable.

Parameter	Estimates	
	Field experiment 1	Field experiment 2
Fixed Effects		
Intercept	−1.151 (SE: 1.027, P = 0.262)	−6.641 (SE: 2.649, P = 0.012)
Treatment (No Light)	4.400 (SE: 1.145, P < 0.001)	6.088 (SE: 2.763, P = 0.006)
Distance	–	1.093 (SE: 0.397, P = 0.006)
Random Effects		
Plot [Beach]	<0.001 (SE: 0.001)	–
Beach	1.565 (SE: 1.251)	–
Patch [Plot]	–	<0.001 (SE: <0.001)
Plot	–	0.994 (SE: 0.997)
pseudo-R^2		
Marginal	0.503	0.796
Conditional	0.664	0.843

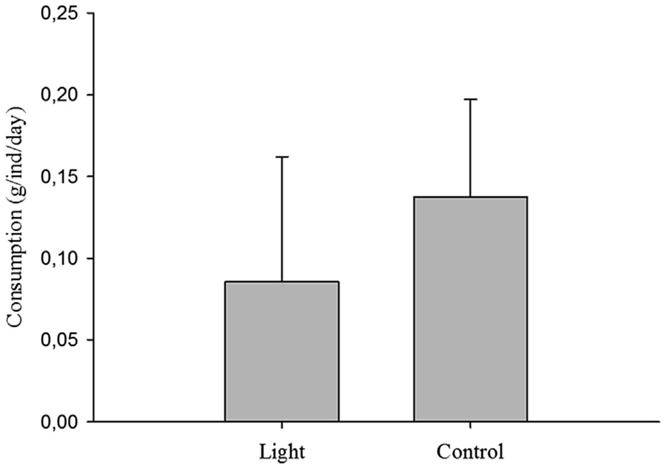

Fig. 4. Mean (+S.D.) amphipod consumption rates in sediments exposed to artificial light and those kept in control conditions.

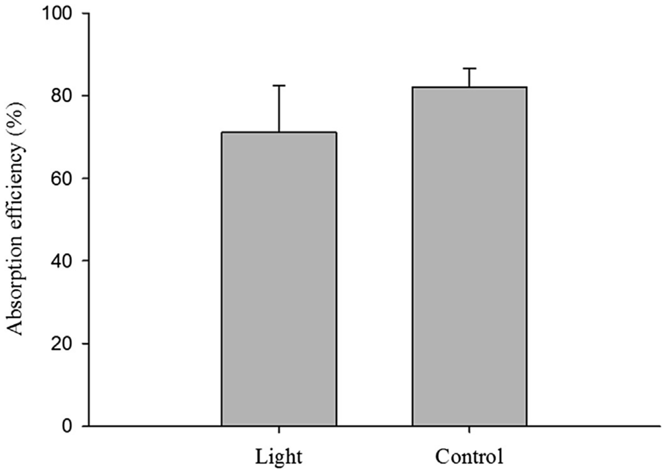

Fig. 5. Mean (+S.D.) amphipod absorption efficiency in sediments exposed to artificial light and those kept in control conditions.

4. Discussion

Ecological light pollution is an emerging threat for biodiversity in general (Perkin et al., 2011; Gaston et al., 2013) and for sandy beach organisms in particular (Schlacher et al., 2016). Nevertheless, to date the effects of ELP on sandy beach organisms (other than sea turtles) have remained largely unexplored (Schlacher et al., 2016). The handful of studies that have addressed ELP impacts on beach invertebrates, have done so by applying correlative analyses (e.g., Giaconni, 2006; González et al., 2014; Fanini et al., 2016). For example, Fanini et al. (2016) found that the activity rhythm of the amphipod *Platorchestia smithi* was similar between a beach exposed to light and a beach that was not. In contrast, Giaconni (2006) found that in a single beach exposed to artificial light *O. tuberculata* was absent contrasting with three beaches without light where this amphipod was present. González et al. (2014) reported that the abundance of a sandy beach beetle was positively correlated with night sky quality (an indirect indicator of ELP) and in turn negatively correlated with level of urbanization. While these observational studies provide mixed evidence for (Giaconni, 2006; González et al., 2014) or against (Fanini et al., 2016) effects of ELP on sandy beach organisms, our field and laboratory experiments provide strong and consistent evidence that ELP affects the locomotor activity levels, foraging behavior and growth rates of a sandy beach organism.

In our study we found that exposure to ELP caused a significant reduction in the locomotor activity both in field and laboratory conditions. In the field, we observed a high reduction in talitrid activity associated to light exposure in two different beaches and, in the case of one of the beaches, in two different seasons (austral summer and winter). The same effects were observed under laboratory conditions, where the individuals exposed to artificial light stayed buried in the sediment most of the time. In light of the multiple sources of experimental evidence obtained we can conclude that light causes a reduction in locomotor activity in *O. tuberculata*. Our results are similar to those reported by Bird et al. (2004) for beach mice in Florida. However, unlike that study, the effects of distance from the light source on *O. tuberculata* activity were not clear. This is partially explained because we could not include the interaction between distance and treatment in the models, and distance effects are expected to occur in the light exposure control but not the ambient conditions treatment. However, the facts that (1) no activity was detected in the first 3 m from the light source in any of the experiments, whereas this was not true for the ambient treatment (activity was nearly always detected at this distance class), and (2) activity was detected in most patches set in the ambient plots, only 50 m away from the light source, suggest that as reported by Bird et al. (2004) the effects of light exposure decrease quickly as distance from the light source increases. The light intensity used in our field experiments (60 lux) reflects the typical conditions to which ground level organisms are exposed in areas with know ELP influence. Regardless, the spatial scales over which artificial lightning influence the behavior of animals will likely depend on the organisms involved, their life stage (Benítez et al., 2016) and also an array of environmental conditions.

In laboratory conditions, ELP has been shown to alter the length (duration) of the daily locomotor activity patterns in other talitrid species (Jelassi et al., 2014) but with contrasting effects. In a diurnal species like *Orchestia montaguii*, ELP induced a reduction on the period of locomotor activity. In contrast, for a nocturnal species like *Orchestia gammarellus*, ELP induced an extension in its locomotor activity. Unexpectedly, we also found evidence of an alteration in the circadian rhythm in these individuals. Amphipods exposed to ELP showed signs of "diurnal" activity seven days after the onset of the experiments. Previous laboratory experiments with this and other sandy beach species have shown that these organisms are able to retain their circadian rhythm for longer periods of time (e.g., Jaramillo et al., 2003). Hence, this alteration is related to ELP and cannot be attributed to the confinement or the laboratory conditions created by our mesocosms. Unfortunately, our field design did not allow us to detect similar rhythm alterations, in case they actually occurred *in situ*. It is therefore unclear if this level of exposure to ELP would promote the changes observed in the laboratory.

To our knowledge, there are no prior studies evaluating the effects of ELP on the feeding behavior and growth rate of sandy beach invertebrates. Rather, the studies available have focused on the effects of ELP on vertebrates (e.g., Lima, 1998; Bird et al., 2004; Julien-Laferrière, 1997; Lewanzik and Voigt, 2014) and invertebrate zooplanktonic species (Moore et al., 2000). Our results indicate that exposure to ELP (60 lux, similar to field conditions at ground level) reduced significantly amphipod consumption and growth rates. These negative effects were not compensated by an increase in absorption efficiency, a physiological response used by some species in response to low food availability (Simpson and Simpson, 1990). These results are consistent with those reported by Vásquez (1994) who found that ELP reduced feeding rates in rodents, and by Boldogh et al. (2007) who documented a reduction in growth in juvenile and especially suckling bats (*Myotis emarginatus* and *M. oxygnathus*). Growth rates have been used before as a proxy of fitness in this and other species of talitrid amphipods (Duarte et al., 2010, 2016). Additional traits reflecting overall species fitness include survival (Porter et al., 2008; Horváth et al., 2009) and reproduction (Rand et al., 1997; De Molenaar et al., 2000), both of which are also negatively affected by ELP. Although our field design did not include measurements of growth or consumption *in situ*, the lower activity levels recorded in the patches associated to ELP, suggest that consumption rates (and potentially growth) could have been reduced as well. We are cautious about (and avoid) extrapolating laboratory results into field settings though. In their natural setting, amphipods are able to feed elsewhere, and potentially migrate in and out the limits of our experimental areas. Hence, even though our results from the laboratory are clear and meaningful, we encourage the implementation of larger scale field manipulations in order to provide further reaching evidence of ALP effects on fitness.

4.1. Scaling up and implications

The relevance of our findings depends on the extent at which artificial light is used now or in the future onto or nearby sandy beach systems. For example González et al. (2014) conducted a study in northern Chile (ca. 400 km north of our study area) and found that night sky quality was negatively correlated with urbanization levels. These authors concluded that for at least a third of the sandy beaches they studied, there was evidence of relative low night sky quality due to high levels of development (González et al., 2014). The quick expansion of ELP into natural settings in this and other regions worldwide (Gaston et al., 2012) suggest that the impacts of ELP may increase in scope as urbanization continues. However, it is important to highlight that there may be considerable variation in the effects of ELP. Our experiments used a light intensity known to reflect ground conditions exposed to ELP (60 lux) and is expected to change with distance from the source or in most cases, with distance from light networks. More importantly, responses to this and other stressors can indeed be diverse in direction and intensity, modifying the interaction balance as proposed by Bennie et al. (2015). Further studies should aim to understand impacts beyond the presence of ELP, and focus on the quality and intensity of ELP (above and below 60 lux), which likely, would affect differentially different taxa (e.g. Witherington and Martin, 2000; Rydell, 1992). Shorebirds and other vertebrates relying on upper shore invertebrates are likely to be indirectly affected (if not directly as well) by ELP. Several studies have in fact documented the dynamics (Hubbard and Dugan, 2003) and reliance (Bower, 1964; Dugan et al., 2003) of Pacific shorebirds like sanderlings, goldwits and several plover species on sandy beach invertebrates like talitrid amphipopds. Furthermore, upper shore invertebrates, and the factors driving their abundance have been also mentioned as key considerations for the conservation of endangered piping plovers (*Charadrius melodus*) in Atlantic Canada sandy beaches (MacMillan and Quijón, 2012). If ELP has an effect on the growth activity and overall availability of invertebrates, it would indirectly affect their predators.

Finally, the strong responses to ELP here reported do not preclude the likely influence of other stressors in combination or not with ELP. Beach grooming, for example, reduces food availability (Dugan et al., 2013) and likely interacts with ELP among the challenges faced by beach invertebrate populations. Other stressors that, like ELP, are expected to grow in scope or intensity in the future include rising sea levels, arrival of non-indigenous species, growing coastal infrastructure, pollution and disturbance associated to human recreational use of beaches (see Schlacher et al., 2007). Aiming at diagnosing and managing a single stressor in this list is not advisable. Conservation policies targeting beach conservation should start by stressing the status of these systems as valuable but fragile ecosystems (see Schlacher et al., 2016).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.envpol.2016.08.068.

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