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Artificial light pollution at night (ALAN) disrupts the distribution and circadian rhythm of a sandy beach isopod[☆]

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ABSTRACT

Coastal habitats, in particular sandy beaches, are becoming increasingly exposed to artificial light pollution at night (ALAN). Yet, only a few studies have this far assessed the effects of ALAN on the species inhabiting these ecosystems. In this study we assessed the effects of ALAN on *Tylos spinulosus*, a prominent wrack-consumer isopod living in sandy beaches of north-central Chile. This species burrows in the sand during daylight and emerges at night to migrate down-shore, so we argue it can be used as a model species for the study of ALAN effects on coastal nocturnal species. We assessed whether ALAN alters the distribution and locomotor activity of this isopod using a light system placed in upper shore sediments close to the edge of the dunes, mimicking light intensities measured near public lighting. The response of the isopods was compared to control transects located farther away and not exposed to artificial light. In parallel, we measured the isopods' locomotor activity in the laboratory using actographs that recorded their movement within mesocosms simulating the beach surface. Measurements in the field indicated a clear reduction in isopod abundance near the source of the light and a restriction of their tidal distribution range, as compared to control transects. Meanwhile, the laboratory experiments showed that in mesocosms exposed to ALAN, isopods exhibited reduced activity and a circadian rhythm that was altered and even lost after a few days. Such changes with respect to control mesocosms with a natural day/night cycle suggest that the changes observed in the field were directly related to a disruption in the locomotor activity of the isopods. All together these results provide causal evidence of negative ALAN effects on this species, and call for further research on other nocturnal sandy beach species that might become increasingly affected by ALAN.

1. Introduction

Most of the natural illumination at night comes from celestial bodies, namely the moon, the stars and the Milky Way. These natural light sources, as well as daily light/night cycles, play a fundamental role on behavioral patterns of marine and terrestrial organisms and the timing of ecological processes (Gaston et al., 2013, 2015; Longcore and Rich, 2004; Luarte et al., 2016).

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Artificial Light Pollution at Night (hereafter ALAN) is the alteration of natural light levels as the result of anthropogenic light sources (Cinzano et al., 2001; Falchi et al., 2016). ALAN has widespread effects on a diverse range of taxa, including birds (McLaren et al., 2018; Montevecchi, 2006), bats (Cravens et al., 2018), marine turtles (Dimitriadis et al., 2018; Lorne and Salmon, 2007; Tuxbury and Salmon, 2005), plants (Bennie et al., 2018), fish (Brüning et al., 2015; Pulgar et al., 2019) and invertebrate communities (Grenis and Murphy, 2018; Jelassi et al., 2014; Underwood et al., 2017; van Langevelde et al., 2018). This stressor also has an effect on predator-prey interactions (Cravens et al., 2018; Yurk and Trites, 2000), species phenology (Bennie et al., 2018; Gaston et al., 2017), foraging behavior (Farnworth et al., 2018; Underwood et al., 2017) and orientation (Lorne and Salmon, 2007).

Behavioral and physiological processes associated with species' circadian rhythms may also be affected by ALAN (Luarte et al., 2016; Pulgar et al., 2019). For instance, the foraging of beach mice (*Peromyscus polionotus leucocephalus*) was negatively altered by light coming from two different sources (low-pressure sodium vapor and bug lights) (Bird et al., 2004). Similarly, in European perch (*Perca fluviatilis*), the natural increase in melatonin production taking place at night hours was found to be inhibited by ALAN (Brüning et al., 2015). In coastal areas, a large number of other species show circadian rhythms in which their locomotor activity is restricted to the night hours (Westin and Aneer, 1987; Nardi et al., 2003; Jaramillo et al., 2003). This is a concern considering that coastal habitats are becoming increasingly exposed to ALAN (Bird et al., 2004), an anthropogenic stressor whose area of influence grows at a near 6% per year (Hölker et al., 2010a).

Sandy beaches constitute nearly 80% of the world's shorelines (Bascom, 1980). In these habitats, circadian and circatidal cycles govern invertebrates' locomotor activity (i.e. the timing and intensity of the movement defining the distribution of these organisms in the beach) (Mezzetti et al., 2010; Scapini, 2006; Jaramillo et al., 2003; Kennedy et al., 2000). Yet, research into the potential effects of ALAN on these organisms is limited to a handful of studies (Dimitriadis et al., 2018; Jelassi et al., 2014; Lorne and Salmon, 2007; Luarte et al., 2016). ALAN can negatively influence the foraging activity and growth rate of intertidal invertebrates such as the Talitrid amphipod *Orchestoidea tuberculata* (Luarte et al., 2016). However, whether ALAN can also alter the abundance, distribution and locomotor activity of this and other intertidal invertebrates is not really known. To address this question we used the Oniscoid isopod *Tylos spinulosus* Dana (Jaramillo et al., 2003, 2006) as a model species. This isopod is a semi-terrestrial species that burrows on upper-shore sediments during daylight and emerges at night to make down-shore migrations and feed upon stranded seaweeds. This invertebrate is very abundant in sandy beaches located in north-central Chile, south east Pacific (23–30°S) and plays an ecologically important role in the turnover of stranded macroalgae (see Jaramillo et al., 2003, 2006).

Our working hypothesis was that ALAN negatively affects *T. spinulosus*' abundance, distribution and locomotor activity. The rationale behind this hypothesis is that this isopod is nocturnal and previous studies have shown that even full moon light conditions appear to inhibit some of the activity of this species (Jaramillo et al., 2003). To test our hypothesis, we conducted field experiments to assess the potential effects of ALAN on *T. spinulosus* abundance and distribution across the intertidal of El Apolillado beach. These field manipulations were complemented with laboratory measurements using actographs attached to mesocosms that allowed us to measure the effects of ALAN on the locomotor activity of this species. To the best of our knowledge, this is the first study to experimentally assess the effects of ALAN on the abundance and distribution of a species like this in the field and to test its relationship with locomotor activity levels in the laboratory.

2. Materials and methods

2.1. Field experiments

We conducted field lighting experiments on a sandy beach located in north-central Chile ("El Apolillado"; 29°10′48.315″S; 71°29′22.918″W). We chose this location because it supports large densities of *Tylos spinulosus* (Jaramillo et al., 2003) and is located far away from urban areas and networks of coastal lighting, providing natural dark conditions at night. This sandy beach possess intermediate morphodynamic characteristics, with a mean grain size of 282 μm and a slope of 1/24 (Jaramillo et al., 2003, 2006). The field experiments were carried out during two separate periods (November 17–19, 2017 and January 15–17, 2018), aiming to measure species responses to ALAN during periods representing austral spring and summer conditions. During night hours, these periods of time are characterized by relatively high humidity levels (means of 86% and 81% during the corresponding weeks in November and January, respectively) and mild temperatures (means of 12.3 °C and 16.1 °C in November and January respectively) as based on Meteorological records gathered from a weather station (290004) located a few miles away from the study area (see at https://climatologia.meteochile.gob.cl/). Both experiments were initiated on the first new moon of each month. These experiments aimed to compare the response of isopods (in terms of abundance and distribution) to two distinct conditions or treatments: natural daylight/dark conditions (control) and exposure to ALAN.

For each of the dates indicated above, each of the treatments included three separate transects (replicates) placed across the intertidal zone, from the base of the dunes to the start of the swash zone (low tide). Along each transect, we placed nine pitfall plastic traps (traps 1–9; 5 cm diameter, 12 cm height) buried into the sand with their rim flush to the beach surface at 3 m intervals. All the traps were filled with a 5% sea water-formalin solution to preserve organisms caught in the traps. Treatments (control versus ALAN) were placed 100 m apart from each other to avoid any potential interference, and were arranged in a systematic way (Hurlbert, 1984), alternating control and ALAN.

Transects associated to the ALAN treatment were exposed to light-emitting diodes lights (SENTRY S 20W driverless 5 K White-light; 220 V) at the top of a 3-m height post connected to a distant power source (EP2500CX Honda generator; 2.2 KVA). This artificial light system was placed 2 m away from the first trap (located near the base of the dune) and provided an average ground-level light intensity of approximately 120 lux. Light intensity gradually decreased from there towards the low-tide end of the transect (trap 9), in which light intensity was approximately 3 lux. In all cases, light intensity was measured with a PCE-L 100 Light meter. As in previous studies (Pulgar et al., 2019), the highest light intensity of this system recreated the light intensity recorded under lighting networks of heavily polluted shorelines, where lights are located at the top of the shore, nearby roads or boardwalks. Transects associated to the control had an identical arrangement of traps (traps 1–9) and were never exposed to ALAN. Repeated measurements of light intensity conducted along these transects at night, consistently recorded 0 lux.

Experimental trials lasted three consecutive nights and started approximately at 10:00 p.m., collecting the first samples at midnight (0:00 is the time known to mark the beginning of the activity in adult *T. spinulosus*, Jaramillo et al., 2003) and lasted 4 h in November 2017 and 5 h in January 2018. On each night and for each transect, the nine pitfall traps deployed along a given transect were removed and quickly replaced on an hourly basis. The content of the pitfall traps was placed on labelled containers and transported to the laboratory (Universidad Andrés Bello) where we recorded the number and size (total length) of all *T. spinulosus* collected.

2.2. Laboratory experiments

To conduct laboratory experiments we collected individuals of *T. spinulosus* using red light in the burrowing zone (upper intertidal zone) of the study area. These collections were conducted by hand during the first new moon of each month in which the experiments were run. The individuals were carefully handled and placed in plastic jars containing damp sand (10–12% water content) and seaweeds. In the laboratory, individuals were kept under continuous darkness and room temperature (16 °C) for an acclimation period of 48 h. The locomotor activity of *T. spinulosus* was then recorded in 40 × 20 × 26 cm (length, height and width) acrylic aquarium tanks equipped with infrared recording systems (actographs; designed and built by Ingeniería y Servicios Paulo Leal EIRL) during the seven day period between October 25 and November 1, 2017, between December 19 and 26, 2017, and between January 18 and 25, 2018 (Fig. 1). The bottom of these tanks was filled to a depth of 6 cm with damp sand from the study area. Measurements of locomotor activity were conducted in two conditions or treatments: natural daylight/dark cycle (control) and exposure to light during night hours (ALAN).

Forty isopods were placed in each tank (one for each light condition) and their (surface) locomotor activity was digitally recorded by the interruption of two infrared beams across the tank. The beams were arranged to pass over the surface of the sediment placed in the tanks. We had two infrared beams per tank to preclude potential data loss due to failure of one of the equipments. After a predetermined download interval per second, the data were uploaded into a computer. For the duration of the experiments (7 d), the tanks were kept at constant room temperature (16 °C), the sand was moistened every day and the animals were maintained with food *ad libitum*.

2.3. Field experiments data analysis

Field data were analyzed using Generalized Additive Models for Location, Scale and Shape (GAMLSS, Rigby and Stasinopoulos, 2005). To model the abundance of *Tylos spinulosus* we used the negative binomial error distribution and a log link function. The negative binomial distribution is adequate to deal with overdispersed count data (Zuur et al., 2009; O'Hara and Kotze, 2010). We modeled the spatio-temporal variation of *T. spinulosus* abundances in response to the treatment (control versus ALAN), the hour (as a factor) and the distance-to-light-source (as a continuum variable; 1–9 units). The distance-to-light-source was fitted nonlinearly using the cubic smoothing splines (Hastie and Tibshirani, 1990) function available in the GAMLSS package. We included additive and interactive effects between the three predictive variables described above. To account for confounding factors due to experimental design (i.e. micro habitat and seasonal differences), in all models we incorporated the micro-zone of the beach,wherea pair of transects (both control and ALAN) was located as a random effect (6 micro-zones, 3 in spring and 3 in summer), with randomly varying intercepts (Bolker et al., 2009; Zuur et al., 2009). In addition, we also modeled the variability (i.e. sigma) of the *T. spinulosus* abundances in response to the same predictors and interactions described above. Incorporating sigma parameters significantly improved the fit of the models (see Results).

We modeled the spatio-temporal variation of *T. spinulosus* sizes (all individuals = 40613 individuals) in response to the same predictors (i.e. fixed and random effects) and interactions described above. For these models, we used log-normal distribution because the size distribution of *T. spinulosus* showed a wide range (min-max = 0.068–7.9 cm) with a positive skewness (skewness = 1.90). Based on diagnose tools described below, models with the log-normal distribution showed a better fit than those with a normal distribution.

For model selection (abundance and size) we use in a complementary way both information-theoretic model comparison and null-hypothesis testing (Stephens et al., 2005). Specifically we used the Generalized Akaike information criterion (AIC; Akaike, 1974) and the likelihood ratio test (Lewis et al., 2011). For the abundance models we used the corrected Akaike Information Criteria (AICc) due to the high dimension of the models in relation to our sample size (Burnham and Anderson, 2002). In addition for all models a marginal (i.e., only fixed effects) and conditional (i.e., fixed and random effects) pseudo-R2 was calculated (Nagelkerke, 1991). Model diagnosis were based on residuals plots available in the GAMLSS package (residuals against fitted values, residuals against explanatory variable, density plot of the residuals and a normal Q-Q plot of the residuals). The analyses were conducted in the GAMLSS package (Rigby and Stasinopoulos, 2005) implemented in software R (R Core Team, 2017).

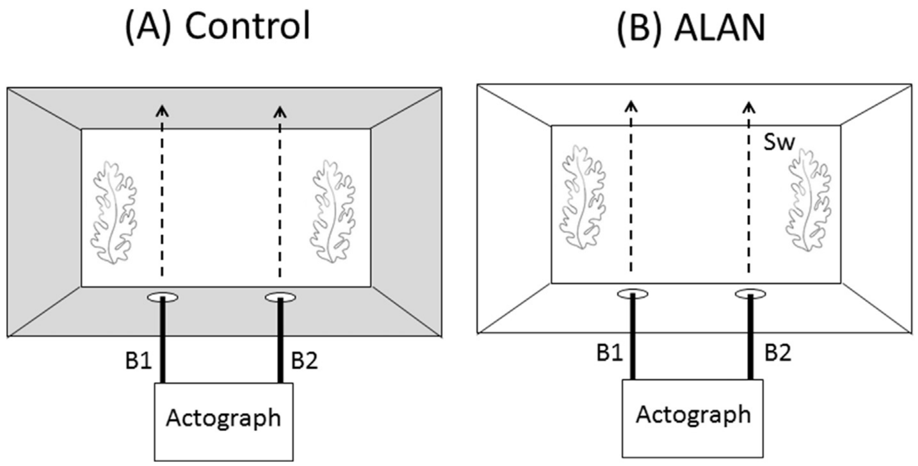

Fig. 1. Top view of the two-tank experimental setup used to evaluate the locomotor activity of *T. spinulosus* under contrasting conditions: (A) control (natural daylight/dark cycle) and (B) ALAN: (light exposure during night hours). Actographs are attached to the acrylic aquarium tanks. B1: Beam 1; B2: Beam 2; Sw: Seaweed.

2.4. Laboratory experiments data analysis

Laboratory data were also analyzed using GAMLSS (Rigby and Stasinopoulos, 2005). Each experiment (October, December and January) was analyzed separately. For each experiment, we grouped the activity recorded by actographs in one minute intervals (October = 19743, December = 19160, January = 17518; intervals, respectively) and we modeled the probability of activity (i.e., at least one activity record within a one minute interval) using a binomial error distribution and a logit link. We included additive and interactive effects between the treatment (as a factor) and the hour of the day (0–23hrs). The hour of the day was fitted non-linearly (in order to adjust the circadian rhythm) using the cubic smoothing splines function available in the GAMLSS package. In order to account for daily variations throughout the experiment, we included the day of the experiment as random effect with randomly varying intercepts. Model selection and diagnosis were done in same manner as in the field experiments section (see above). In addition, for all models we calculated the receiver operating characteristic curve (ROC curve). ROC curves and the area under the ROC curve were estimated using the pROC package in R (Robin et al., 2011). Figures were produced using the stat_smooth function available in the ggplot2 package (Wickham, 2009) in R.

3. Results

3.1. Field experiments

The abundance of *Tylos spinulosus* in the field was significantly affected by treatment (control versus ALAN), hour, and distance to the light source ($P < 0.001$, Tables 1 and 2; fitted using cubic smoothing splines). The best AICc model explaining the variation of *T. spinulosus* variance (up to 46%) included the interactive effect between predictive variables (only mu; Table 1; Pseudo-R2, Table 1). Models that also included the variability of *T. spinulosus* (mu and sigma, Table 1), in response to predictors and their interaction, increased the explained variation up to 61% (Table 1, Table 2). Overall, *T. spinulosus* exhibited significantly higher abundances ($P < 0.0001$, Table 2) in control (mean ± SE = 170 ± 19 individuals per pitfall trap) than under light conditions (31 ± 5 individuals per pitfall trap; $P < 0.0001$; Table 2; Fig. 2a), with a peak in abundance in control conditions at 2:30 a.m. (214 ± 30 individuals per pitfall trap; Fig. 2a).

The interaction of treatment and distance-to-light was the main source of variation in the abundance of *T. spinulosus* ($P < 0.0001$, Tables 1 and 2, Fig. 2b). Under control conditions, *T. spinulosus* exhibited the highest mean abundances at intermediate tidal levels with 269 (±51) individuals per pitfall trap recorded between stations 4 and 5 from the light source (Fig. 2b). From mid to low tide levels a decrease in abundance and a simultaneous increase of variability were observed (Fig. 2b). In field transects exposed to ALAN, *T. spinulosus* exhibited low mean abundances at close and intermediate distances to the light source (6 ± 2 individuals at stations 1 to 4 in relation to distance -to -the-light -source, Fig. 2b). In contrast, the isopod highest mean abundance (77 ± 17 individuals, Fig. 2b) was recorded at stations 6 and 7 in relation to distance-to-light-source. Micro-zones — as random effect — explained 15% of *T. spinulosus* variation (Table 1), which could be attributed to micro-habitat variations.

The size of *T spinulosus* was significantly affected ($P < 0.001$, Tables 3 and 4) by treatment, hour and distance-to-light-source (fitted using cubic smoothing splines). The best model (Table 3) included the interaction between predictive variables, explaining 40% of the distribution of *T. spinulosus* sizes (Pseudo-R2, Table 3). The mean size (±95% CI) of *T. spinulosus* was significantly larger ($P < 0.0001$, Table 4) in control (0.876 ± 0.004 cm) than under ALAN (0.751 ± 0.006 cm; Fig. 3a). Regarding to the distance-to-light-source under control conditions, *T. spinulosus* exhibited the largest sizes at high to mid tide levels (0.91 ± 0.01 cm at station 3 from the light source), decreasing in size towards low tide levels. Conversely, under light pollution conditions *T. spinulosus* exhibited the smallest mean sizes at high tide levels (0.64 ± 0.04 cm, Fig. 3b) increasing in mean size towards mid tide levels (0.78 ± 0.01 cm at station 6 from the light source; Fig. 3b).

Table 2

Spatio-temporal variation of *T. spinulosus* abundances in response to the treatment (control and ALAN), the hour of the experiment and the distance-to-light-source. It is shown a likelihood-ratio test of dropping each term (for *mu* and *sigma*) from the saturated model (M6, Table 1).

	Term	LRT	Pr(Chi)
Mu	Treatment	150.3	<0.0001
	Hour	51.0	<0.0001
	cs(Distance)	20.9	0.0003
	Treatment x Hour	25.2	0.0003
	Treatment x cs(Distance)	145.5	<0.0001
	Random (micro-zone)	185.4	<0.0001
	Term	LRT	Pr(Chi)
Sigma	Treatment	8.2	0.0043
	Hour	25.7	0.0003
	cs(Distance)	25.5	<0.0001
	Treatment x Hour	16.75	0.01014
	Treatment x cs(Distance)	4.36	0.03677

LRT; Likelihood ratio test, cs; cubic smoothing splines, x; indicates interaction between predictive variables.

Table 1

Model selection for spatio-temporal variation of *T. spinulosus* abundances (*mu*) in response to the treatment (control and ALAN), the hour of the experiment and the distance-to-light-source. All models contained micro-zones (see methods) as a random effect. The best model (M6) contained the variability (i.e. *sigma*) of *T. spinulosus* abundances in response to predictors.

Model	Formula	df	AICc	ΔAICc	R^2 (F + R)	R^2 (F)
M1	*mu* ~ Treatment + Hour + cs(Distance)	16.0	3655	202	0.54	0.28
M2	*mu* ~ Treatment x Hour + cs(Distance)	22.0	3644	190	0.57	0.33
M3	*mu* ~ Treatment x Hour + cs(Distance) x Treatment	23.0	3501	47	0.70	0.46
M4	*mu* ~ Treatment x Hour + cs(Distance) x Treatment *sigma* ~ Treatment x Hour	38.9	3474	21	0.74	0.55
M5	*mu* ~ Treatment x Hour + cs(Distance) x Treatment *sigma* ~ Treatment x Hour + cs(Distance)	42.9	3455	2	0.76	0.60
M6	*mu* ~ Treatment x Hour + cs(Distance) x Treatment *sigma* ~ Treatment x Hour + cs(Distance) x Treatment	43.9	3453	0	0.76	0.61

Models GAMLSS with a negative binomial error distribution are sorted by decreasing AIC values. df; degrees of freedom, AICc; corrected Akaike Information Criterion, ΔAICc; shows AICc differences between *i*th model and the best model, R^2 (F + R); Generalized (pseudo) R-squared for fixed and random terms, R^2 (F); Generalized (pseudo) R-squared for fixed terms, cs; cubic smoothing splines, x; indicates interaction between predictive variables. See Table 2 for likelihood-ratio tests for the best model (M6).

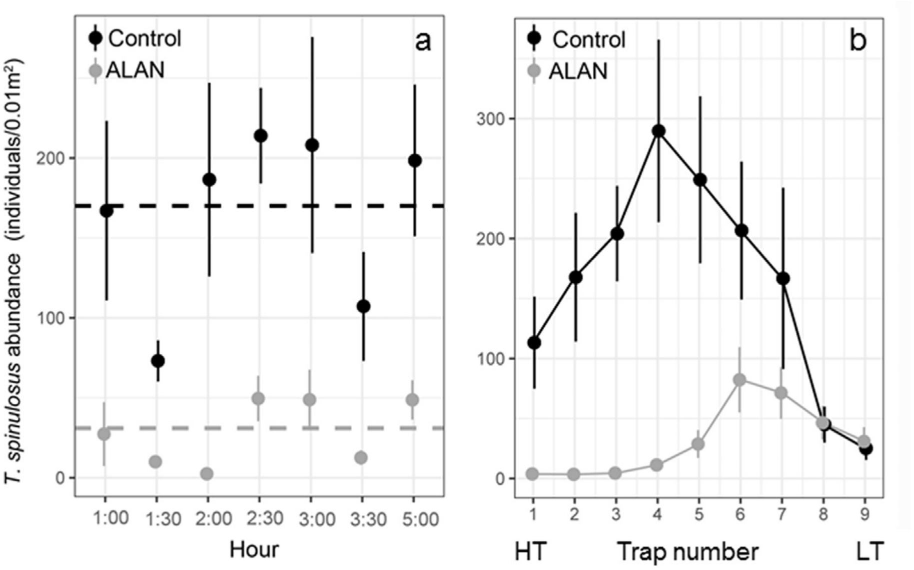

Fig. 2. Mean (±SE) of *Tylos spinulosus* abundance (individuals per pitfall trap) in response to control and ALAN conditions and to the hour of the experiments (a) and the position of the traps in relation to light source (b). Dotted lines in the left plot (a) show the overall mean throughout the experiment.

Table 3
Model selection for the spatio-temporal variation of *T. spinulosus* sizes in response to the treatment (control and ALAN), the hour of the day and the distance-to-light-source. All models contained micro-zones as a random effect.

Model	Formula	df	AIC	ΔAIC	R^2 (F + R)	R^2(F)
M1	Size ~ Treatment + hour	15	5780	685	0.46	0.31
M2	Size ~ Treatment x hour	21	5305	210	0.51	0.37
M3	Size ~ Treatment x hour + cs(Distance)	25	5125	30	0.53	0.39
M4	Size ~ Treatment x hour + cs(Distance) x Treatment	26	5096	0	0.53	0.40

Models (GAMLSS with lognormal error distribution) are sorted by decreasing AIC values. df; degrees of freedom, AIC; Akaike's Information Criterion, ΔAIC; shows AIC differences between *i*th model and the best model, R^2 (F + R); Generalized (pseudo) R-squared for fixed and random terms, R^2 (F); Generalized (pseudo) R-squared for fixed terms, cs; cubic smoothing splines, x; indicates interaction between predictive variables. See Table 4 for likelihood-ratio tests for the best model (M4).

Table 4
Spatio-temporal variation of *T.spinulosus* sizes in response to the treatment (control and ALAN), the hour of the experiment and the distance-to-light-source. It is shown a likelihood-ratio test of dropping each term from the saturated model (M4, Table 3).

Term	LRT	Pr(Chi)
Treatment	361.94	<0.0001
Hour	547.16	<0.0001
cs(Distance)	274.81	<0.0001
Treatment x Hour	407.91	<0.0001
Treatment x cs(Distance)	31.7	<0.0001
Random (micro-zone)	1301.28	<0.0001

LRT; lihelihood ratio test, cs; cubic smoothing splines, x; indicates interaction between predictive variables.

3.2. *Laboratory experiments*

The probability of *T. spinulosus* locomotor activity (i.e. presence of activity per minute) in the laboratory trials was significantly affected by treatment (control versus ALAN) and the hour of the day (fitted cubic smoothing splines; $P < 0.001$, Tables 5 and 6). In the three trials, the best model included the interactive effect of both predictors explaining 34, 54 and 60% of the variation (Pseudo-R2, Tables 5 and 6) of *T. spinulosus* probability of locomotor activity. In general, the day of the experiment as random effect explained a low percentage of *T. spinulosus* locomotor activity (average of 9% across models, Table 5), showing that the interactive effect between the treatment and the hour of the day was consistent throughout the experiment. In all three experiments *T. spinulosus* showed a clear circadian rhythm under control conditions, with a slight increase of locomotor activity at 8 p.m. (~at sunset) and a peak around 2:00 a.m. (mean probability of 0.72 and 95% confidence interval 0.69–0.75) of locomotor activity across the three trials (Fig. 4). A decrease in locomotor activity was detected from 6:00 a.m. to 8:00 a.m. (~sunrise) followed by a very low locomotor activity during daylight (9:00 a.m. - 8:00 p.m.) with a mean probability of 0.038 (95% confidence interval = 0.07–0.11) across the three trials (Fig. 4). In contrast, *T. spinulosus* exposed to ALAN showed a drastic inhibition of circadian rhythm. In these conditions, the highest probability of locomotor activity throughout the day was recorded at 3 a.m. (0.063 of mean probability with a 95% confidence interval of 0.05–0.08) across the three experiments (Fig. 4).

4. Discussion

During the last few decades, light/dark natural conditions have been changing as a result of an unprecedented increase in Artificial Light Pollution at Night (ALAN, e.g. Davies et al., 2013). Not surprisingly, ALAN is now perceived as a threat to biodiversity both in terrestrial and coastal areas worldwide (Davies et al., 2014; Falchi et al., 2016). Sandy beaches are among the best represented habitats in the coastline (Bascom, 1980). These habitats are being increasingly urbanized (González et al., 2014) and, as a result, their resident fauna is at risk from this stressor (e.g. Luarte et al., 2016). Despite this rather alarming scenario, studies evaluating the potential effects of ALAN on sandy beach organisms—other than sea turtles—remain scarce (Schlacher et al., 2016; Gonzalez et al., 2014)

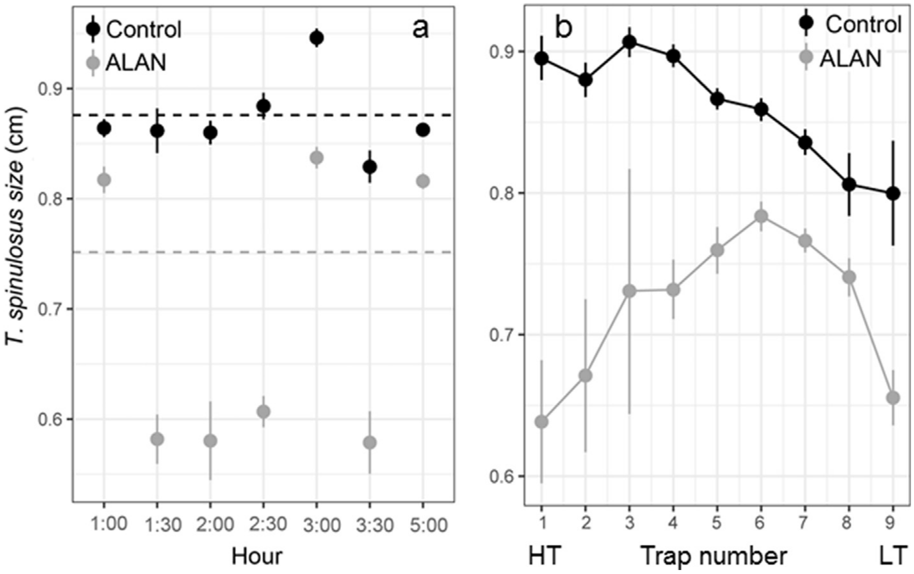

Fig. 3. Mean (±95% CI) of *Tylos spinulosus* sizes in response to control and ALAN conditions and to the hour of the experiments (a) and the position of the traps in relation to light source (b). Dotted lines in the left plot (a) show the overall mean throughout the experiment.

Table 5
Model selection for the probability of locomotor activity of *T. spinulosus* in response to the treatment (control and ALAN), the hour of the day and the day of the experiment as random effect. For each experiment, the best model (GAMLSS with a binomial error distribution) contained the interaction between predictive variables.

Experiment	Model	Formula	df	AIC	AUC	R^2(F + R)	R^2(F)
October	M1	Sensor ~ cs(hour) + Treatment + Day	13.5	5563.0	0.93	0.55	0.34
	M2	Sensor ~ cs(hour) x Treatment + Day	14.6	5497.3	0.93	0.56	0.34
December	M1	Sensor ~ cs(hour) + Treatment + Day	13.7	9315.4	0.92	0.58	0.53
	M2	Sensor ~ cs(hour) x Treatment + Day	14.8	9200.4	0.92	0.58	0.54
January	M1	Sensor ~ cs(hour) + Treatment + Day	13.2	6916.5	0.94	0.61	0.59
	M2	Sensor ~ cs(hour) x Treatment + Day	14.4	6851.9	0.94	0.61	0.60

df; degrees of freedom, AIC; Akaike's Information Criterion, AUC; area under the ROC curve, R^2 (F + R); Generalized (pseudo) R-squared for fixed and random terms, R^2 (F); Generalized (pseudo) R-squared for fixed terms, cs; cubic smoothing splines, x; indicates interaction between predictive variables. See Table 6 for likelihood-ratio tests for the best models.

Table 6
Probability of locomotor activity of *T. spinulosus* in response to the treatment (control and ALAN), the hour of the day and the day of the experiment as random effect. It is shown a likelihood-ratio test of dropping each term from the saturated models (GAMLSS with a binomial error distribution, Table 5).

	Term	LRT	Pr(Chi)
October	Treatment	1909.9	<0.0001
	cs (hour)	2039.1	<0.0001
	cs (hour) x Treatment	68.1	<0.0001
	Random(Day)	2273.8	<0.0001
December	Treatment	4110.0	<0.0001
	cs (hour)	4433.3	<0.0001
	cs (hour) x Treatment	87.6	<0.0001
	Random(Day)	750.0	<0.0001
January	Treatment	2758.1	<0.0001
	cs (hour)	4504.4	<0.0001
	cs (hour) x Treatment	67.2	<0.0001
	Random(Day)	228.9	<0.0001

and, so far, have shown only indirect evidence of ALAN impacts (but see Luarte et al., 2016).

The results of this study show that ALAN has a strong effect on the distribution and circadian rhythm of *Tylos spinulosus*. In comparison to natural light/dark conditions (controls), exposure to ALAN significantly reduced the abundance and distribution of the isopods across different tide levels. Such changes are likely associated to a reduction in locomotor activity, a hypothesis that we tested with actograph measurements in the laboratory. Those measurements unequivocally showed that individuals exposed to ALAN lost—at least temporarily—their circadian rhythm of activity: they remained most of the time buried in the sediment or exhibited diurnal activity, a behavior never recorded before in the field (see Jaramillo et al., 2003). Interestingly, in field transects exposed to ALAN we found an upturn of abundance in the sediments located farther away from the light sources, which is consistent with the premise that ALAN locally inhibits or reduces locomotor activity. These results are also in agreement with the activity recorded in beach mice in Florida (Bird et al., 2004). Those authors showed a negative effect of artificial light on the foraging behavior of mice, reducing patch use near artificial lights and harvesting significantly more seeds as distance from the light source increased.

Under natural dark (night) conditions, populations of *T. spinolosus* exhibited their highest abundance at mid-tide levels, where they feed on readily available stranded seaweed (e.g. Jaramillo et al., 2003). However, when exposed to ALAN, isopods were only collected farther down in the intertidal, suggesting that ALAN is forcing individual *T. spinulosus* to move towards suboptimal tide levels. A previous study assessing the distribution of a sympatric species, the sand hopper *Orchestoidea tuberculata* (Luarte et al., 2016) showed that ALAN had also a negative effect on the

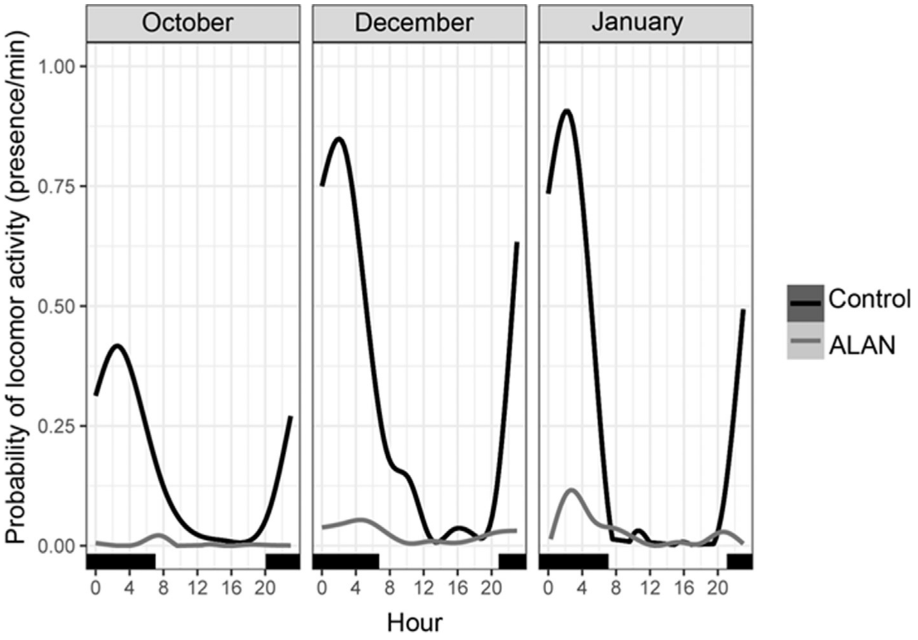

Fig. 4. Mean probability of locomotor activity of *Tylos spinulosus* throughout the day in response to control and ALAN conditions.

distribution of this species. However, unlike the results gathered with *T spinulosus*, Luarte et al. (2016) did not evaluate if the distance to the light source was related to the activity of the amphipods. Other studies evaluating ALAN effects on the abundance of sandy beach invertebrates have been primarily observational in nature and, so far, have not provided conclusive results (e.g. Gonzalez et al., 2014; Fanini et al., 2016). However, a recent study addressing ALAN effects on endogenous physiological performance and behavior in a rock fish (*Girella laevifrons*; Pulgar et al., 2019) offers conclusions similar to ours.

The influence of ALAN on *T. spinulosus* field distribution and abundance suggests that continued exposure to this stressor may reduce this species' foraging area, with possible consequences for its fitness as shown for other species (Luarte et al., 2016; Pulgar et al., 2019, Duarte, unpublished data). We cannot speculate on the exact consequences a long-term exposure to ALAN may have on the fitness of *T. spinulosus*. However, the likelihood of some effects is also supported by the known sensitivity of *T. spinulosus* to light variations. For instance, full moon light intensity (0.1–0.3 lux, Gaston et al., 2013) has been shown to partially inhibit the activity of *T. spinulosus* (Jaramillo et al., 2003). Such sensitivity would explain the strong effects of ALAN on the activity of this - but not necessarily other - species. *T spinulosus* coexists with species such as *Orchestoidea tuberculata* which use identical food resources (algal wrack). If exposure to ALAN alters *T spinulosus* foraging area and potentially its fitness, this could indirectly modify the interactions that have previously been recorded between these two species (Jaramillo et al., 2003) with unpredictable community-level consequences. Even though both species are affected by ALAN, such responses have not been measured in an integrative framework that would allow us to assess simultaneously the direction of those effects.

Responses to ALAN are likely to change with ontogeny and, although we did not explicitly focus on age groups, some of our results seem to reflect that. The body size of individuals collected from sediments exposed to ALAN was smaller (near juvenile-size range) than those collected under control conditions. A plausible explanation for this difference could simply be adult-juvenile behavioral differences in locomotor activity, as those described previously for other crustaceans (e.g. Fallaci et al., 1999; Kennedy et al., 2000). However, different physiological conditions and requirements along the ontogeny should also promote different responses to ALAN or other environmental stressors (Benitez et al., 2016; Farnworth et al., 2018). Given that we do not know the precise underlying mechanisms by which ALAN alters circadian rhythms, differences along the ontogeny are an interesting venue to further exploration. Studies evaluating ALAN effects on circadian rhythms in general, are also required given that they are still scarce for aquatic invertebrates (e.g. Bregazzi and Naylor, 1972; Jelassi et al., 2014; Luarte et al., 2016). Similarly, studies addressing the potential long-term effects of exposure to ALAN are also critical. Seasonal variations in light intensity, ALAN exposure, and a myriad of other factors changing within and among seasons are likely to play a role on ALAN impacts on the life cycle of species like *Tylos spinulosus*.

In the three laboratory trials in which *T. spinulosus* was exposed to natural day/light (control) conditions, this species showed a marked circadian rhythm of locomotor activity. Activity slightly increased at dusk and reached a peak by 2 a.m., concurrently with the low tide, and subsequently its activity declined again at dawn. Such pattern reflects closely what has been observed repetitively in the field, and suggests that *T. spinulosus* has a strict nocturnal activity pattern with an endogenous circadian component, as shown for this (Jaramillo et al., 2003) and other species (e.g Kennedy et al., 2000; Dhouha et al., 2018). Likely, this pattern of nocturnal activity is associated with the environmental conditions that only occur at night. For example, a relative humidity of 80% (normally recorded only at night) is optimal for *Talitrus saltator* to survive (Dhouha et al., 2017). Similarly, low temperatures occurring at night are essential for efficient oxygen consumption in the oniscoid isopod *Tylos europaeus* (Marsh and Branch, 1979).

In the trials exposing individuals of *T. spinulosus* to ALAN, activity decreased at night, when they are normally expected to be most active. Moreover, some activity was observed during daylight hours, when this species is expected to be least active (see Jaramillo et al., 2003). Other studies exposing sandy beach organisms to

ALAN have showed contrasting results. While some reported an extended period of activity (e.g. Dhouha et al., 2017), others reported an inhibition of locomotor activity or, as seen in this study, an abnormal diurnal activity (e.g. Luarte et al., 2016). Of course, locomotor activity is not the only phenomenon regulated by circadian rhythms. Several studies have reported distinct patterns (e.g. foraging behavior, enzyme activity, movements, and photosynthetic activity) to be closely related, if not regulated, by circadian rhythms (e.g. Gaston et al., 2017; Longcore and Rich, 2004). Once the natural cycles of day/night are modified as a result of ALAN, such phenomena become disrupted in ways we don't fully understand. For instance, under constant artificial light, the Atlantic tarpon (*Megalops atlanticus*) stopped its retino-motor movements, a phenomenon known to be controlled by a circadian clock (Kopperud and Grace, 2017).

The effects of ALAN on circadian rhythms are broad and likely include a wide variety of taxa and biological processes. Our study provides solid evidence gathered from field and laboratory experiments, indicating that ALAN disrupts the circadian rhythm activity of an intertidal sandy beach isopod. In the field, our results suggest that individuals of *T. spinulosus* exposed to ALAN reduce their foraging area and, potentially, see their fitness negatively affected. The ongoing spread of ALAN into an increasing number of natural areas (Cinzano et al., 2001; Falchi et al., 2016) suggests that its impacts will become more evident as urbanization continues to occur along our shorelines (Hölker et al., 2010b). We stress the need for more studies addressing the impact of this stressor on other species and geographic locations, incorporating also the study of ALAN effects on multiple species and on their potential interactions. Finally, futures studies should incorporate the combined effects of different light characteristics (e.g. spectrum and intensity) to better understand the ecological consequences of ALAN (Davies et al., 2017).

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