

Flagship species as subterranean monitoring tools: a case study in anchialine ecosystems in Lanzarote (Canary Islands)

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Research Article

Keywords: flagship species, umbrella species, coastal aquifers

Posted Date: March 20th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-9141619/v1>

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Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Biodiversity and Conservation on July 8th, 2026. See the published version at <https://doi.org/10.1007/s10531-026-03389-7>.

Abstract

Anchialine ecosystems support distinct biological communities that sustain key biogeochemical functions. Yet, they are increasingly threatened by global change and local anthropogenic disturbances. Because routine sampling is hard, long-term biodiversity baselines are rare, limiting evidence-based management. We compiled and standardized 1980–2025 abundance records from Lanzarote (Canary Islands) for protected crustaceans that act as conservation flagships: the jameíto *Munidopsis polymorpha* (Decapoda, Munidopsidae) and the Canarian morlocks *Morlockia ondinae* and *M. atlantida* (Remipedia, Morlockiidae). We integrated and analysed data from dive transects, direct counts and photo-quadrats with generalized additive models to test for (i) interannual changes and (ii) effects of tidal forcing and light regime across cave sectors. The jameíto showed strong spatial aggregation, with densities 3–4 orders of magnitude higher in food-enriched entrances and depositional areas than in dark passages, whereas the morlocks occurred sparsely in water-column habitats. Apparent interannual changes were highly specific to cave localities and sections for both taxa, consistent with their redistribution within the anchialine network rather than a system-wide population trend. Tidal dynamics explained short-term variability in both species, with densities decreasing as tidal range increased. Light effects were detectable only for the jameíto in illuminated sectors, where densities were lower during daytime. Together, these complementary bottom and water column indicators provide a practical, long-term framework for monitoring anchialine ecosystems and guiding management actions in Lanzarote and comparable coastal aquifers.

1. Introduction

Global subterranean ecosystems are increasingly threatened by anthropogenic activities (Mammola et al. 2019), and yet, their biodiversity is not systematically monitored, protected, and managed (Sánchez-Fernández et al. 2021; Wynne et al. 2021). The intrinsic inaccessibility of most subterranean ecosystems, logistical constraints, and dependence on specialized sampling techniques severely limit the feasibility of systematic surveys, resulting in fragmented records and a striking scarcity of long-term time series (Ficetola et al. 2019; Mammola et al. 2021; Salvidio et al. 2025). As a consequence, population trends for subterranean species remain largely unknown (Salvidio et al. 2025)—with the possible exception of some conspicuous groups such as bats (e.g., Machado et al. 2017; Whiting et al. 2021). It follows that assessments of conservation status are frequently based on indirect evidence, expert judgement, or habitat-level proxies rather than quantitative demographic indicators (Mammola et al. 2022; Nanni et al. 2023; Salvidio et al. 2025). This lack of temporal resolution constrains the detection of gradual population declines, delayed responses to disturbance, early warning signals of ecosystem change and, ultimately, hampers the setting and implementation of effective conservation objectives and measures.

The challenges highlighted above are particularly prevalent in subterranean ecosystems that require additional effort for sampling and monitoring: subterranean aquatic environments in general, and in flooded cave passages in particular. Density-stratification in unconfined coastal aquifers separates a meteoric freshwater lens from underlying recirculating seawater. At their interface, a subterranean estuary creates a biogeochemical reaction zone that modulates the chemistry of groundwater before its discharge to the coastal sea (Moore 1999; Santos et al. 2021). The functioning of coastal aquifers strongly depends on specialized microbial and animal communities that drive key biogeochemical processes along salinity

gradients in groundwater (Brankovits et al. 2017). Many of these organisms exhibit high levels of local endemism and belong to lineages that are rare or absent in marine or inland waters (Iliffe and Kornicker 2009). Because of this distinctive biota and their characteristic hydrological settings, caves and pools in coastal aquifers were originally termed ‘anchialine’, to denote that they are influenced by tides despite their inland position and the absence of apparent connection to the ocean (Holthuis 1973; Stock et al. 1986).

Lanzarote, a volcanic island in the Canary Islands archipelago (Spain), offers a compelling case for studying anchialine biodiversity and developing general conservation approaches. Over 130 years of research have led to the discovery of 38 endemic species with remarkable phylogenetic origins and specialized functional traits (Martínez et al. 2016). Some of these organisms remain with uncertain phylogenetic affinities and have historically been referred to as “living fossils” (García-Valdecasas, 1985; Koenemann et al. 2009), whereas others exhibit strong affinities to deep-sea lineages (Gonzalez et al. 2018, 2021; Martínez et al. 2013). However, the importance of Lanzarote’s anchialine ecosystems extends beyond its species list. This ecosystem supports a broad range of ecosystem services, including provisioning, regulating and cultural functions, ranging from irrigation and salt production to tourism, scientific research, and education (Martínez et al. 2019; Mammola et al. 2026). These services depend on groundwater quality, which ultimately relies on the structure of these communities of organisms and their functions (Di Nezio et al. 2025). In Lanzarote, anchialine habitats have long been protected through area-based conservation measures, namely the designation of a network of protected areas aimed at safeguarding the physical habitat structure and hydrological connectivity, while regulating human fruition and disturbance. While area-based conservation approaches offer broad spatial coverage (Mammola et al. 2024), their effectiveness depends not only on managing direct and indirect pressures, including diffuse pressures, but also on addressing drivers that often originate beyond protected area boundaries (Huggins et al. 2023). As a complementary strategy, species-based conservation often focuses on conspicuous, charismatic organisms whose habitat requirements overlap with those of many other anchialine taxa (umbrella species) and that can be used as ambassadors for biodiversity conservation (flagship species). Flagship and umbrella species can concentrate monitoring efforts, generate public engagement, and provide tractable indicators of ecosystem change (Bowen-Jones and Entwistle 2002; Jarić et al. 2025).

Lanzarote’s anchialine ecosystems harbours iconic species that not only represent outstanding examples of cave evolution, but also have notorious popularity amongst the human inhabitants of the island (Iliffe et al. 2025). These species are the Canarian morlocks (*Morlockia ondinae* García-Valdecasas, 1985 and *M. atlantida* Koenemann et al. 2009; named after the monsters in H.G. Wells’ novel ‘The Time Machine’), the top predators along the saline water column of La Corona lava tube (García-Valdecasas 1984); and the squat lobster (*Munidopsis polymorpha*), popularly known as “jameíto” or “grillo blanco” (Koelbel 1892), a ubiquitous bottom consumer feeding on detritus and carrion through the anchialine system (Wilkens et al. 1986; 1990; Wilkens, 2022). *Morlockia ondinae* and *Munidopsis polymorpha* are currently listed as at risk of extinction in the Spanish Catalogue of Threatened Species and the Canary Islands Catalogue of Protected Species and have been selected as umbrella species by the Government of the Canary Islands and the UNESCO Geopark of Lanzarote and the Chinijo Islands (Martínez et al. 2019; Iliffe et al. 2025). Furthermore, the jameíto was officially designated as the animal symbol of Lanzarote under Law 7/1991. This role has recently been reinvigorated through multi-channel communication campaigns that aimed to position the jameíto as a flagship species, leveraging its striking morphology and charisma to raise awareness of anchialine ecosystems and their

distinctive conservation challenges. The jameíto is ubiquitous in Lanzarote's cultural heritage (Camacho et al. 2025) and has more recently been reimagined as a comic-style character for science outreach ("fictional flagship" *sensu* Jarić et al. 2025), serving as the official mascot of the Lanzarote and Chinijo Islands UNESCO Global Geopark. This role builds on a much older heritage, as documented by Oskar Simony, who collected the type material after local shepherds pointed him to a flooded coastal cave where they reported "grillos blancos" (white crickets, Koelbel, 1892). Indeed, the jameíto is depicted in the coat of arms of the municipality of Haría—a municipality in the Northeastern tip of Lanzarote, where most anchialine ecosystems concentrate. In contrast to the jameíto, the morlocks represent the hidden fraction of Lanzarote's anchialine biodiversity and the strict protection constraints that come with it. All sites where remipedes occur are inaccessible to the general public, which limits direct encounter, making representation through illustration, storytelling, and mediated imagery especially important (Mammola et al. 2025). Together, these two species offer complementary flagship potential: the jameíto as a culturally embedded, conspicuous symbol, and the morlocks as an emblem of rarity, endemism, and the conservation value of the unseen subterranean realm.

In this study, we synthesize and analyse the available data on the distribution of the Canarian morlocks and jameíto to improve their management and exploit their potential as flagship and umbrella species in the anchialine ecosystems of Lanzarote. We integrate published information (peer-reviewed literature and grey sources between 1980–2015) with newly conducted standardized surveys (2015, 2024–2025) to address two critical objectives for the management of these species. First, we test whether interannual changes in abundance are detectable across localities and cave sectors, which could indicate population decline or redistribution within the anchialine network. Second, we quantify the extent to which short-term environmental cycles, specifically tides and light, explain observed variability in abundance, using snapshot surveys across the system and high-frequency time series in Los Jameos del Agua anchialine pool. We hypothesize stronger light effects in passages near skylight and stronger tidal effects within dark passages, with species-specific responses reflecting ecological differences. Specifically, we expect greater light effects on the jameíto due to its benthic foraging, and greater tidal effects on the Canarian morlocks due to their feeding in the water column on periodic prey fluxes. Using generalized additive models, we estimate the effects of tides and light on the response scale to inform and support conservation decision-making.

2. Material and methods

2.0. Rationale

We analysed the abundances of the jameíto (*Munidopsis polymorpha*) and the morlocks (*Morlockia ondinae* and *M. atlantida*) in the anchialine ecosystems of Lanzarote accounting for tidal and sunlight effects using two complementary sampling approaches: (1) snapshot surveys, which provide broad spatial and interannual coverage across localities, and (2) iterative count series, which quantify high-frequency variability in the jameíto within a day and allow inference on short-term tidal and light effects (Fig. 1A-C).

Morlocks' abundances are reported as *Morlockia* spp. because *M. ondinae* and *M. atlantida* are distinguished by subtle morphological and limited genetic differences that cannot be resolved during non-invasive underwater surveys (Koenemann et al. 2009). Individuals were therefore pooled and treated as a single

operational taxonomic unit, assuming comparable ecological roles of the two morlocks within the cave system.

Snapshot surveys consisted of a single 0.5–2 h visit to a locality. These surveys provide a broader temporal perspective for assessing differences among sites and years, while allowing us to account for confounding ecological factors such as sunlight and tidal cycles. Importantly, snapshot surveys represent the only feasible approach for estimating abundances inside flooded cave passages, where the challenging environment prevented us from performing iterative count series (Mammola et al. 2021). Snapshots were implemented using three sampling designs: (i) direct counts in the entrance of Túnel de la Atlántida and Charcos de Luis (Fig. 1E), (ii) diving transects in Cueva de los Lagos and Túnel de la Atlántida (Fig. 1F), and (iii) photo-quadrats in Los Jameos del Agua (Fig. 1G).

Iterative count series, in contrast, consisted of repeated observations conducted every 15 minutes at fixed points over 3–5 h periods (Fig. 1H). Fixed points were defined by selecting individual rocks of known surface that have been previously used for abundance estimates in the 1980s (Wilkins et al. 1990). Iterative count series were specifically designed to capture short-term variability in abundance associated with diel changes in sunlight and tidal dynamics within a single day. This approach was implemented in Los Jameos del Agua, where pronounced fluctuations in abundance of the jameíto were observed over short time spans.

The adoption of these non-invasive approaches was necessary because current conservation regulations governing both species prohibit the manipulation or handling of large numbers of individuals, precluding the use of capture–recapture or other intrusive population-estimation methods.

2.1. Sampling design

We carried out snapshot surveys by diving transects in Cueva de los Lagos and Túnel de la Atlántida (Fig. 2E, G-L). SCUBA divers surveyed Cueva de los Lagos (Fig. 2G) and the twilight section of Túnel de la Atlántida (1–30 m). In addition, rebreather divers equipped with diver propulsion vehicles (*a.k.a.* scooters) surveyed the dark passages of Túnel de la Atlántida, reaching as far as Montaña de Arena at 700 m penetration (García-Valdecasas, 1985; Lario et al. 2022; Fig. 2M). Divers operated in pairs, each covering one flank of the lava tube. When an individual was observed, the sighting was announced to avoid double counts. To standardize transects of varying length, sampling effort was quantified as surveyed distance, and abundances were expressed as densities (individuals per linear meter of cave).

Snapshot surveys by direct counts were performed at the entrance of Túnel de la Atlántida and Charcos de Luis (Fig. 1E; 2I; 2K), where two observers counted all visible animals from the water's edge (Fig. 1E). Search time was standardized to 20 minutes per locality. To obtain densities comparable to other cave sites, abundances were expressed as densities (individuals per linear meter): at Charcos de Luis, counts were standardized to the length of each pool; whereas at the entrance of Túnel de la Atlántida, they were standardized to 10 meters, corresponding to the maximum distance visible from the water's edge, before the drop-off leading to the main cave passage.

Snapshot surveys using photo-quadrats were conducted at Los Jameos del Agua, where high densities of the jameíto and bottom complexity render both transects and direct counts inefficient (Fig. 1G; Espino and

Herrera, 2002b). Abundances were therefore quantified from photographs of non-overlapping, randomly located bottom patches taken with a camera mounted on a 1-meter rod to maintain a constant focal distance. Each image was treated as an independent spatial replicate (non-overlapping quadrat) for estimating within-survey density. To avoid pseudoreplication, photoquadrat counts were summarized at the survey/event level before interannual analyses. Counts were normalized to area (m²) using focal-distance calibration.

Iterative count series using fixed points were performed at Los Jameos del Agua, where abundances of the jameíto exhibit pronounced short-term fluctuations at dusk and dawn (Fig. 1H). Repeated counts were conducted every 15 minutes over a 3–5 h period on pre-selected rocks of ca. 0.25 m² surface (modified from Wilkens et al. 1990). Fixed points were defined at both the eastern (Jameo Chico; cave downstream) and western (Jameo Grande; upstream) ends of the cave pool, which differ in sunlight exposure and tidal influence (Figure S1).

Additional information on the morphology of each locality as well as the methods followed to make the counting is included in the Supplementary Information 1; specific methods followed in Túnel de la Atlántida twilight section are described in Supplementary Information 3.

2.2. Compilation of the dataset

Data were collected during monitoring surveys performed in 2015, 2017, 2023 and 2024 promoted by the Government of the Canary Islands as part of conservation programs targeting the jameíto and the morlocks.

These new data were complemented with records compiled from publications and technical reports. All those published data were collected by members of our team, ensuring comparability of our surveys. For Cueva de los Lagos, we included diving transects performed in 2002, 2006, and 2008 (Espino and Herrera 2002a,b; Martínez and Palmero 2006; Núñez and Brito 2008a, b). For Túnel de la Atlántida, we compiled diving transects and direct counts performed in 1994 and 2008 (Jantschke 1994; Núñez and Brito, 2008a, b). For Los Jameos del Agua, we included fixed point iterative count series performed in 1980, 1983, 1984, 1986, and 1989 (Wilkens et al. 1990), and snapshot survey by photo-quadrats taken in 2002 (Espino and Herrera 2002b). Unfortunately, raw data for the 1980s was lost, and we could only include the monthly average numbers per time in our models, limiting the interpretation of the long term model of the iterative counting in Los Jameos del Agua, and preventing us from including tidal effects on it (Wilkens et al. 1990).

The final dataset was recorded from 155 unique sampling events (119 targeting jameíto; 36 targeting the morlocks) spanning 44 years and 5 localities. Details of each survey, whether published or not, including raw data, dates, localities, and sampling methods are available along with the code used in the analyses at github.com/amartinezgarcia/flagshipspeciesLanzarote.

2.3. Data analysis and visualization

2.3.1. Covariates and effort offset

Each snapshot survey was treated as a unique sampling event defined by a combination of date, time interval, and locality. Events were further subdivided by cave section to capture spatial heterogeneity in illumination, organic matter availability, and tidal dynamics that are expected to influence species abundance. Cueva de los

Lagos was divided into four sections, all surveyed using diving transects: the three phreatic tidal lakes (Lakes 1–3) and the terminal flooded sump, all located in complete darkness (Fig. 1E, 1G). Túnel de la Atlántida was divided into four sections: the entrance section, corresponding to a shallow area before the cave drop-off that is artificially illuminated between 10:00 and 20:00 h each day; the twilight section (1–30 m penetration), which receives attenuated artificial light; the dark passages (30–650 m), in complete darkness; and Montaña de Arena (650–700 m), a section accumulating sediments that traps organic matter and supports presence of meiofauna (Martínez et al. 2019) (Fig. 1E, 1K, 1L, 1M). The entrance was evaluated by direct counts, the twilight section by SCUBA transects, and the dark section and Montaña de Arena by rebreather diving transects. Iterative count series were considered as separated series defined by date and time interval.

Due to the cave morphology, divers need to use the twilight section of Túnel de la Atlántida to check the gear before each dive, making it impossible to regularly count the abundances of the jameíto in the dives devoted to surveying the entire section. Therefore, twilight section abundances were counted only in dedicated dives with adapted methodology (Jantschke et al. 1994), which is summarized and presented in the Supplementary Information 3. Summary of the results are still shown in the main text and figures.

To define tide-related environmental variables, for each event we identified the preceding and subsequent sea-level peaks (high and low tide) (Fig. 1C). Sea-level peaks between 2009 and 2025 were extracted from the Arrecife tide gauge available at IOC Sea Level Monitoring site; earlier records were obtained from the tidal annuaries compiled in the ADMIRALTY TotalTide software (UK Hydrographic Office, Taunton, UK), either directly from the Arrecife tide gauge or extrapolated from the tide gauges at Puerto del Rosario or Casablanca. A fixed 90-min lag was added to all tide peaks to approximate the delay of tidal propagation inside the cave relative to the ocean (Wilkens et al. 2009; Martínez et al. 2016). From these tidal peaks, we computed the following variables: (i) semidiurnal cycle length (minutes), (ii) tide direction (ebb/flood), (iii) tidal semirange (difference between successive sea-level peaks in meters, used as a proxy for tidal strength), and (iv) cave tidal phase, scaled from 0 to 1, where values near 0 or 1 indicate tidal peaks, i.e. slack water, and 0.5 indicates mid-cycle, i.e. maximal currents).

Sunlight-related variables were computed from the sunrise and sunset times for each date, calculated at Los Jameos del Agua (WGS84: 29.157°N, 13.432°W) (Fig. 1B). From these values we derived: (i) day length (minutes), a day/night indicator, (ii) solar phase (scaled 0–1, where 0 corresponds to sunrise, 0.5 to sunset, and 1 to the following sunrise), and (ii) time to sunrise/sunset (minutes relative to these events).

We standardized sampling effort to obtain comparable density estimates across methods. For transects (Cueva de los Lagos, Túnel de la Atlántida), and direct counts (entrance of Túnel de la Atlántida, Charcos de Luis), effort was quantified as surveyed distance (m), and abundances were modelled as individuals per linear meter using a log(distance) offset. We preferred linear meters over surface because the three-dimensional cave bottom and the tidal fluctuations in water level render surface estimates unreliable. For photographic quadrats (Los Jameos del Agua), effort was the photographed area (m²). Abundances were modeled as individuals per square meter, using a log(area) offset. For descriptive figures, densities were transformed to individuals per linear meter for better comparison with other localities within the cave. In the iterative count series (Los Jameos del Agua), the sampled rocks had constant area; therefore, no offset was required, but rock identity and time-series were included as random effects.

Because Los Jameos del Agua and Túnel de la Atlántida are embedded within a touristic building, as is officially called, sampling dates and working hours were constrained by the opening schedule and operational requirements of the visitor centre, with monitoring activities developed after 5pm.

2.3.2. Data analyses

We analyzed counts of the jameíto and the morlocks using generalized additive models (GAMs) implemented with the function 'gam' in the package 'mgcv' version 0.1.11 (Wood 2011; 2017). We did not fit a single unified model across all localities because response units and sampling designs differ substantially among sites, and because distance from sea is confounded with locality-specific morphology and hydrological setting. Instead, we fit a separate additive model for the data in each locality (Túnel de la Atlántida, Los Jameos del Agua, Cueva de los Lagos, and Charcos de Luis) using a unified modelling framework, which allows consistent inference while respecting sampling structure. Counts were assumed to follow a negative binomial distribution with a log link to account for overdispersed count data, and smoothing parameters were estimated using restricted maximum likelihood (REML). Sampling effort was incorporated as a log-offset as described above. We selected GAMs to account for the non-linear responses of abundances to the cyclic changes in the tide and sunlight cycle.

Our two objectives, (1) assessing interannual variation in abundance and (2) quantifying the relative importance of tidal versus light-related drivers, were addressed within a unified generalized additive modelling framework. Snapshot survey models were fitted separately for each locality and species to account for differences in sampling design and environmental context. To strengthen inference on objective 2 at high temporal resolution, we additionally analysed fixed-point time series from Los Jameos del Agua, which capture within-day variability in the jameíto under changing tidal and light conditions.

For snapshot data for each species and locality (i.e. transects and direct counts), we fitted GAMs that simultaneously accounted for long-term annual change and short-term environmental variability. Interannual change was modelled by including a continuous, centered decimal year covariate, which estimates monotonic trends in abundance over the study period. Models were fit separately by locality and species to accommodate differences in sampling design, environmental context, and data availability. Where relevant, spatial heterogeneity within localities arising from physically isolated (e.g. Lagos 1–3 and Sifón within Cueva de los Lagos) or ecologically distinct (e.g. entrance, passages and Montaña de Arena within Túnel de la Atlántida) sections were accounted for by including them explicitly as a parametric factor, and, where justified by the sampling design, by allowing section-specific smooths or section x year interactions.

Within this unified modelling structure, the relative importance of tidal versus light-related drivers was evaluated by comparing alternative model specifications that differed in the environmental covariates included (Fig. 1A). Specifically, for each locality we fitted three candidate models including (i) tidal covariates only, (ii) sunlight covariates only, or (iii) both sets of covariates. Tidal predictors included tide direction (ebb/flood) and tidal strength (tidal semirange, z-scored) as parametric terms, as well as a cyclic smooth for tidal phase using cyclic cubic regression splines ($bs = "cc"$, knots fixed at 0 and 1) to enforce periodicity. Sunlight predictors included a day/night factor, a cyclic smooth for solar phase (same basis specification), and, where sample size permitted, a non-cyclic smooth for day length (min) using thin-plate regression splines to capture non-linear photoperiod effects independent of daily phase.

We set `select = TRUE` so unsupported smooths shrink to zero, reducing overfitting. Model selection was based on Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC), with lower values indicating better expected out-of-sample performance.

Because observations within series were time-ordered and moderately large, we fitted GAMs using the function `'bam'` in the package `'mgcv'` version 0.1.11 (Wood 2011, 2017), assuming negative binomial errors. Parametric terms included centered decimal year and position (upstream versus downstream). Series identity and fixed point were included as random-effect smooths to account for persistent differences and avoid pseudo-replication. Environmental variation within days was represented using the same tidal and light covariates as in the snapshot analyses. Temporal autocorrelation was addressed by fitting an AR(1) error structure, with ρ estimated from the median lag-1 Pearson residual correlation across series (truncated to 0.01–0.95) and using `AR.start` to reset the correlation at the first observation of each series. Competing tide-only, light-only, and combined models were compared using AIC and BIC.

For all models, we assessed residual diagnostics and smooth adequacy with the functions `'gam.check'` (R package `'mgcv'`) and `'appraise'` (R package `'gratia'` v. 0.10.0; Simpson, 2024). We examined non-linear collinearity using the function `'concurvity'` (R package `'mgcv'`). Where relevant, overdispersion was assessed with the function `'check_overdispersion'` (R package `'performance'` v. 0.11.0; Lüdtke et al. 2021). Effect sizes are reported as predicted linear densities (ind/m) with 95% CIs. Those are referred to as 'densities' subsequently for simplicity.

Figures were produced with the R package `'ggplot2'` (v3.5.1). For descriptive displays we show event-level abundances or densities by section and year, and (where appropriate) smooth relationships with phase variables, using the same cyclic basis used in the models. Interannual patterns are colour-coded by year to aid interpretation.

3. Results

3.1. Description of the observations

The jameíto *Munidopsis polymorpha* was recorded at all sampled localities, but with lower frequencies at Charcos de Luis (presence in 30% of surveys) and in the dark passages of Túnel de la Atlántida (62.5%).

Densities in Cueva de los Lagos varied between 0.03–0.15 ind/m in 2024 (N = 7 surveys), 0.01 ind/m in 2017 (N = 2) and 0.01–0.08 ind/m between 2002 and 2008 (N = 5) (Fig. 2H). We recorded densities in a similar range in the dark passages of Túnel de la Atlántida (0–0.018 ind/m; N = 12 in 2024; 0.01–0.03 ind/m, N = 4 in 2017; and 0.017–0.075 ind/m in 2008; Fig. 2H). In both sections, observations typically corresponded to scattered, wandering individuals, occasionally forming small aggregates (Fig. 2E).

Densities in Los Jameos del Agua and the entrance of Túnel de la Atlántida were up to four orders of magnitude higher. Specifically, we observed densities of 1.24–42.06 ind/m in Los Jameos del Agua between 2002 and 2024 (N = 18 surveys; Fig. 2H) and between 1.20–25.80 ind/m in the entrance of Túnel de la Atlántida between 2008 and 2024 (N = 38 surveys; Fig. 2H). Densities in these localities largely fluctuated during the daytime and tidal cycle (Section 3.3). In both localities, individuals were frequently observed in fixed

locations, feeding on the substrate. Intermediate densities were recorded in Montaña de Arena (0.17–0.73 ind/m; N = 12 surveys in 2024; Fig. 2H) and at the twilight section (0.13–5.13 ind/m; N = 8 surveys in 1994 and 2024; Figure S02).

We recorded scattered individuals of morlocks swimming in the dark water column of Cueva de los Lagos and Túnel de la Atlántida. In Cueva de los Lagos, we counted 1–2 individuals in 9 out of 13 surveys between 1994 and 2024 (~ 0.01 ind/m; Fig. 2B), whereas in the dark section of Túnel de la Atlántida we recorded 1–8 individuals in 21 out of 24 surveys between 2008 and 2024 (~ 0.01 ind/m; Fig. 2B). Morlock individuals were always observed swimming in the water column, at variable distances from both the cave walls and the bottom (Fig. 2E-F). During the study period, the species was not recorded at Charcos de Luis and only once in Los Jameos del Agua.

3.2. Interannual trends in abundance

Interannual trends in abundance the jameíto and the morlocks were inferred from the year term of the generalized additive models described above and selected after AIC and BIC criteria (Section 3.3, Table 1).

We observed a significant increase in abundance of the jameíto in Cueva de los Lagos (GAM, estimate = 0.23, $p = 0.001$; Table 2). In contrast, Túnel de la Atlántida exhibits spatially heterogeneous temporal trends among cave sections, with a significant decline in the dark passages (GAM, $\beta = -0.31$, $p = 0.020$; β = locality estimate - level trend estimate) and the twilight (estimate = - 0.06, $p = 0.008$, Table S2) sections; but a marginally significant, weakly positive trends in the entrance (GAM, $\beta = 0.01$, $p = 0.080$; Table 2) and Montaña de Arena (GAM, estimate = 1.25, $p = 0.070$). At Los Jameos del Agua, we observed a weak but significant decline in abundance over time (GAM, estimate = - 0.06, $p < 0.001$; Table 2), whereas no significant interannual trend was detected at Charcos de Luis (GAM, estimate = - 0.03, $p = 0.681$; Table 2).

We did not detect significant trends in abundance of *Morlockia* spp. in Cueva de los Lagos (GAM, estimate = 0.15, $p = 0.157$; Table 04), whereas a significant decrease in abundance was observed in Túnel de la Atlántida (GAM, estimate = - 0.11, $p = 0.004$; Table 04).

3.3. Role of tides and sunlight on abundances

Following our biological expectations, both Akaike and Bayesian information criteria (AIC, BIC) favoured the tide-only model in Cueva de los Lagos for the jameíto (Table 1), showing significant abundance difference among cave sections (GAM, Table 2), due to lower densities in the terminal sump compared with all three phreatic lakes, while differences among the lakes themselves were not significant (Tukey-adjusted pairwise comparisons test, Table 3). Abundance also varied significantly and non-linearly with tidal phase (Table 2). The model explained 77% of deviance.

Table 1

Summary of the model selection, across species (the jameíto *Munidopsis polymorpha* and the remipedes *Morlockia* spp.) and localities. The tidal model ('tidal') included semidiurnal cycle length (in minutes), tide direction (ebb/flood), tidal semirange (in meters) and cave tidal phase (scaled from 0 to 1). The solar model included sun position (day/night), solar phase (scaled from 0 to 1), and day length (in minutes). Degree of freedom (df), and values for the Akaike (AIC) and Bayesian (BIC) information criteria are summarized. Best values are highlighted in bold.

		<i>Munidopsis polymorpha</i>			<i>Morlockia</i> spp.		
		df	AIC	BIC	df	AIC	BIC
Cueva Lagos	Tidal	10.172	158.700	173.287	7.000	48.843	58.652
	Solar	9.793	191.306	207.344	6.000	50.024	59.525
	Combined	11.101	159.840	175.759	8.000	50.788	61.998
Jameos Agua	Tidal	5.000	162.795	167.247	na	na	na
	Solar	7.672	146.920	153.751	na	na	na
	Combined	9.833	140.245	149.000	na	na	na
Túnel Atlántida	Tidal	15.150	501.892	535.956	7.061	83.653	91.971
	Solar	10.330	515.851	539.078	6.242	84.690	92.044
	Combined	20.891	478.720	525.694	8.032	85.609	95.071
Charcos Luis	Tidal	7.636	80.668	98.953	na	na	na
	Solar	4.000	81.966	91.544	na	na	na
	Combined	11.993	75.385	104.101	na	na	na

Table 2

Results of generalized additive models describing the effects of tidal forcing on the abundance of the jameito in Cueva de los Lagos, Los Jameos del Agua, Túnel de la Atlántida, and Charcos de Luis. Parametric coefficients (estimates, standard errors, z values, and p values) are reported for tidal direction, tidal semirange, cave section (where applicable), and temporal trend (Year). The significance of the cyclic smooth for tidal phase is reported using estimated degrees of freedom (Est df), reference degrees of freedom (Ref df), Chi-square statistics, and p values. Model fit is summarized by adjusted R^2 and percentage of deviance explained.

Cueva de los Lagos (Tidal, R-sq.(adj) = 0.422; Dev. = 77.5%)				
	Estimate	Std Error	z value	p value
(Intercept)	-3.3376	0.4562	-7.316	2.56E-13
Tide dir. (flood)	-0.2540	0.3345	-0.759	0.4477
Tidal semirange	0.0674	0.1969	0.342	0.7321
Section (Lago2)	-0.0194	0.2792	-0.069	0.9447
Section (Lago3)	0.6218	0.2842	2.188	0.0287
Section (Sifón)	-2.1470	0.6143	-3.495	0.0004
Year	0.2306	0.0709	3.254	0.0011
	Est df	Ref df	Chi sq	p value
s(tidal phase)	1.624	4	6.333	0.015
Jameos del Agua (Combined, R-sq.(adj) = 0.818; Dev. = 87.7%)				
	Estimate	Std. Error	z value	p-value
(Intercept)	2.8396	0.1696	16.7470	< 2.00E-16
s(tidal phase)	0.5464	0.2078	2.6290	0.0086
Tidal semirange	0.1971	0.1163	1.6950	0.0901
Sun position (day)	-0.1924	0.2864	-0.6720	0.5016
Year	-0.0562	0.0161	-3.4950	0.0005
	Est df	Ref df	Chi sq	p value
s(tidal phase)	0.0007	4	0.0010	0.3313
s(sun phase)	0.0000	4	0.0000	0.9010
s(day length)	3.3100	9	49.1930	0.0701
Túnel de la Atlántida (Combined, R-sq.(adj) = 0.736; Dev. = 95.8%)				
	Estimate	Std Error	z value	p value
(Intercept)	-5.7234	2.8135	-2.0340	0.0419
Tide dir. (flood)	0.0498	0.1465	0.3400	0.7341

Cueva de los Lagos (Tidal, R-sq.(adj) = 0.422; Dev. = 77.5%)				
	Estimate	Std Error	z value	p value
Tidal semirange	-0.4837	0.0921	-5.2500	0.0000
Sun position (day)	-0.4308	0.1816	-2.3720	0.0177
Section (Entrance)	7.8747	2.7703	2.8420	0.0045
Section (Passage)	0.3955	2.7706	0.1430	0.8865
Year	1.2543	0.7027	1.7850	0.0743
Zone(Entrance):Year	-1.2395	0.7029	-1.7630	0.0778
Zone(Passage):Year	-1.5686	0.7072	-2.2180	0.0266
	Est df	Ref df	Chi sq	p value
s(tidal phase): Section (Montaña)	1.7633	4	6.0360	0.0221
s(tidal phase): Section (Entrance)	1.7750	4	6.3130	0.0173
s(tidal phase): Section (Passage)	1.9664	4	8.0360	0.0085
s(sun phase): by_light	3.1351	4	23.2460	0.0000
s(day length)	0.0013	9	0.0010	0.3693
Charcos de Luis (Combined, R-sq.(adj) = 0.463; Dev. =52.1%)				
	Estimate	Std. Error	z value	p-value
(Intercept)	-3.0344	1.1163	-2.7180	0.0066
Tide dir. (flood)	-1.4605	1.4787	-0.9880	0.3233
Tidal semirange	0.3468	0.9280	0.3740	0.7087
Sun position (day)	0.7261	2.5543	0.2840	0.7762
Year	-0.0278	0.0675	-0.4110	0.6808
	Est df	Ref df	Chi sq	p value
s(tidal phase)	2.3744	4	8.5910	0.0097
s(sun phase)	2.5536	4	5.6050	0.0696
s(day length)	0.0001	9	0.0000	0.5423

Table 3

Tukey post hoc pairwise comparisons of spatial sections for the jameíto based on generalized additive models (GAMs). Pairwise contrasts among sampling sections within Cueva de los Lagos (Lake 1–3, sump) and Túnel de la Atlántida (entrance, passage, Montaña de Arena) derived from the best-supported GAM. Values are expressed as estimated ratios of mean densities between sections, with associated standard errors (SE), degrees of freedom (df), t ratios, and adjusted p values. Significant contrasts ($\alpha = 0.05$) are highlighted in bold. Results indicate strong and consistent differences between lake sections and the sump in Cueva de los Lagos, as well as pronounced density contrasts between the entrance and inner passages of Túnel de la Atlántida, whereas differences between Montaña de Arena and the main passage are not significant

contrast	ratio	SE	df	t ratio	p value
Lago 1 vs. Lago 2	1.020	0.285	22.4	0.069	0.9999
Lago 1 vs. Lago 3	0.537	0.153	22.4	-2.188	0.1572
Lago 1 vs. sump	8.559	5.258	22.4	3.495	0.0101**
Lago 2 vs. Lago 3	0.527	0.145	22.4	-2.323	0.1228
Lago 2 vs. sump	8.395	5.125	22.4	3.485	0.0103**
Lago 3 vs. sump	15.939	9.768	22.4	4.518	0.0009**
Montaña vs. passage	0.271	0.7695	52.4	-0.460	0.8902
Montaña vs. entrance	0.001	0.001	52.4	-2.938	0.0134**
Passage vs. entrance	0.001	0.000	52.4	-18.831	< .0001**

In contrast, AIC and BIC strongly supported the model including both tidal and sunlight predictors in Túnel de la Atlántida (Table 1). Abundance significantly varied non-linearly with tidal phase across entrance (GAM, $\chi^2 = 6.31$, $p = 0.017$; Table 2), dark passages (GAM, $\chi^2 = 8.04$, $p = 0.008$; Table 2) and Montaña de Arena (GAM, $\chi^2 = 6.03$, $p = 0.022$; Table 2) sections and showed a significant relationship with solar phase in the entrance section (GAM, $\chi^2 = 23.24$, $p < 0.001$; Table 2). In addition, abundance was higher at night and decreased with increasing tidal semirange (GAM, estimate = -0.48 , $p < 0.001$; Table 2). Abundances also differed among cave sections, being significantly higher at the entrance than both at the dark section (Tukey-adjusted pairwise ratio = 0.01, $p < 0.001$) and at Montaña de Arena (ratio = 0.00, $p = 0.013$). No significant difference was detected between the dark section and Montaña de Arena (ratio = 0.27, $p = 0.890$; Table 3). The model explained 87.7% of deviance. In its separate model, no significant ecological drivers were observed in the twilight section, although we observed reduction in densities towards the dark passage sections (Table S2; Figure S2).

For Los Jameos del Agua, AIC and BIC favored the model including both tidal and sunlight predictors (Table 1). Abundances were significantly affected by tide direction, with higher counts during flood tide (GAM, estimate = 0.55, $p = 0.009$; Table 2), while effects of tidal and solar phase were weak and shrank towards zero. Photoperiod showed a non-linear effect that was only marginally supported (GAM, $\chi^2 = 49.19$, $p = 0.070$; Table 2). The model explained 95.8% of deviance.

At Charcos de Luis, model selection was sensitive to the information criterion used. AIC favoured the combined model, whereas BIC penalized its added complexity, favoring the tidal one (Table 1). The only significant effect detected was a non-linear relationship with the tidal phase (GAM, $\chi^2 = 8.59$, $p = 0.010$; Table 2). The overall model fit was low (deviance explained = 52.1%), probably due to the scarcity of records in that locality.

Model comparisons for the morlocks supported the tidal model in both Cueva de los Lagos and Túnel de la Atlántida (Table 1). However, models explained relatively low deviance (< 50%), consistent with the lower number of observations of this taxon. No significant effects were recovered in Cueva de los Lagos (Table 4), whereas abundance declined significantly with increasing tidal semirange in Túnel de la Atlántida (GAM, estimate = - 0.46, $p = 0.004$, Table 4). In this locality, a non-linear effect of tidal phase was also marginally supported (GAM, $\chi^2 = 3.34$, $p = 0.088$). However, deviance explained for those models was only 24.4% and 45.8% for Cueva de los Lagos and Túnel de la Atlántida, respectively.

Table 4

Results of generalized additive models describing the effects of tidal forcing on the remipedes *Morlockia* spp. abundance in Cueva de los Lagos and Túnel de la Atlántida. Parametric coefficients (estimates, standard errors, z values, and p values) are reported for tidal direction, tidal semirange, cave section (where applicable), and temporal trend (Year). The significance of the cyclic smooth for tidal phase is reported using estimated degrees of freedom (Est df), reference degrees of freedom (Ref df), Chi-square statistics, and p values. Model fit is summarized by adjusted R^2 and percentage of deviance explained.

Cueva de los Lagos (Tidal, R-sq.(adj) = 0.0461; Dev. = 24.4%)				
	Estimate	Std Error	z value	p value
(Intercept)	-6.8880	1.2230	-5.6320	0.0000
Tide dir. (flood)	1.1623	1.0623	1.0940	0.2740
Tidal semirange	0.3960	0.3552	1.1150	0.2650
Section (Lago2)	-0.0527	0.6708	-0.0790	0.9370
Section (Lago3)	-0.8557	1.1180	-0.7650	0.4440
Year	0.1547	0.1094	1.4140	0.1570
	Est df	Ref df	Chi sq	p value
s(tidal phase)	0.0000	4	0	0.779
Túnel de la Atlántida (Combined, R-sq.(adj) = 0.338; Dev. = 45.8%)				
	Estimate	Std Error	z value	p value
(Intercept)	-5.2748	0.2412	-21.8680	< 2e-16
Tide dir. (flood)	-0.4025	0.3481	-1.1560	0.2475
Tidal semirange	-0.4589	0.2132	-2.1530	0.0313
Year	-0.1115	0.0383	-2.9110	0.0036
	Est df	Ref df	Chi sq	p value
s(tidal phase)	1.4740	4	3.3690	0.0882

3.4. Short-term effect of tides and sunlight on densities.

Short-term variation in counts of the jameíto at Los Jameos del Agua was calculated based on fixed-point time series between 2017–2025. Both AIC and BIC favour the model with tides and light effects (Table S3), which shows lower abundance during daytime (GAM, estimate = -0.28 , $p < 0.001$; Fig. 3, Table 5) and at Jameo Grande (GAM, estimate = -1.72 , $p < 0.001$; Table 5); as well as a significant non-linear relationship with tidal phase (GAM, $\chi^2 = 24.17$; $p = 0.031$). After accounting for these effects and for strong among-series heterogeneity, we found no evidence for additional effects of solar phase or day length (Table 5).

Table 5

Results of the generalized additive model (GAM) describing short-term fluctuations in the abundance of the jameño in Los Jameos del Agua based on iterative counting time series from 2017–2025. The results of the model including all observations and only solar variables is included in Supplementary Material. The model integrates tidal forcing, solar incidence, spatial position within the cave (Jameo Grande vs. Jameo Chico, reference), and temporal trend (Year), while accounting for repeated high-frequency observations through a random smooth of counting series. Parametric coefficients are reported with estimates, standard errors, z values, and p values. Smooth terms are summarized by estimated degrees of freedom (edf), reference degrees of freedom (Ref df), Chi-square statistics, and p values. Model fit is indicated by adjusted R^2 and percentage of deviance explained.

Jameos del Agua (Combined, R-sq.(adj) = 0.890; Dev. = 90.2%)				
	Estimate	Std Error	z value	p value
(Intercept)	3.6448	0.3117	11.6920	< 2.00E-16
Tide dir. (flood)	0.0726	0.0611	1.1870	0.2360
Tidal semirange	0.1543	0.0994	1.5530	0.1210
Sun position (day)	-0.2876	0.0689	-4.1730	0.0000
Position (Jameo grande)	-1.7177	0.1814	-9.4690	< 2.00E-16
Year	-0.0319	0.0405	-0.7860	0.4320
	Est df	Ref df	Chi sq	p value
s(tidal phase)	2.8007	4	24.1720	0.0312
s(sun phase)	3.6321	4	158.9310	0.1210
s(day length)	0.2788	5	2.0330	0.8031
s(series)	64.5545	74	16.3800	< 2e-16

We obtained partially consistent results when we included earlier campaigns (1980–1989), which only include monthly summaries and lack tidal covariates: abundances were again lower during daytime (GAM, estimate = - 0.19, $p = 0.006$) and at Jameos Grande (GAM, estimate = - 1.14, $p < 0.006$), but, in this case, the model indicated a modest long-term decline in mean abundance through time (GAM, estimate = - 0.016, $p = 0.004$; Table S7).

4. Discussion

Our analyses highlight a pronounced spatial structure in the distribution of both species, strongly modulated by tides, light availability, and cave zonation. However, they do not reveal consistent, system-wide interannual trends in the abundance across sampled localities. These patterns emphasize the importance of local ecological context and aquifer–ocean exchange in shaping anchialine communities, and caution against interpreting localized abundance changes as direct proxies for population-level trends. Importantly, the localities surveyed here represent only a fraction of the total habitat utilized by both species within the Corona

lava tube and the surrounding groundwater system, which extends through crevices and fissures of the volcanic bedrock beyond the human-accessible passages (Wilkins et al. 1986; Martinez and Gonzalez 2019). Therefore, observed changes in local abundance should be interpreted as redistribution within the anchialine system rather than direct proxies for total population size.

In addition to environmental constraints, since both taxa are legally protected, capture–mark–recapture and other approaches for population estimation that implied direct interaction with the species were not feasible. Therefore, our inference relies on non-invasive abundance indices standardized by sampling effort. This implies that the observations presented here constitute among the most complete and current evidence that can reasonably be obtained.

4.1. Spatial structure and ecological drivers of abundance

For the jameíto, abundance patterns were strongly structured by cave sectors associated with enhanced resource availability. Individuals were consistently recorded in Los Jameos del Agua, at the entrance of Túnel de la Atlántida, and in Montaña de Arena at densities that were 3–4 orders of magnitude higher than in the darker passages. Those three sections differ among them in light regime and geomorphology but share a common feature of trophic enrichment (Martinez et al. 2016). In the illuminated sector of Los Jameos del Agua and at the tunnel entrance, local photosynthetic production by diatoms provides abundant trophic resources, whereas in Montaña de Arena, the direct connection to the ocean allows sediment and marine sinking particulate organic matter to accumulate (Garcia-Valdecasas 1985; Martinez et al. 2019). High trophic enrichment appears to play a key role in enabling the jameíto to achieve high population densities, given that its larger body size and higher baseline metabolic rate, compared with coexisting taxa, result in the highest energy use recorded among Lanzarote stygofauna (Boulamail et al. 2026). The strong tidal modulation detected in several models further supports the interpretation that the jameíto responds dynamically to short-term fluctuations in resource delivery at all those localities.

Interannual changes in abundance varied among cave sections over the last 30 years. The jameíto showed a significant increase in Cueva de los Lagos and a decline in the dark passages of Túnel de la Atlántida, accompanied by weak, marginal increases in entrance of the tunnel and in Los Jameos del Agua. This pattern is consistent with a redistribution of individuals within the lava tube system, potentially toward deeper, often more thermally stable sections. We propose that such redistribution could be favored under scenarios where temperature increases in shallow groundwater layers linked to ongoing ocean warming around the Canary Islands (Siemer et al. 2021). However, the lack of long-term temperature records for most localities limits direct testing of this hypothesis. Recent continuous monitoring at Túnel de la Atlántida started as part of Proyecto Subtlántida (Lario et al. 2022) indicates a measurable warming trend ($\sim 0.04^{\circ}\text{C}/\text{yr}$; Figure S3), at least at the entrance of the tunnel. However, equivalent long-term temperature data are not available for other localities, especially Cueva de los Lagos, limiting our ability to evaluate spatial variation in thermal change across the coastal aquifer in Lanzarote and highlighting an important gap that warrants future research.

Although the jameíto exhibits some degree of physiological tolerance to warming (Boulamail et al. 2026), such redistribution may nonetheless be functionally detrimental to species' fitness. Even if individuals shift toward deeper and more thermally stable sections of the cave to offset the increased metabolic demand associated

with higher atmospheric temperatures and thermoregulatory costs, they will remain exposed to warmer groundwater driven by marine warming, thereby likely increasing mass-specific energy requirements (Boulamail et al. 2026). Concurrently, resource availability in these lower cave sections is not expected to increase, as it is primarily constrained by limitations in allochthonous inputs, which may intensify under reduced precipitation, rather than by local primary production that could be boosted as well by increasing temperature. Under these conditions, the balance between energy intake and expenditure would deteriorate, with potential negative consequences for reproductive output and population densities (Yvon-Durocher et al. 2012). Moreover, temperature-driven increases in basal metabolic rate may further constrain aerobic scope, reducing physiological tolerance (Sokolova 2021; Metcalfe 2025) and ability to exploit low-density or low-quality resource patches (Cozzoli et al. 2019), which are likely crucial for survival in anchialine groundwater ecosystems.

In contrast, the drivers of abundance patterns of the morlocks remain more elusive. While our models supported tide-related effects particularly in Túnel de la Atlántida, they explained a substantially lower proportion of variance than those for the jameíto. This difference may partly reflect lower encounter rates and reduced sample sizes, but it might also be indicative of a distinct ecological strategy of the species (see section 4.2). Despite these limitations, our models indicate an overall reduction in abundances in Túnel de la Atlántida and suggest a trend of increase in Cueva de los Lagos, congruent with the patterns observed for the jameíto.

4.2. Contrasting ecological strategies: benthic versus water-column indicators

The contrasting responses of the crawling and swimming species reflect their fundamentally different ecological roles within the anchialine system. The jameíto *Munidopsis polymorpha* is a benthic detritivore that aggregates in areas with high availability of trophic resources, integrating signals of resource deposition, aquifer–ocean exchange, and local photosynthetic productivity (Wilkins et al. 1990). The morlocks are swimming predators that move in the water column (Kohlhage and Yager 1994).

A plausible mechanistic explanation for the pattern observed for the bottom-dweller jameíto is that individuals reduce their movement range to remain in these food-rich areas, while increasing it when food becomes scarcer and they need to disperse through resource-poor sectors. More generally, organisms adjust their space use in response to resource heterogeneity, contracting their movement ranges in favourable habitats and expanding them when resources are scarce. This behaviour can be captured with mathematical models of resource-dependent movement, which often include a random-walk description in which the characteristic step length is shorter in resource-rich areas and longer in resource-poor ones; or equivalently, in a diffusion formulation, the effective diffusion coefficient decreases where resources are high and increases where they are low. Such movement rules can generate spatial aggregation even in the absence of social attraction or coordinated behaviour (Okubo and Levin 2002; Kareiva and Odell 1987).

Resource-dependent movement rates would therefore persistently drive local aggregations in trophically enriched cave sections, without requiring any form of social attraction or coordinated behaviour. Because the jameíto is characterized by intrinsically high baseline energy requirements relative to other species inhabiting the tunnel, the fact that it occupies resource-rich areas, where food can be accessed with minimal additional

locomotor effort, can be interpreted as a strategy to avoid additional costs and increase energy use efficiency. This behavioural strategy may be plesiomorphic in the genus *Munidopsis*. Many deep-sea congeners persist in otherwise food-poor benthos by locating and exploiting small, spatially discrete resource patches such as hydrothermal vents, cold seeps, and organic falls (Bernardino et al. 2012). The tendency of the jameíto to accumulate in energetic hotspots within anchialine caves may therefore reflect an ancestral deep-sea foraging strategy, retained and repurposed in the spatially constrained but trophically heterogeneous subterranean environments of volcanic islands.

Importantly, sustained aggregation of individuals of the jameíto in resource-rich habitats over evolutionary timescales could contribute to fine-scale genetic differentiation, even in the absence of strong physical barriers (Levin 1992). This is supported by recent microsatellite analyses that revealed detectable genetic structuring between populations of the jameíto within the interconnected La Corona anchialine lavatube and Charcos de Luis, consistent with restricted dispersal and prolonged residence of individuals within specific cave sectors (Martínez et al. 2026).

The nutrient-rich sectors where the jameíto concentrates are also areas of the system more prone to colonization by marine opportunistic species (Nuñez et al. 1997; Martínez et al. 2009). For example, we registered a proliferation of the green spoonworm *Bonellia viridis* in Los Jameos del Agua during the 2000s, which generated fine organic-rich faecal deposits, and substantially altered benthic habitat structure (Brito et al. 2009). More generally, opportunistic colonizers with high local retention and strong sediment-processing capacity can rapidly amplify trophic enrichment and modify benthic conditions in ways that may disadvantage cave-adapted meiofauna. Under current conditions, the jameíto, which occupies the same sectors and exploits similar detrital resources, may help limit the establishment or expansion of such colonizers through competition and predation. We therefore speculate that climate-driven or anthropogenic stressors (e.g. global warming, pollution) that reduce or redistribute the jameíto could relax this biotic control, increasing the likelihood of cascading habitat changes driven by opportunistic marine species.

In contrast, the morlocks, like other remipedes, are mobile predators hunting throughout the dark water mass of the cave (Koenemann et al. 1997). Their occurrence is likely shaped by the distribution of prey and by fine-scale water structure, including variation in salinity, turbulence, and internal circulation. Potential prey includes several taxa that live and feed in the water, such as the mysid crustaceans *Heteromysis cotti*, *Halosbaena fortunata*, and *Megadrilus pelagicus* (Martínez et al. 2016). These preys rely on suspended organic particles, whose distribution within the cave likely responds to similar physical processes. Although ultimately linked to tides, such processes can create uneven and short-lived prey concentrations that are not well captured by coarse descriptors such as tidal phase or range (Genin 2004; Kiørboe 2009; Kiørboe and Saiz 1995). As a result, observed counts of the morlocks may reflect brief foraging episodes rather than stable residence in each passage, which would naturally weaken apparent relationships with the environmental covariates included in our models. This interpretation is consistent with reports from other anchialine systems (e.g. Ox Bel Ha and Aerolito in Mexico), where communities living in the water form transient aggregations linked to stratification and circulation, whereas bottom-associated organisms more consistently track areas where organic matter accumulates (Calderón et al. 2018; Benítez et al. 2019).

4.3. Charcos de Luis: a suboptimal habitat for the jameíto?

Population densities measured at Charcos de Luis exhibited comparatively low resolution and weak temporal signal, which may reflect a combination of methodological and ecological factors. Methodologically, this pattern could arise from detectability bias in earlier studies that reported visits to Charcos de Luis only when individuals of the jameíto were present, thereby inflating the frequency of the species and obscuring calculation of abundance trends.

Ecologically, Charcos de Luis differs from the natural cave sectors analysed here in hydrology, structural complexity, and exposure to epigean predators. The jameíto may be attracted into these shallow pools by locally enhanced food availability, but persistence may be low due to intense predation (e.g. gobiid and eel fish) and competition with large decapods (e.g. *Palaemon*, *Xantho*) (Wilkens et al. 1993), as well as direct exposure to sunlight and elevated local temperatures. Under this scenario, Charcos de Luis would function as an ecological trap or sink (Pulliam 1988; Schlaepfer et al. 2002): individuals arrive attracted by food, but are rapidly removed, preventing the build-up of permanent populations and making densities from Charcos de Luis poorly comparable to those from cave sectors where individuals survive and accumulate. This also implies a shift in trophic role. Within the cave, the jameíto tends to retain energy acting as a trophic dead-end; in Charcos de Luis, it may instead act as a transient consumer that transfers energy to higher trophic levels through predation. Together, these mechanisms provide a plausible explanation for the weak temporal structure observed at this site and illustrate how surface-connected settings can alter both persistence and functioning of anchialine fauna.

Charcos de Luis also appears to be, at least in part, an artificial habitat, most likely linked to cinder extraction during the 20th century (Rodrigo 2009). The shape of its shallow pools and the presence of extensive unconsolidated cinder deposits suggest excavation or enlargement of natural depressions to access and stockpile volcanic material. More broadly, this case is a powerful reminder of the sensitivity of the La Corona anchialine system to surface disturbance. Because the water table is shallow and the lava field relatively flat, the Malpaís de la Corona has been proposed as a Ramsar wetland type Z(k) by the Government of the Canary Islands. This category includes coastal terrains with pools, sinkholes, and other features that expose groundwater that is connected to carbonate or volcanic aquifers inhabited by highly specialized endemic fauna. In this context, Charcos de Luis provides a concrete example of how surface interventions, whether historical extraction or contemporary land use, can have long-lasting and disproportionate effects on groundwater-dependent ecosystems, reinforcing the need for integrated surface–subsurface management.

4.4. Beyond flagships: a data-driven, integrative approach to anchialine ecosystem conservation

This study highlights the value of the jameíto *Munidopsis polymorpha* and of the remipedes *Morlockia* spp. as complementary indicators of different compartments of the same anchialine ecosystem, the cave bottom versus the water column. The strength of this dual-indicator framework is reinforced by the evolutionary origin of both taxa. The jameíto, one of the earliest described groundwater-restricted species, belongs to an evolutionary lineage adapted to exploit patchy trophic resources in otherwise vast and resource-limited deep-sea environments (Koelbel, 1892). Its tendency to concentrate in trophic hotspots within anchialine caves likely represents the retention of this ancestral strategy in a spatially constrained subterranean setting.

The morlocks, in turn, represent a phylogenetically distinctive lineage whose presence in Lanzarote has played a pivotal role in shaping our understanding of anchialine biodiversity and evolution (Ilfiffe et al. 1984). As specialized, mobile top-predators adapted to stratified and sometimes low-oxygen waters, remipedes respond primarily to prey fluxes and internal circulation within the cave, rather than to localized accumulation of organic matter. Their low densities, high mobility, and sensitivity to water-column structure make them ideal sentinels of changes in stratification and energy transfer through anchialine waters.

From a conservation perspective, in-tandem monitoring of these taxa provides a broader picture of ecosystem change than either species alone. Disturbances affecting organic matter inputs and deposition are likely to be detected first through shifts in the crawler jameíto, whereas changes affecting stratification, circulation, or prey supply should be more readily reflected in the swimmer morlocks. Framing these species as sentinels of complementary ecosystem functions strengthens the case for conservation strategies that explicitly integrate ecological processes in management decisions. Crucially, the interpretability of these biological signals depends on a parallel characterization of the physical environment. Moreover, joint monitoring can mitigate the logistical constraints of accessing confined environments by combining pelagic and benthic sampling in a single visit, avoiding the need for separate sampling events. Long-term monitoring efforts should be embedded within hydrological and environmental frameworks, as set out in both the Habitats Directive (Directive 92/43/EEC) and the Marine Strategy Framework Directive (Directive 2008/56/EC). We suggest these efforts should focus on groundwater monitoring wells and continuous measurements of water level, temperature, and water chemistry, to place population trends in the context of soil–aquifer–ocean connectivity and climatic forcing that drive eco-evolutionary processes in the island aquifer ecosystem.

Building on this environmental foundation, three complementary research directions emerge as priorities. First, spatially explicit, agent-based models parameterized with empirical abundance and behavioural data (Grimm and Railsback 2013), as well as geological and hydrological information would allow formal testing of mechanistic hypotheses linking resource heterogeneity, movement behaviour, and aggregation patterns (Nathan et al. 2008), helping to distinguish redistribution within the anchialine network from true population decline. Second, targeted studies on metabolic rates, trophic interactions, and food-web structure integrating stable isotopes, gut-content analyses, and microbial functional data are essential to quantify energy flow and identify critical thresholds beyond which altered energy transfer or resource limitation may compromise population persistence (Layman et al. 2012). Third, genomic approaches offer a powerful avenue to resolve population structure, connectivity, and adaptive potential at biologically relevant temporal and spatial scales, thereby informing the delineation of management units and the resilience of populations under environmental change. In particular, the generation of high-quality, chromosome-level reference genomes for the jameíto and the morlocks would be transformative for anchialine conservation (Allendorf et al. 2010). Such resources enable robust genome-wide inference of effective population sizes through time, helping to distinguish long-term evolutionary rarity from recent demographic decline (Ellegren 2014). Chromosome-scale assemblies further provide the framework to detect cryptic population subdivision, restricted gene flow, and potential local adaptation across cave sectors, all of which are essential for defining biologically meaningful management units in these complex subterranean systems. Importantly, reference genomes also allow the integration of historical and museum specimens into population genomic analyses, adding a temporal dimension that can reveal genetic erosion or fragmentation across decades.

Finally, because both taxa also function as cultural and symbolic flagships, conservation effectiveness will ultimately depend on coupling environmental and biological monitoring with sustained dissemination and public-engagement strategies. Citizen science initiatives promoted by the local administrations and the UNESCO Geopark have demonstrated how anchialine flagship species can reconnect scientific knowledge with local memory, education, and stewardship, while simultaneously generating observations relevant for conservation (Camacho et al. 2025). Integrating participatory frameworks with environmental monitoring, mechanistic models, trophic studies, and genomic data would transform the jameíto *Munidopsis polymorpha* and the remipedes *Morlockia* spp. from descriptive indicators into fully operational sentinels—linking ecosystem processes, public engagement, and clearly defined conservation triggers. Without such integration, long-term monitoring risks remaining an exercise in documentation rather than a tool for timely intervention, echoing concerns raised for biodiversity monitoring more broadly (Lindenmayer et al. 2013).

Declarations

Funding

Surveys in 2017 were supported by the project “Elaboración del Plan de Manejo de las especies amenazadas *Munidopsis polymorpha* y *Morlockia ondiniae*” to AM, co-funded by the Government of the Canary Islands and the European Regional Development Fund (ERDF–FEDER) through the Canary Islands Operational Programme 2014–2020. Surveys in 2024 was supported by the PRTR-ESMOLINCO project, developed under Contract TEC00006101 between the Euskoiker Foundation (in collaboration with the Spanish Malacological Society, SEM) and Tecnologías y Servicios Agrarios S.A., S.M.E., M.P. (TRAGSATEC), within the Recovery, Transformation and Resilience Plan funded by the European Union (NextGenerationEU) to AM. Additional support was provided by Biodiversa+ (project ‘DarCo’), the European Biodiversity Partnership under the 2021–2022 BiodivProtect joint call for research proposals, co-funded by the European Commission (GA N°101052342) and with the funding organizations Ministry of Universities and Research (Italy), Agencia Estatal de Investigación–Fundación Biodiversidad (Spain), Fundo Regional para a Ciência e Tecnologia (Portugal), Suomen Akatemia–Ministry of the Environment (Finland), Belgian Science Policy Office (Belgium), Agence Nationale de la Recherche (France), Deutsche Forschungsgemeinschaft e.V. (Germany), Schweizerischer Nationalfonds (Grant No. 31BD30_209583, Switzerland), Fonds zur Förderung der Wissenschaftlichen Forschung (Austria), Ministry of Higher Education, Science and Innovation (Slovenia), Ministry of Agriculture of the Czech Republic (MZe RO0425, Czechia) and the Executive Agency for Higher Education, Research, Development and Innovation Funding (Romania). RMG was supported by the Center for Advanced Systems Understanding (CASUS), which is financed by Germany's Federal Ministry of Research, Technology, and Space (BMFTR) and by the Saxon Ministry for Science, Culture and Tourism (SMWK) with tax funds on the basis of the budget approved by the Saxon State Parliament; the São Paulo Research Foundation (FAPESP, Brazil) through ICTP-SAIFR Grant 2021/14335-0 (RMG). We thank the Cabildo de Lanzarote and the Centros de Arte, Cultura y Turismo (CACT) for their support. We are especially grateful to the staff at Los Jameos del Agua, particularly Suso Fontes and Alexis Guadalupe, for facilitating access and fieldwork at the site. We are grateful to the divers Antonio Martín, Juan Valenciano, Alexander Standler, Diego Nicolás Penno, Iñaki Galilea Benito, José Manuel Golderos Tena, Loic Jacques V. Bichet, Marina López Fernández, and Santiago Eduardo Ramos Martín for their support in the field. We are indebted to GISMACAN SL and Alejandro Martínez y Sánchez de Neyra for the management of the projects. FC and SB were funded by the project PRIN

2022 STIGE-CLIMAQUIFERI DTA.PN010.014 2022MM8P88_LS8_PRIN2022 - CUP: B53D23012170006. AM was further supported by PRIN 2022 ANCHIALOS: Diversity, function, and resilience of Italian coastal aquifers upon global climatic changes (2022LLNF3N, CUP: B53D23012140006). SB was further supported by the Company of Biologists for the travelling fellowship, reference number of the grant (JEBTF24081567). RF acknowledges support from the Agencia Estatal de Investigación (project PID2019-108824GA-I00 funded by MCIN/AEI/10.13039/501100011033) and the European Research Council (ERC) under the European's Union's Horizon 2020 research and innovation programme (grant agreement no. 948281)).

Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Author Contributions

Data collection was performed by Alejandro Martinez, Guillermo Garcia-Gomez, Alvaro Garcia-Herrero, Alvaro Roldan, Marta Garcia-Cobo, Sarah Boulamail, Zacarias Fresno, Cristina Camacho, Marcia N. Kurtz, Marika Maranzano, Enrique Dominguez, Carola D. Jorge, Horst Wilkens, and Francesco Di Nezio. Alejandro Martinez, Sarah Boulamail, Leopoldo Moro and Rosa Fernandez obtained funding. Alejandro Martinez was the main project coordinator, together with Enrique Dominguez, Leopoldo Moro and Elena Mateo. Data was managed by Alejandro Martinez, Marta Garcia-Cobo, Zacarias Fresno, Alvaro Garcia-Herrero and Guillermo Garcia-Gomez. Alejandro Martinez analysed the data, with support of Diego Fontaneto and Guillermo Garcia-Gomez. Javier Lario, Francesco Cozzoli, Sarah Boulamail and Ricardo Martinez-Garcia provided additional analyses or data. Alejandro Martinez and Guillermo Garcia-Gomez lead the data interpretation, with expert input from Ricardo Martinez-Garcia, Stefano Mammola, Francesco Cozzoli, Sarah Boulamail, Rosa Fernandez and Javier Lario. Alejandro Martinez and Marika Maranzano did the figures. Elena Mateo and Leopoldo Moro managed the permits.

Data Availability

All data and scripts are available at github repository,
<https://github.com/amartinezgarcia/flagshipspeciesLanzarote>

Permits

Sampling at all the localities were authorized by Gobierno de Canarias, Cabildo de Lanzarote and Centros de Arte y Turismo de Lanzarote, and supported by the Lanzarote and Chinijo Islands UNESCO Geopark.

Ethics approval

This study did not involve human participants, human data, human tissue, or clinical trial procedures. Therefore, ethics approval was not required.

Consent to participate

Not applicable.

Human Ethics and Consent to Participate declarations

Not applicable.

Clinical trial number

Not applicable.

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92. Statements & Declarations

Figures

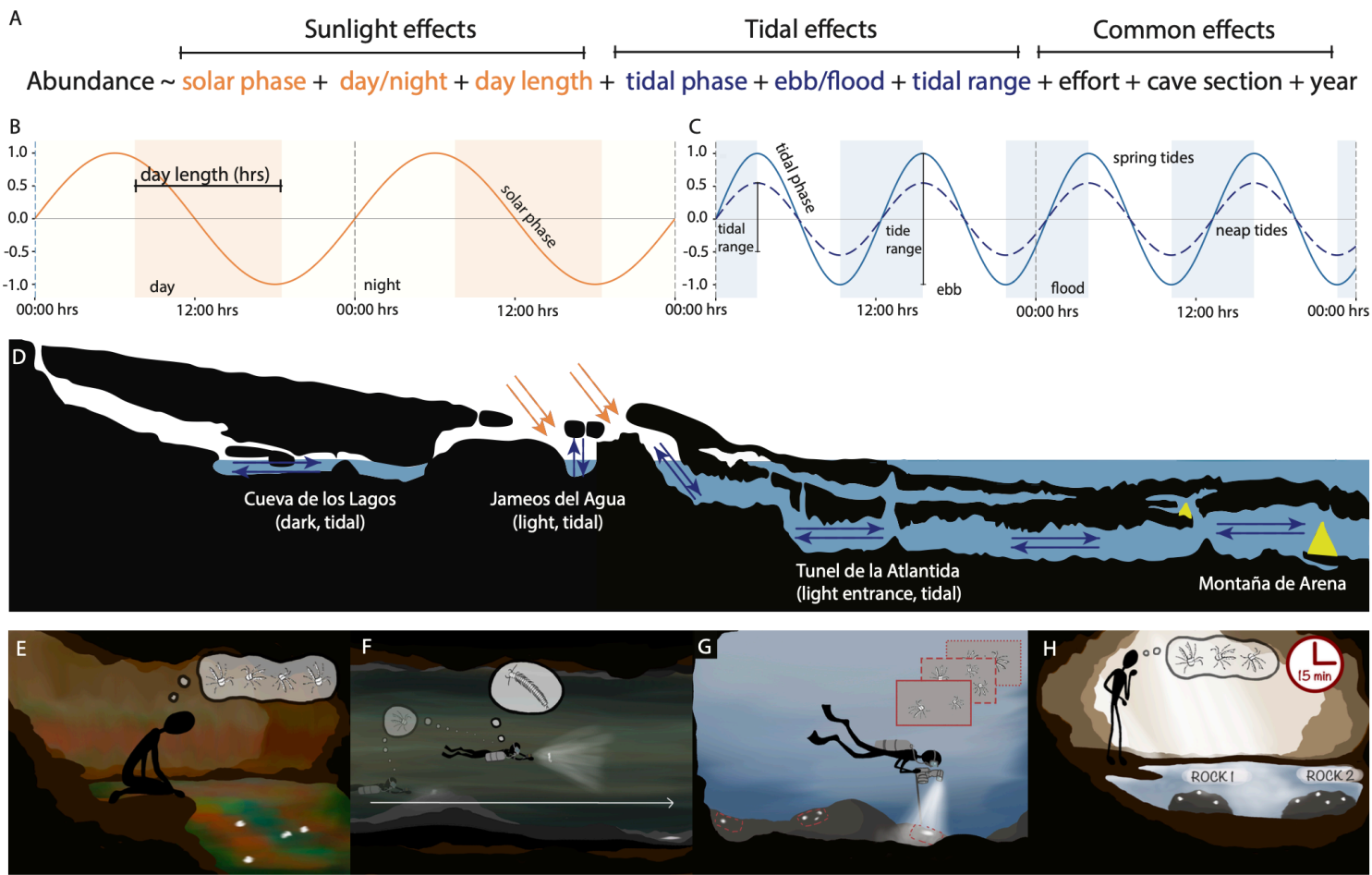


Figure 1

Conceptual model used to analyse abundance of the jameíto *Munidopsis polymorpha* and the remipedes *Morlockia* spp. in Lanzarote's anchialine systems. **A**. Additive modelling framework: abundance (or density, using an effort offset where applicable) was modelled as the sum of light effects (solar phase, day/night, day length), tidal effects (cave tidal phase, ebb/flood, tidal strength), and common effects (effort offset, cave section, year). For each locality (panel D), we compared tide-only, light-only, and combined models, always retaining common terms. **B**. Light covariate day length, day/night, and solar phase (0 = sunrise, 0.5 = sunset, 1 = next sunrise), modelled with a cyclic smoother. **C**. Tidal covariates derived from sea-level peaks lagged to the cave, cave tidal phase (0/1 = tidal peaks with slack water; 0.5 = mid-cycle with maximal currents), tide direction (ebb/flood), and tidal strength (tidal semirange, |post – pre|; z-scored). Stronger and weaker forcing is illustrated by *mareas vivas* (spring tides, solid line) and *mareas muertas* (neap tides, broken line). **D**. Localities and the sections used as model factors, and the expected gradients in light exposure and tidal

influence (Redrawn from Tomasi et al., 2022). Notice that, in profile view, length of different sections might appear distorted. Charcos de Luis (affected by tidal and sunlight effects) is now shown as they do not make part of La Corona lava tube (see Figure 2A). **E–H.** Survey vignettes: direct counts (E), transects (F), photo-quadrats (G), and fixed-point iterative counts (H).

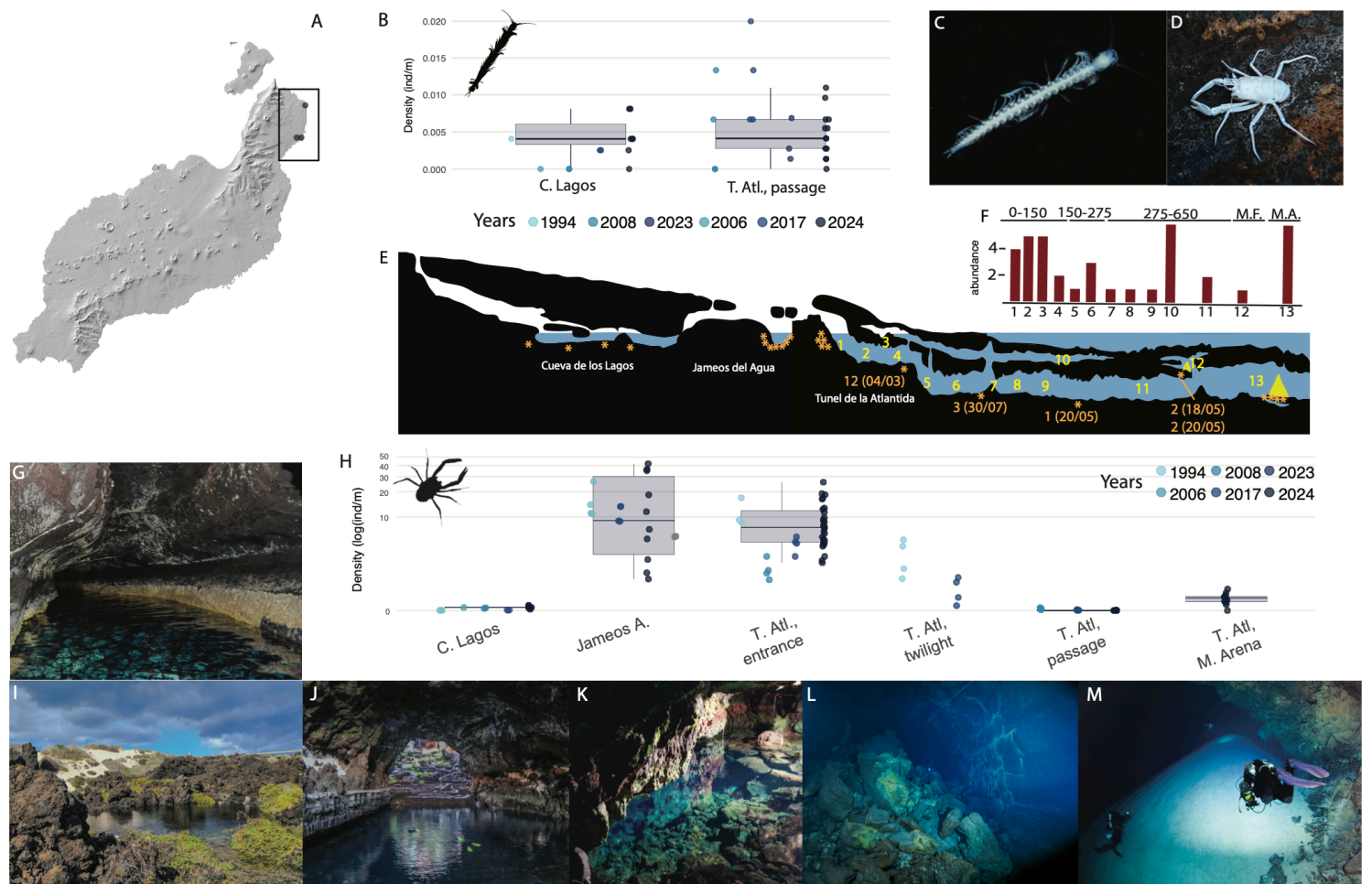


Figure 2

Overview of the results. **A.** Island of Lanzarote showing the position of the sampled localities. **B.** Densities of the remipedes *Morlockia* spp. in Cueva de los Lagos and the passages of Túnel de la Atlántida per year. The number of surveys are indicated at the right of each panel, densities are transformed to allow for comparable plots. **C.** *Morlockia ondinae* photographed swimming in the water column. **D.** The jameíto *Munidopsis polymorpha* photographed in Cueva de los Lagos. **E.** Profile diagram representing the anchialine localities in La Corona lavatube. Asterisk represents the localities where individuals of the jameíto were observed in 2025. Areas with high density of asterisk represent the nutrient enriched localities where the species is always present. Numbers and dates in orange, refer to specific dates in 2025. Numbers in yellow represent the position where the morlocks were observed in 2025. Yellow triangles represent the fossil dune and Montaña de Arena. **F.** Individuals of the morlocks counted in the positions marked with the numbers during the surveys of 2025, grouped according to the following cave sections: 0–150 m, 150–275 m, 275–650 m, Montaña Fósil (MF), and Montaña de Arena (MA). **G.** First lake of Cueva de los Lagos. **H.** Log₁₀ transformed densities of the jameíto in Cueva de los Lagos, Los Jameos del Agua, and Túnel de la Atlántida (entrance, passage, twilight

section and Montaña de Arena) per year, to capture the wide range in density variation. Number of surveys are indicated at the right of each panel and year on the left, densities are transformed to allow for comparable plots. **I.**Charcos de Luis. **J.** Los Jameos del Agua lake. **K.** Entrance of Túnel de la Atlántida. **L.** Dark passage in Túnel de la Atlántida. **M.**Montaña de Arena. Pictures: Suso Fontes (G), A. Martinez (I-K), E. Dominguez (L), J. Heinerth (M). All reproduced with permission.

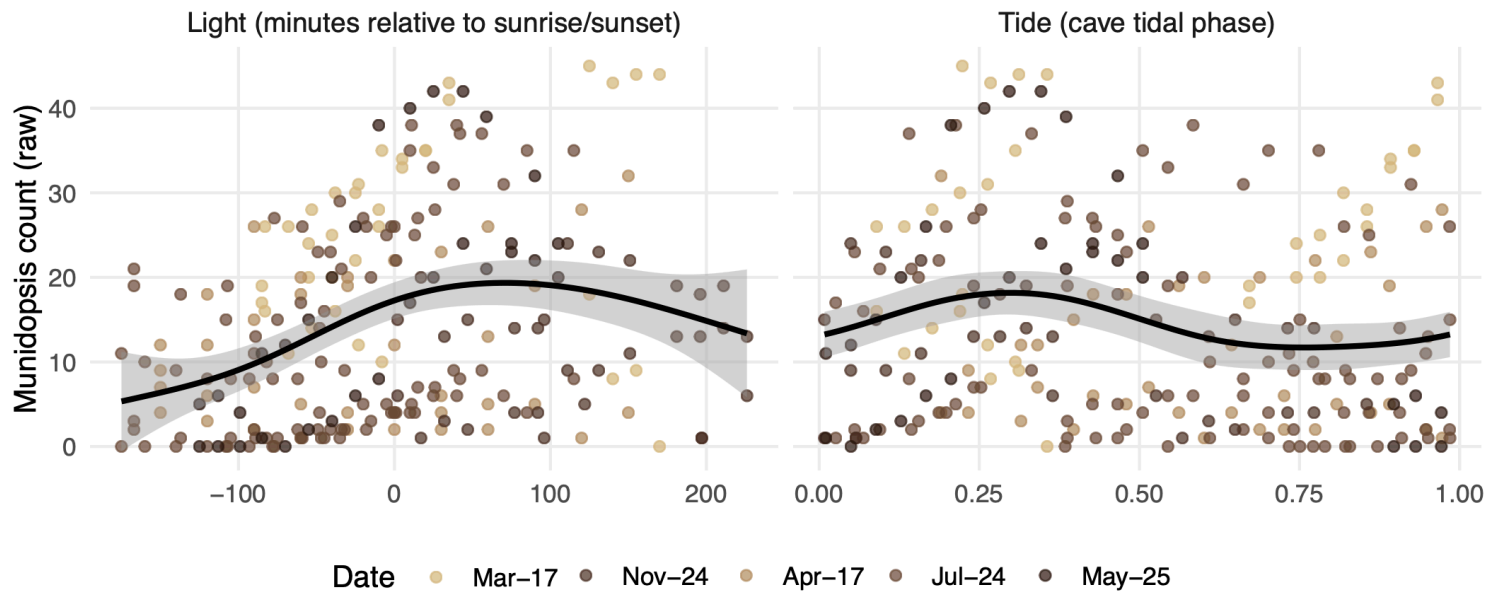


Figure 3

Short-term activity patterns of the jameíto in Los Jameos del Agua. A. Evening time-series of the jameíto counts aligned to sunset (minutes; 0 = sunset), showing raw observations from fixed-point surveys. B. The same observations plotted as a function of cave tidal phase (scaled 0–1, where 0 and 1 = tidal peaks with slack water; 0.5 = mid-cycle with maximal currents), illustrating short-term variability associated with tidal forcing. Points represent individual observations, coloured by sampling date. Black lines represent generalized additive model (GAM) smoothers fitted to the pooled data, with shaded areas indicating 95% confidence intervals. Light-related effects are modelled using a non-cyclic smoother, whereas tidal effects are modelled using a cyclic smoother to account for the periodic nature of the tidal cycle. This figure summarizes the relative influence of diel light transitions and tidal dynamics on short-term fluctuations in the activity of the jameíto.

Supplementary Files

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