

ORIGINAL RESEARCH

## Artificial light at night and apparent predation on juvenile *Neohelice granulata* during two deployment periods at Mar Chiquita, Argentina

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**ABSTRACT.** Over the past decade, artificial light at night (ALAN) has become one of the most spatially extensive anthropogenic disturbances along coastlines worldwide, yet whether its capacity to alter predation is a fixed property of illumination intensity or depends on the ecological context in which it occurs has received little attention. Here we evaluate this question using replicated tethering experiments at the microtidal lagoon of Mar Chiquita (south-western Atlantic coast of Argentina) in two deployment periods (spring and summer), quantifying apparent predation on juvenile *Neohelice granulata* under ALAN (cold-white LED,  $\approx 38$  lux) and natural-darkness controls. A Generalised Linear Mixed Model with experimental night as a random intercept revealed a significant interaction between light condition and season. In spring, ALAN significantly increased the probability of juvenile predation relative to natural darkness, whereas no detectable effect was found in summer. Placed alongside the published effect at a macrotidal, structurally simpler site, ALAN sensitivity follows an ordered gradient consistent with an amplifying-effect hypothesis, whereby ALAN would amplify predation in proportion to the underlying susceptibility state of predators and prey (adult nutritional condition, juvenile developmental vulnerability and habitat structural complexity) rather than being a fixed property of light intensity alone, although adult nutritional condition was not measured directly and is inferred from published seasonal values for this population. These results indicate that the same habitat may shift between high- and low-sensitivity states across seasons, that single-season assessments may systematically underestimate cumulative predation exposure, and that targeted light management during juvenile settlement is, in principle, a more efficient conservation approach than year-round restrictions, although we did not evaluate its costs or feasibility.

**Key words:** Predation risk, light pollution, coastal urbanization, predator-prey interactions.

**Luz artificial nocturna y depredación aparente sobre juveniles de *Neohelice granulata* durante dos períodos de despliegue en Mar Chiquita, Argentina**

**RESUMEN.** En la última década, la luz artificial nocturna (ALAN, por sus siglas en inglés) se ha convertido en una de las perturbaciones antropogénicas de mayor extensión espacial en las costas de todo el mundo; sin embargo, se ha prestado poca atención a si su capacidad para alterar la depredación es una propiedad fija de la intensidad luminica o si depende del contexto ecológico en el que se produce. En este estudio evaluamos dicha cuestión mediante experimentos replicados de sujeción de presas (*tethering*) en la laguna micromareal de Mar Chiquita (costa atlántica del suroeste

de Argentina) durante dos periodos de muestreo (primavera y verano), cuantificando la depredación aparente sobre juveniles de *Neohelice granulata* bajo condiciones de ALAN (LED de luz blanca fría,  $\approx 38$  lux) y controles de oscuridad natural. Un modelo lineal mixto generalizado, con la noche experimental como intercepto aleatorio, reveló una interacción significativa entre la condición lumínica y la estación. En primavera, ALAN aumentó significativamente la probabilidad de depredación de juveniles en comparación con la oscuridad natural, mientras que en verano no se observó ningún efecto detectable. Al comparar estos resultados con los publicados para un sitio macromareal de estructura más simple, se observa que la sensibilidad a la ALAN sigue un gradiente ordenado coherente con la hipótesis de un efecto amplificador: ALAN amplificaría la depredación en proporción al estado de susceptibilidad subyacente de depredadores y presas (condición nutricional de los adultos, vulnerabilidad del desarrollo de los juveniles y complejidad estructural del hábitat), en lugar de ser una propiedad fija derivada únicamente de la intensidad de la luz (si bien la condición nutricional de los adultos no se midió directamente, sino que se infirió a partir de valores estacionales publicados para esta población). Estos resultados indican que un mismo hábitat puede alternar entre estados de alta y baja sensibilidad según la estación, que las evaluaciones realizadas en una sola estación pueden subestimar sistemáticamente la exposición acumulada a la depredación y que la gestión específica de la iluminación durante el asentamiento de los juveniles constituye, en principio, un enfoque de conservación más eficiente que las restricciones aplicadas durante todo el año, aunque no evaluamos los costos ni la viabilidad de dicha medida.

**Palabras clave:** Riesgo de depredación, contaminación lumínica, urbanización costera, interacciones depredador-presa.

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## INTRODUCTION

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The Earth's night is getting brighter at a rate of 6% per year because of the global expansion of artificial light at night (ALAN) (Hölker et al. 2010). Over the past two decades, ALAN has emerged as one of the most spatially extensive anthropogenic disturbances, with notorious impacts on populations and communities in both terrestrial and marine ecosystems (Davies et al. 2014; Gaston et al. 2015; Bennie et al. 2018; Sanders et al. 2018). Coastal and intertidal zones are among the most affected, given the continuing urbanization of coastlines worldwide (Perkin et al. 2011; Garratt et al. 2019; Zapata et al. 2019). ALAN's direct modification of natural lightscapes may have critical consequences for species interactions by disrupting the biological rhythms, locomotion patterns, and refuge-seeking behaviors of benthic vertebrates (Bolton et al. 2017) and invertebrates (Underwood et al. 2017; Nuñez et al. 2021b) and modifying the environmental contexts under which predator-prey encounters occur (see Davies et al. 2013; Gaston et al. 2013; Bolton et al. 2017). In particular, artificial illumination can extend the foraging window of visually oriented predators, increase prey detection

efficiency, and erode the diel temporal refuge that prey species rely on for safety (e.g. Cerri 1983; Batty et al. 1990; Bolton et al. 2017; Sanders et al. 2018; Czarnecka et al. 2019; McMahon et al. 2022). Nevertheless, the outcome is not uniform: under broad-spectrum white light, a shore crab attacked fewer snails overall and the pattern of color-based prey selection was reversed (Moyse et al. 2023), which indicates that the consequences for predation depend on the species and the ecological context.

Although the effects of ALAN on predation have recently begun to be documented in several taxa (see Hampton 2004; Underwood et al. 2017; Sanders et al. 2018), whether the magnitude of ALAN-driven predation amplification is a fixed function of light intensity or depends on the ecological context in which illumination occurs remains poorly understood. If ALAN sensitivity varies predictably with measurable ecological attributes such as habitat complexity, nutritional state of predators, or developmental stage of prey, then risk assessment becomes tractable and management interventions could be prioritized accordingly. If it does not, any single-site, single-season measurement may misrepresent the broader impact.

In size-structured populations of benthic invertebrates, where adults cannibalize recently settled juveniles (Polis 1981; Elgar and Crespi 1992), the

conditions generating ALAN sensitivity may be particularly dynamic. Cannibalism intensity depends on the interaction among adult motivation (nutritional state, reproductive energetics), juvenile vulnerability (developmental stage, refuge establishment), and habitat structure (refuge density, visual complexity of the substrate; Luppi et al. 2001; Claessen et al. 2004; Moksnes 2004; Hines et al. 2026). Each of these parameters changes both seasonally and geographically, so the same population may shift between high- and low-sensitivity states as the year progresses. A 37-year tethering experiment on the blue crab *Callinectes sapidus* has examined cannibalism, predation and refuges of juveniles (Hines et al. 2026), and tethering can serve as a comparative index of predation when applied consistently across treatments (Aronson and Heck 1995; Baker and Waltham 2020).

The burrowing crab *Neohelice granulata* (Dana, 1851) provides an ideal model system to evaluate context-dependence in ALAN-predation interactions. This species is the dominant ecosystem engineer of south-western Atlantic salt marshes, distributed along more than 4000 km of Argentine and Brazilian coast (Spivak et al. 1994), and modulates sediment biogeochemistry, organic-matter cycling, and benthic community structure through its extensive burrowing activity (Botto and Iribarne 2000; Alberti et al. 2015; Martinetto et al. 2016). Adults prey heavily on recently settled conspecifics, with cannibalism strongly mediated by refuge availability, predator hunger, and juvenile developmental stage (Luppi et al. 2001; Méndez Casariego et al. 2009, 2011). Nuñez et al. (2021a) provided the first field evidence that ALAN substantially amplifies juvenile mortality in *N. granulata* at the macrotidal, structurally simple site of San Antonio Oeste (SAO), where the combination of open sediment flats and chronically nutritionally stressed adult populations (Bas et al. 2019) seems to generate extreme ALAN sensitivity. A related study further documented that *N. granulata* exhibits strong behavioural plasticity in its ALAN responses depending on ecological context (Nuñez et al. 2021b).

Whether such sensitivity extends to the structurally complex, high-quality lagoon habitat of Mar Chiquita (MCH), and whether it varies across seasons, had not been tested.

Although the general prediction that ALAN enhances predation by extending the foraging window of visual predators is well supported (e.g. Becker et al. 2013; Bolton et al. 2017; Sanders et al. 2018; Czarnecka et al. 2019), the magnitude of this effect may not be independent of the predatory context of the system. In this sense, we identify four non-exclusive, heuristic hypotheses (not models formally discriminated by the present design) about how ALAN effects on predation interact with the underlying susceptibility state of the system, understood as the combined outcome of adult nutritional condition, juvenile developmental vulnerability, and habitat structural complexity, for which within-site baseline (no-ALAN) predation provides an empirical proxy (Figure 1): (HA) Additive effect. ALAN adds a constant increment to predation regardless of the susceptibility state of the system, implying no interaction between light pollution and the predatory state of the system (see Gaston et al. 2013; Bolton et al. 2017). (HB) Amplifying effect. The ALAN effect scales with susceptibility: systems already characterized by high predatory pressure would experience the greatest absolute increase under ALAN, for instance if nutritionally stressed or behaviorally active predators exploit the extended foraging window more intensively (e.g. Becker et al. 2013; Sanders et al. 2018; Czarnecka et al. 2019), as has been suggested for protein-limited populations of *N. granulata* at SAO (Bas et al. 2019). (HC) Compensatory effect. ALAN effects are largest in low-susceptibility systems, where prey detection under natural darkness is most constrained. This implies that habitat complexity and resource availability may buffer ALAN's influence (Luppi et al. 2001; Méndez Casariego et al. 2009). (HD) non-linear (threshold) effect. The ALAN effect may peak at an intermediate susceptibility state: too few motivated predators in low-susceptibility systems, while high-susceptibility systems

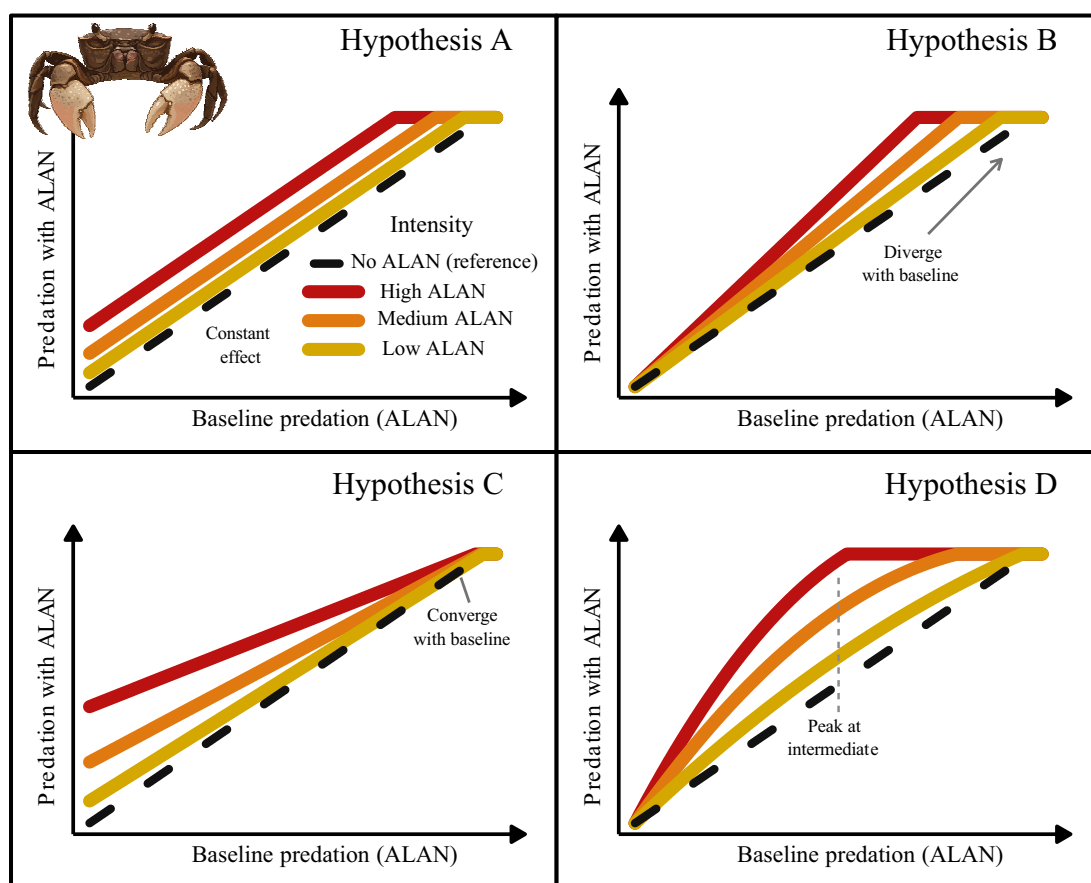


Figure 1. Conceptual hypotheses for how ALAN may modify predation as a function of the susceptibility state of the system. The x-axis ('baseline predation') indexes this susceptibility state via no-ALAN predation intensity; within a single site and protocol this is a direct empirical measure, whereas across independent studies (as for the San Antonio Oeste comparison in this manuscript) it should be interpreted qualitatively rather than as a strictly commensurable metric (see Caveats and limitations). A) Additive effect (HA): ALAN adds a constant increment to predation regardless of susceptibility, so the ALAN and no-ALAN lines remain parallel. B) Amplifying effect (HB): the ALAN effect diverges from baseline as susceptibility increases, so contexts already characterised by high predation show the largest absolute increase under ALAN. C) Compensatory effect (HC): the ALAN effect converges with baseline as susceptibility increases, so low-susceptibility contexts show the largest relative increase under ALAN. D) Non-linear (threshold) effect (HD): the ALAN effect peaks at an intermediate susceptibility state. In all panels, line colour indicates ALAN intensity (low, medium, high) and the black dashed line marks the 1:1 reference (no ALAN effect).

could already be behaviorally saturated (see Gaston et al. 2013). These hypotheses are not mutually exclusive and may operate at different spatial or temporal scales. Our design combines a within-site seasonal contrast at MCH, where susceptibility was expected to differ between a higher-risk spring period and a lower-risk summer period, with a contextual comparison against the published, chroni-

cally high-susceptibility population at San Antonio Oeste (SAO; a macrotidal site with limited habitat complexity and protein-limited adults; Bas et al. 2019). This design provides an empirical basis to evaluate which hypothesis best describes ALAN's influence on predation in *N. granulata*, while recognizing that the SAO comparison draws on an independent study and is treated as a qualitative

contextual anchor rather than a third quantitative point on a common baseline-predation axis. Here we report novel tethering data from two deployment periods at MCH: austral spring (September 2021), when we expected adult energy reserves to be low and juveniles to be highly vulnerable, and summer (February 2022), when we expected adults to be nutritionally replete and juveniles to have had time to establish burrow refuges. We predicted that ALAN would significantly amplify predation in spring (high susceptibility) but not in summer (low susceptibility), and that the spring MCH response would fall between the absent summer MCH effect and the extreme, chronic SAO sensitivity, consistent with the amplifying hypothesis (HB). We emphasize that baseline (no-ALAN) predation is used here strictly as an empirical proxy for the system's overall susceptibility state, not as a direct measurement of its underlying mechanistic components; the candidate mechanisms linking adult nutritional condition and juvenile vulnerability to this pattern are developed in the Discussion as *post-hoc*, non-measured interpretations, so as to keep the classification of contexts (via baseline predation) and the mechanistic explanation of the observed pattern logically separate.

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## MATERIALS AND METHODS

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### Study system and sites

*Neohelice granulata* is a semiterrestrial burrowing crab (adults 30–45 mm carapace width, CW) that dominates intertidal sediments of south-western Atlantic salt marshes along more than 4,000 km of Argentine and Brazilian coast. The juveniles used in our experiments measured 12–14 mm CW. Primary experiments were conducted at the Mar Chiquita coastal lagoon (MCH; 37° 45' S, 57° 26' W; Figure 2), a Ramsar-listed microtidal system (tidal range 0.3–0.8 m) on the Buenos Aires Province coast of Argentina. Mar Chiquita is char-

acterized by organic-rich muddy sediments and a dense, persistent burrow network of *N. granulata* that provides structural microrefugia for juveniles. Adults from Mar Chiquita maintain higher somatic energy reserves than conspecifics at structurally simpler sites (Bas et al. 2019). Paired exclusion/inclusion cage experiments at the structurally simpler SAO site identified adult conspecifics as the dominant source of juvenile mortality there (Nuñez et al. 2021a); no equivalent exclusion experiment has been conducted at MCH, so predator identity at this lagoon was inferred rather than directly established (see Caveats and limitations). Published tethering data from San Antonio Oeste (SAO; 40° 47' S, 65° 02' W; Figure 2), a macrotidal bay (tidal range 5–7 m) characterized by exposed sand-cobble intertidal flats with sparse burrow networks and chronically protein-limited *N. granulata* populations (Bas et al. 2019; Nuñez et al. 2021a), were used as a contextual reference only.

### ALAN treatment

The ALAN was simulated using a cold-white LED lamp (30 W, color temperature  $\approx$  6,000 K) mounted on a 3 m PVC mast powered by a solar panel, programmed to operate automatically from dusk to dawn. At each site, multiple independently located ALAN/control station pairs ('blocks') were deployed simultaneously, each block consisting of one ALAN station and one natural-darkness control station 30 m apart (Figure 2): four blocks in summer and three in spring, each sampled across five and four experimental nights per season respectively. Spring sampling was originally scheduled for five nights; one night was excluded after two of the three lighting units were stolen and the remaining unit was damaged in the same incident, leaving no usable data for that night. Control stations maintained  $< 0.1$  lux and ALAN stations  $\approx$  38 lux at ground level throughout each night, as verified with a calibrated luxmeter (Mastech MS6610). This intensity was chosen to match that used in the companion San Antonio Oeste study (Nuñez

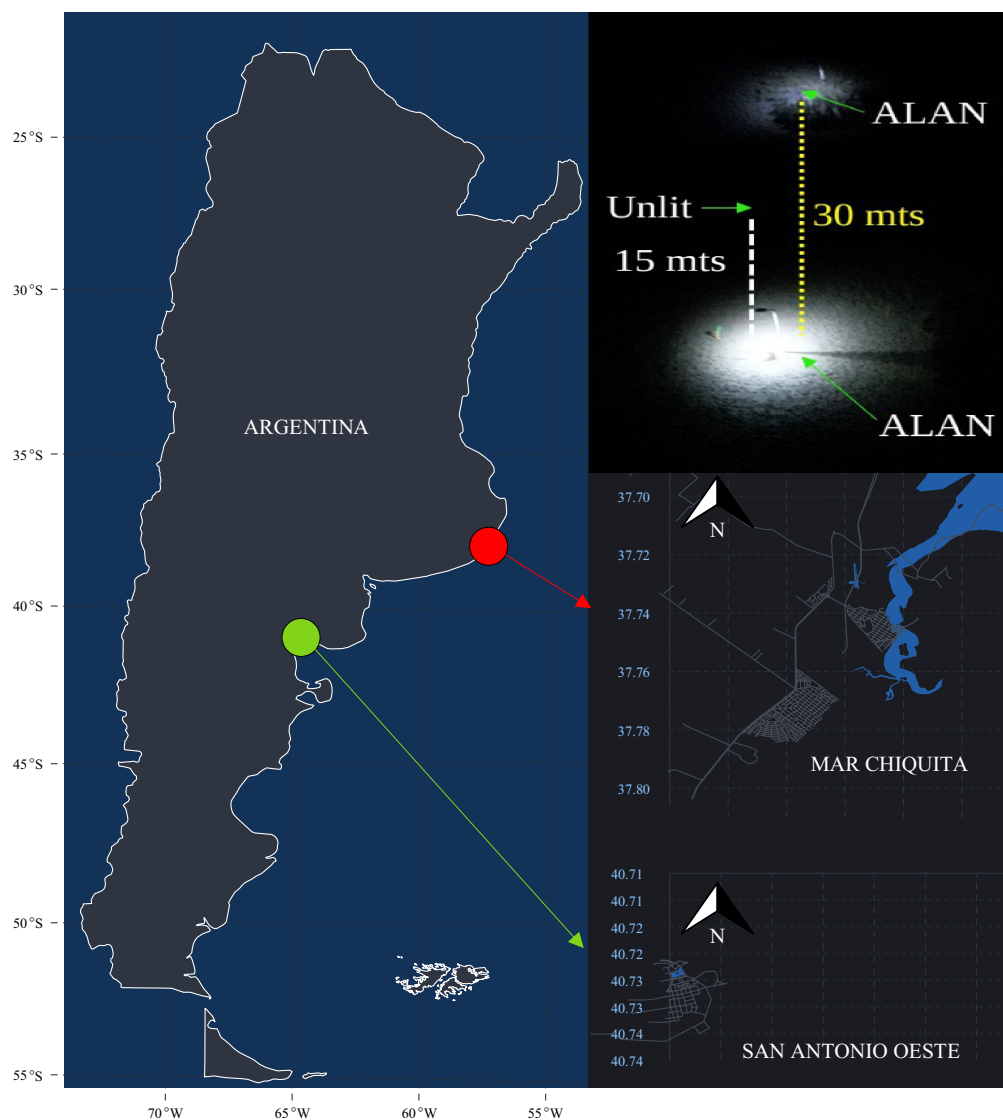


Figure 2. Study area and experimental design. Locator map of Argentina (left) showing the two study sites: Mar Chiquita (MCH; red circle, this study) and San Antonio Oeste (SAO; green circle, published reference site, Nuñez et al. 2021a), each linked by an arrow to a detailed inset map (right) giving latitude/longitude grid lines and a north arrow for that site. Top-right panel: night-time photograph illustrating the ALAN experimental set-up, showing an unlit reference point and illuminated (ALAN) stations, with the inter-station distance (30 m, matching the block spacing described in ALAN treatment) marked.

et al. 2021a), enabling direct cross-site comparison, and corresponds to the mean level previously measured under coastal lighting installations in the study region. All experiments were conducted during new-moon phases ( $\pm 3$  d) to minimize ambient lunar illumination.

### Tethering experiments

A tethering experiment was conducted at MCH in two deployment periods: austral spring 2021 (September; 4 usable experimental nights; 9 ALAN and 9 control replicates;  $N = 88$  crabs) and sum-

mer 2022 (February; 5 experimental nights; 23 ALAN and 23 control replicates;  $N = 223$  crabs). Juvenile *N. granulata* (CW  $13 \pm 1$  mm; intermolt individuals) were collected from unlit intertidal areas immediately before deployment to minimize handling stress. Each juvenile was tethered with 25 cm transparent nylon monofilament (0.20 mm diameter) attached to the posterior carapace with cyanoacrylate adhesive, which is biologically inert once cured and is standard practice in crustacean tethering studies (Baker and Waltham 2020), and fixed individually to its own sediment stake (a 5 mm-diameter, 35 cm-tall plastic stake driven into the sediment; one tethered juvenile per stake), permitting free movement within a 25-cm radius including partial burial. Three to five stakes per treatment and block were deployed each night, and the outcomes of these stakes were pooled into a single replicate (Table 1); crabs were deployed at dusk and retrieved at dawn after one tidal cycle ( $\approx 12$  h). At retrieval, each individual was classified as: (i) alive and uninjured; (ii) predated (dead with carapace damage characteristic of large-crab attack); (iii) sublethal injury; (iv) missing from tether; or (v) dead without apparent injury. The response variable was the number of predated and surviving individuals per replicate, analyzed as bi-

nomial data. Because tethering removes an individual's capacity to actively evade predators, absolute predation proportions from this design should not be extrapolated as estimates of natural, untethered predation rates in the field; instead, tethering was used to hold baseline vulnerability constant across treatments and thereby isolate the relative effect of ALAN, expressed as an odds ratio between ALAN and control replicates. All analyses were performed in R 4.3.3 (R Core Team 2024).

### Data analysis

A Generalized Linear Mixed Model was fitted to MCH data only using glmmTMB (Brooks et al. 2017). The response was the number of predated and surviving individuals per replicate (binomial, logit link). Fixed effects were light condition (ALAN versus natural-darkness control), season (spring versus summer), and their interaction. Experimental night was included as a random intercept to account for night-to-night variation. The need for the interaction term was assessed via likelihood-ratio test (LRT) comparing the full model against an additive model under maximum likelihood. Type-III Wald  $\chi^2$  tests (car package; Fox and Weisberg 2019) provided complementary inference.

Table 1. Descriptive summary of tethering experiments at Mar Chiquita (MCH) across two deployment periods and contextual comparison with the published San Antonio Oeste (SAO) result. Values are mean  $\pm$  SD across replicates per treatment per deployment period. MCH data are primary (this study); SAO data are from Nuñez et al. (2021a) and are incorporated solely in the secondary contextual analysis.

| Season                  | Treatment                | N replicates | Total crabs/total predated | Mean proportion $\pm$ SD |
|-------------------------|--------------------------|--------------|----------------------------|--------------------------|
| Spring                  | Natural darkness         | 9            | 43/27                      | $0.66 \pm 0.35$          |
| Spring                  | ALAN ( $\approx 38$ lux) | 9            | 45/39                      | $0.87 \pm 0.22$          |
| Summer                  | Natural darkness         | 23           | 113/17                     | $0.15 \pm 0.20$          |
| Summer                  | ALAN ( $\approx 38$ lux) | 23           | 110/13                     | $0.11 \pm 0.18$          |
| SAO (published), summer | Natural darkness         | 20           | 100/22                     | $0.22 \pm 0.20$          |
| SAO (published), summer | ALAN                     | 20           | 100/69                     | $0.69 \pm 0.26$          |

Note: each replicate pools the outcomes of three to five stakes, each holding one individually tethered juvenile (mean  $\approx 4$ -5 crabs per replicate); see Tethering experiments.

Marginal ( $R^2_m$ ) and conditional ( $R^2_c$ ) coefficients were estimated with the performance package (Nakagawa and Schielzeth 2013). Residual diagnostics used DHARMA (Hartig 2018). Pairwise contrasts (ALAN versus natural darkness within each season) were computed using emmeans (Lenth et al. 2020) and are reported as odds ratios (OR) with 95% confidence intervals. Unlike the GLMM, which appropriately weights each replicate by its own number of tethered individuals through the binomial structure, the descriptive summary in Table 1 (mean proportion  $\pm$  SD) is an unweighted average across replicates, giving each replicate equal weight regardless of how many individuals it contained.

As a sensitivity check on the choice of random-effect structure, we additionally fitted two block-sensitivity models on the MCH data: one adding block identity nested within season as a further random intercept alongside night, and one adding it as a fixed effect. Both models supported the same qualitative conclusions as the primary model (light effect and light  $\times$  season interaction both remained significant,  $p < 0.01$  in both cases), and the block-random model was preferred by AIC ( $\Delta AIC = 13.5$  relative to the primary model; likelihood-ratio test for the added block term:  $\chi^2_1 = 15.46$ ,  $p < 0.001$ ). We nonetheless report the primary model (night only) as our main result because it directly matches the random-effect structure used in the published SAO reference model, keeping the three contexts compared under one consistent specification; the block-sensitivity results are summarized here to demonstrate that our main conclusions do not depend on this choice.

To visualise the ALAN-sensitivity gradient across all three empirical contexts and construct the forest plot (Figure 3 B), we additionally fitted a GLMM replacing season with a three-level context factor (MCH summer, MCH spring, SAO summer), retaining night as a random intercept, and including the published SAO dataset (Nuñez et al. 2021a) alongside the primary MCH data. This model was used solely to generate model-predicted probabilities and odds ratios for all three contexts on a common parameter scale; all primary inference

is based on the MCH-only model. The published SAO summer survival OR (OR<sub>surv</sub> = 0.12, 95% CI [0.04-0.35]; Nuñez et al. 2021a) was independently verified by algebraic inversion (OR<sub>pred</sub> =  $1/0.12 = 8.33$ , 95% CI [2.86-25.00]).

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## RESULTS

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### Descriptive patterns

At MCH, baseline predation (natural-darkness control) differed markedly between seasons: the mean predation proportion was  $0.66 \pm 0.35$  (SD) in spring versus only  $0.15 \pm 0.20$  in summer, reflecting the substantial difference in predation pressure between the settlement season and the post-recruitment period (Table 1). Under ALAN, spring predation rose to  $0.87 \pm 0.22$ , whereas summer predation remained essentially unchanged at  $0.11 \pm 0.18$ , a divergence that suggests a season-dependent ALAN response already at the descriptive level (Figure 3 A). At the published SAO site, mean control predation was  $0.22 \pm 0.20$  and rose to  $0.69 \pm 0.26$  under ALAN (Nuñez et al. 2021a), producing the highest absolute ALAN effect among the three contexts examined.

### Light $\times$ season interaction at MCH

The MCH-only GLMM explained a large proportion of total variation ( $R^2_c = 0.884$ ;  $R^2_m = 0.591$ ), with the night random intercept absorbing substantial residual variation (variance = 0.94, SD = 0.97; ICC  $\approx 0.22$ ), confirming that night-to-night differences warranted their inclusion in the model. DHARMA residual diagnostics showed no violations of model assumptions (uniformity  $p = 0.141$ ; dispersion  $p = 0.146$ ; outliers  $p = 1.000$ ). The LRT confirmed that the light  $\times$  season interaction significantly improved fit over the additive model ( $\chi^2_1 = 6.09$ ,  $p = 0.014$ ,  $\Delta AIC = 4.09$ ). Type-III Wald tests supported the importance of season ( $\chi^2_1 = 8.99$ ,  $p$

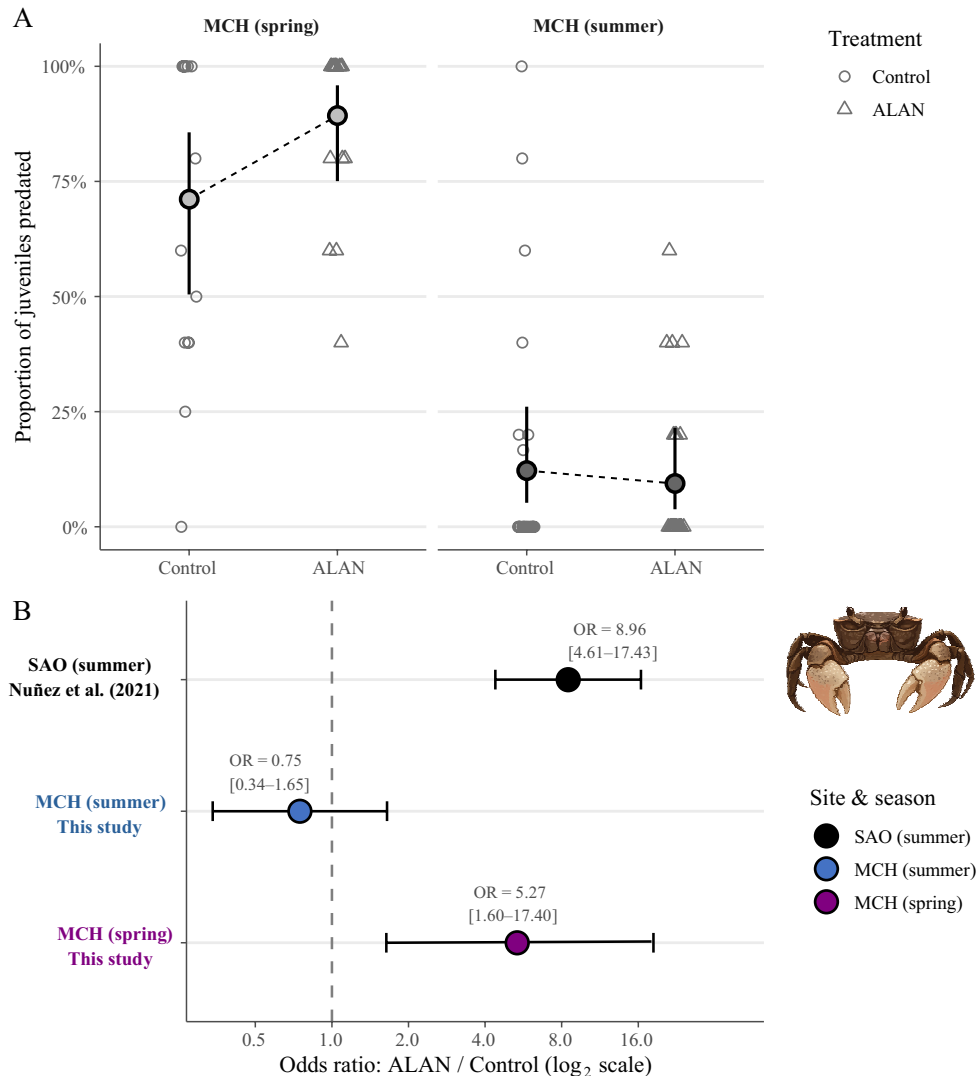


Figure 3. Experimental results for *Neohelice granulata* at MCH and contextual comparison with SAO. (A) Proportion of juveniles predated per replicate, by season. Open circles/triangles show individual replicates (circle = Control, triangle = ALAN); filled symbols show the GLMM-estimated marginal probability  $\pm$  95% CI for each treatment, connected by a dashed line. (B) Forest plot of ALAN effect sizes (odds ratio, log<sub>2</sub> scale; dashed line at OR = 1, the null). Points show the estimated OR and bars the 95% CI. Numeric OR values with 95% CI are given for each context.

= 0.003) and the interaction ( $\chi^2_1 = 7.42$ ,  $p = 0.006$ ; Table 2).

Pairwise contrasts showed that the ALAN effect was strongly season-dependent (Figure 3 A and B; Table 2). In spring, ALAN significantly increased predation odds relative to natural darkness (OR = 5.77, 95% CI [1.67–19.89],  $p = 0.006$ ): the odds of

a juvenile being predated were approximately 5.8 times higher under ALAN, with GLMM marginal probabilities of 0.91 (ALAN) versus 0.64 (control). In summer, by contrast, ALAN had no detectable effect on predation probability (OR = 0.75, 95% CI [0.34–1.65],  $p = 0.470$ ), with marginal probabilities of 0.09 (ALAN) and 0.12 (control).

Table 2. Model estimates for ALAN effects on juvenile predation. Primary analysis (MCH-only GLMM):  $R^2m = 0.591$ ,  $R^2c = 0.884$ ; LRT for light  $\times$  season:  $\chi^2_1 = 6.09$ ,  $p = 0.014$ ,  $\Delta AIC = 4.09$ . DHARMA diagnostics: no violations. Secondary analysis (three-context GLMM, MCH + SAO):  $\chi^2_2 = 22.69$ ,  $p < 0.001$ . OR > 1 indicates ALAN increases predation odds.

| Context     | Model     | OR   | 95% CI        | p/data source                      |
|-------------|-----------|------|---------------|------------------------------------|
| MCH, summer | Primary   | 0.75 | [0.34, 1.65]  | $p = 0.470$ ; this study           |
| MCH, spring | Primary   | 5.77 | [1.67, 19.89] | $p = 0.006$ ; this study           |
| MCH, summer | Secondary | 0.75 | [0.34, 1.65]  | $p > 0.05$ ; this study            |
| MCH, spring | Secondary | 5.27 | [1.60, 17.40] | $p < 0.05$ ; this study            |
| SAO, summer | Secondary | 8.96 | [4.61, 17.43] | $p < 0.001$ ; Nuñez et al. (2021a) |

OR = odds ratio (ALAN/Control); CI = 95% confidence interval. The SAO odds ratio used throughout (secondary three-context model) is independently cross-checked by algebraic inversion of the published SAO survival OR (Nuñez et al. 2021a):  $OR_{pred} = 1/0.12 = 8.33$ , 95% CI [2.86-25.00], consistent with the model-based estimate.

Contextual gradient in ALAN sensitivity

The secondary three-context model confirmed that the ALAN effect differed significantly across contexts (light  $\times$  context interaction:  $\chi^2 = 22.69$ ,  $df = 2$ ,  $p < 0.001$ ; conditional  $R^2 = 0.809$ , marginal  $R^2 = 0.654$ ). Effect sizes for each context: SAO summer OR = 8.96 [4.61-17.43], MCH spring OR = 5.27 [1.60-17.40], MCH summer OR = 0.75 [0.34-1.65]. These results reveal a clear ordered gradient in ALAN sensitivity (Figure 3 B; Table 2): SAO summer > MCH spring > MCH summer, which parallels the seasonal ranking in baseline (no-ALAN) predation at MCH itself (0.66 in spring versus 0.15 in summer; Table 1).

DISCUSSION

The seasonal variation in the ALAN effect at MCH (significant in spring, entirely absent in summer) together with the published extreme sensitivity at SAO (Nuñez et al. 2021a), produces an ordered gradient that is most consistent with the amplifying hypothesis (HB): the capacity of ALAN to amplify predation scales with the susceptibility state of the system (the combined outcome of adult

nutritional condition, juvenile vulnerability and habitat complexity) rather than with light intensity alone. Within MCH, where site and protocol are held constant, this susceptibility state is directly indexed by seasonal baseline predation itself; the SAO comparison extends this pattern to an independently studied, chronically high-susceptibility population, though its raw baseline predation value is not directly comparable across studies (see Caveats and limitations). These results indicate that the impact of ALAN on predation may be as dependent on the ecological state of the system as on the intensity of the light itself.

Among the four hypotheses considered, the observed pattern is not consistent with the compensatory hypothesis (HC), which would predict the strongest effect at the lowest-susceptibility context (MCH summer) rather than the weakest, nor with the additive null (HA), which would predict a detectable effect even at MCH in summer. The pattern is also not consistent with a non-linear threshold model (HD) in its simplest form, since the ALAN effect continued to increase from MCH spring to SAO rather than plateauing or declining at the most susceptible end of the gradient. Taken together, these results are consistent with studies showing that ALAN affects foraging most strongly where predators are most motivated

(e.g. Becker et al. 2013; Czarnecka et al. 2019) and that food-web strengthening by ALAN scales with predator activity levels (Sanders et al. 2018). It is emphasized, however, that with only three, non-equivalent contexts, namely two deployment periods at one site plus a single external, independently studied population, our design can rule out the two hypotheses whose qualitative predictions are clearly violated (HC, HA) but cannot formally discriminate between the amplifying (HB) and threshold (HD) hypotheses, nor test any functional form statistically; doing so would require a continuous gradient of independently sampled susceptibility states, which was beyond the scope of the present study (see Caveats and limitations below).

### Adult nutritional state as a motivational gateway for ALAN effects

A plausible explanation for why ALAN amplified predation at MCH in spring but not in summer may lie in the difference in adult energetic state, although we did not measure nutritional condition directly in the crabs used in this study. Spring corresponds to the onset of the reproductive season of *N. granulata* at MCH (Luppi et al. 2013) and published hepatosomatic indices for this population reach their seasonal minimum in spring (Bas et al. 2014), a nutritional context that transiently resembles the chronic protein limitation reported for SAO adults year-round (Bas et al. 2019). If nutritionally stressed adults are more motivated to exploit any increase in foraging opportunity, ALAN could provide exactly that by extending the period of effective visual predation on the intertidal surface (see Sztarker et al. 2020; Nuñez et al. 2021b). This remains a proposed mechanism consistent with the seasonal pattern we observed, rather than a directly tested one; by summer, adults have presumably restored somatic reserves after reproduction, which could explain the complete absence of an ALAN effect during this season.

### Juvenile vulnerability and the temporal window of settlement-season risk

We did not measure megalopa settlement in this study, so the timing of settlement relative to our two deployment periods is not resolved by our data. The juveniles used in our tethering experiments (12-14 mm CW) were small relative to the adults (30-45 mm CW) and are likely to be vulnerable to adult predation: at this size they may still shelter opportunistically in adult burrow networks rather than in individual burrows, which would confer only incomplete refuge from surface-active predators (Méndez Casariego et al. 2009). Predation by adults is size-dependent in *N. granulata*, with larger juveniles being less vulnerable (Luppi et al. 2001). At the population level, juveniles recruiting in spring are expected to outgrow the most vulnerable size classes within a few months, and by February most individuals present in the population would have had time to excavate individual burrows; because summer animals in our tethering trials were freshly collected rather than tracked from the spring cohort, this is presented as a population-level seasonal pattern rather than a demonstrated trajectory of the same individuals. The temporal coincidence of maximum juvenile vulnerability and adult nutritional stress in spring therefore creates a narrow but critical window during which MCH's normally buffering habitat complexity is partially bypassed.

### Habitat complexity as a partial buffer against ALAN effects

Even within the spring vulnerability window, the MCH spring ALAN effect (OR = 5.27, from the secondary three-context model) was lower than that at SAO (OR = 8.96, same model, with broadly overlapping confidence intervals; the published SAO survival OR is independently cross-checked in Table 2), which suggests that the dense burrow network at MCH partially, but not completely, buffers juveniles even before self-excavation is

complete. Habitat complexity appears to act as a sensitivity floor: the dense burrow network at MCH reduces the effective foraging range of adult crabs under ALAN by providing refugia to pre-burrow juveniles (Méndez Casariego et al. 2009), and the organic-rich muddy substrate may limit the visual advantage conferred by illumination compared with the open sand-cobble flats of SAO. The quantitative difference between spring MCH and SAO, approximately 0.8 units on the log OR scale (a ratio of  $\approx 1.7$  between the two odds ratios), could be attributed to habitat structural complexity as a third buffering axis, dampening but not eliminating ALAN-driven predation when the motivational and vulnerability axes are simultaneously elevated (Czarnecka et al. 2019).

### Demographic consequences and cumulative population impact

The spring window of ALAN sensitivity at MCH coincides with the settlement period that contributes to annual cohort size (Luppi et al. 2013; Bas et al. 2019). We did not measure population-level recruitment or perform demographic modelling in this study, so we cannot quantify the net effect of ALAN on cohort size. We note, however, a tension worth flagging for future work: Nuñez et al. (2025) reported that ALAN increased megalopa settlement at MCH, while the present results show that a larger proportion of juveniles present during the spring settlement window are predated under ALAN. Whether these two effects combine to increase or decrease net recruitment cannot be determined from either study alone and would require tracking settlement and post-settlement survival concurrently.

### Caveats and limitations

Several lines of evidence support the robustness of the spring result despite its narrower replication history: the light  $\times$  season interaction remains significant whether block is included or excluded from

the model, the effect is consistent in direction and approximate magnitude across the primary model, the block-sensitivity models, and the secondary three-context model, and the resulting OR (5.27–5.77 depending on model specification) sits within the ordered gradient observed across all three predatory contexts.

A second limitation concerns predator identity. At SAO, paired exclusion/inclusion cage experiments identified adult conspecifics as the dominant source of juvenile mortality (Nuñez et al. 2021a); no equivalent experiment was conducted at MCH in the present study. Cannibalism by adult conspecifics remains the most parsimonious explanation for the MCH results, given the well-documented importance of cannibalism in this species (Luppi et al. 2001), but we cannot exclude a contribution from other predators (shorebirds or fish, for instance) active during tidal flooding at MCH.

A further limitation is temporal: our comparison spans a single spring and a single summer at MCH, rather than multiple years of each season. Inter-annual variation in adult condition, juvenile settlement timing, or predator abundance could all shift the magnitude of the ALAN effect independently of season *per se*, and our design cannot distinguish a true seasonal effect from a one-off difference between these particular spring and summer deployments. Accordingly, throughout this manuscript ‘spring’ and ‘summer’ should be read as labels for these two specific 2021–2022 deployment periods, used as an interpretive framework, rather than as a replicated seasonal factor in the statistical sense.

Finally, and most importantly, with only three available contexts we can rule out the additive (HA) and compensatory (HC) hypotheses as sole explanations, but we cannot formally discriminate between the amplifying (HB) and non-linear threshold (HD) hypotheses, nor treat the amplifying hypothesis as statistically confirmed; doing so would require a larger number of independently sampled contexts spanning a continuous susceptibility gradient than the three available here, which was beyond the scope of the present study.

## Management implications and concluding remarks

The temporal dynamics of ALAN sensitivity documented here suggest that targeted, rather than uniform, lighting restrictions during the juvenile settlement season could be a more efficient conservation approach than year-round restrictions, though we did not evaluate the costs or feasibility of any specific lighting management scheme. Two concrete, testable interventions follow directly from our results: (i) shifting ALAN spectral output toward amber or red, long-wavelength lighting in areas adjacent to settlement habitat, which is expected to reduce visual conspicuousness of prey to crustacean predators relative to cold-white LED (this expectation should be verified for *N. granulata* specifically before implementation); and (ii) targeted night-time lighting curfews strictly confined to the settlement window once it has been defined locally, rather than year-round dimming. Neither option has been tested experimentally here, and both would need site-specific cost and feasibility assessment. The period of highest risk at structurally complex intertidal sites appears to be the juvenile settlement season of *N. granulata*, whereas at structurally simpler sites like SAO, risk may be elevated for longer given the year-round nutritional stress reported there (Nuñez et al. 2021a). Season-specific reductions in ALAN intensity or duration during the settlement window, where feasible, represent one potential option for balancing coastal lighting needs against conservation of intertidal crab populations.

Over two deployment periods at the same site, the capacity of ALAN to amplify apparent predation in *N. granulata* was strongly context-dependent and scaled with the susceptibility state of the system, a pattern most consistent with, though not a formal statistical confirmation of, the amplifying hypothesis (HB). The ordered gradient in ALAN sensitivity (SAO summer > MCH spring > MCH summer) is plausibly explained by the combined severity of adult nutritional stress, juvenile pre-refuge vulnerability, and habitat openness (fac-

tors we did not measure directly and infer from the seasonal and site context) rather than by baseline predation intensity *per se*. These results indicate that even high-quality, complex habitats may be seasonally susceptible to ALAN, that single-season assessments may underestimate cumulative predation exposure at the population level (a hypothesis we could not test directly without demographic data), and that the conservation value of darkness is highest, and targeted lighting management most justified, during the juvenile settlement window.

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## Ethics and integrity statement

All experimental procedures complied with Argentine wildlife research regulations (Resolution MAA 264/06 and subsequent provincial permits) and with institutional guidelines for the use of animals in research and sampling of intertidal invertebrates.

## Data availability statement

The datasets and code generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Funding declaration

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## Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Declaration of use of Artificial Intelligence tools

During the preparation of this manuscript, the authors used an AI language model (Claude, Anthropic) solely to improve the English of the text. The authors reviewed and edited the output and took full responsibility for the content of the publication.

## Author contributions

Jesús D. Nuñez: methodology design; laboratory work; field work; writing original draft; writing-review and editing. Ruben A. Robles: methodology design; laboratory work; field work. Macarena Pérez García: field work; writing original draft; writing-review and editing. Camila B. Merodio: field work; writing-review and editing. M. Guadalupe Vázquez: laboratory work; field work. Tomás A. Luppi: methodology design; laboratory work; field work; writing-review and editing.

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