

TYPE OF TIDE POOL AS A DOMINANT FACTOR OVER TIDAL INFLUENCE ON INTERTIDAL FISH ASSEMBLAGES IN A SUBTROPICAL ISLAND

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ABSTRACT

Tide pools are dynamic intertidal habitats that host specialized fish communities adapted to extreme and fluctuating environmental conditions. This study investigates how tidal cycles influence the diversity and abundance of ichthyofauna in natural and artificial tide pools along the coast of Gran Canaria, Canary Islands. Ten pools (five of each type) were sampled during both high and low tides over a two-month period. Fish species were identified and quantified using visual census techniques, and the data were analyzed using multivariate statistics. Results revealed that, while species richness remained relatively stable across tidal stages, fish abundance was generally higher during low tide (largely due to the increased presence of juvenile individuals). Furthermore, clear differences in community structure were found between natural and artificial pools: artificial pools supported greater fish abundance, whereas natural pools hosted a higher proportion of native, specialized species such as gobies and blennies. These findings highlight the ecological role of tide pools as both nursery and refuge areas and emphasize the importance of considering habitat type and tidal dynamics when assessing coastal biodiversity in subtropical marine ecosystems.

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INTRODUCTION

Human populations have historically concentrated in coastal areas due to the moderate climate, abundant food resources, and generally favourable living conditions these environments provide (Small and Nicholls, 2003). This settlement pattern has persisted into the present and is projected to continue in the coming decades (Neuman et al., 2015; Cosby et al., 2024). This highlights the importance that this environment holds for humanity due to all the resources it contains, from intertidal zones to deep coastal waters.

The intertidal zone is an area highly influenced by the tides (Zhu et al., 2016). Since it refers to the zone that emerges at low tide and submerges at high tide, it undergoes significant daily changes with each low and high tide (Raffaelli and Hawkins, 1996; Steneck et al., 2002). It is one of the most ecologically and socioeconomically valuable habitats in the world (Wilson et al., 2005). It hosts rich biodiversity, from algae and other benthic organisms to a great variety of fish, and this diversity is strongly influenced by the physical characteristics of the substrate. In particular, Fernández-Martín et al. (2024) emphasized that substrate heterogeneity plays a crucial role in shaping the distribution of intertidal organisms in the Canary Islands, with less disturbed habitats allowing the persistence of species better adapted to cope with environmental stress. It also serves as a nursery for juveniles of many species and provides fishing resources and recreational activities for local communities (González-Delgado et al., 2018; López et al., 2020; Moreno-Borges et al., 2022). Although intertidal zones and tide pools have been the focus of ecological research for decades, tide pools in certain regions—particularly in tropical areas—remain relatively understudied. In contrast, Espadero et al. (2020) specifically highlighted the limited attention given to intertidal seagrass beds, which have also been overlooked and put at risk in recent decades. Recent studies have also emphasized that intertidal fish communities respond strongly to tidal cycles, which drive short-term fluctuations in abundance, diversity, and species interactions (Faria and Almada, 2006; White et al., 2020; Andrades et al., 2023). Because of this, the intertidal zone offers a wide range of opportunities for studies and research on diverse dynamics and a great variety of species (Rullens et al., 2022).

One of the typical structures found in intertidal zones worldwide are tide pools (Andrades et al., 2023). These tide pools, despite not being formally recognized as a coastal management model and lacking a fully precise definition (Luengo Barreto, 2018), are identified by several distinct criteria: they are naturally filled and replenished by the simple flow of the tide, possess an impermeable substrate that allows them to retain water during both high and low tide, are located in the intertidal zone or, if elevated, are filled by the tides, and, in most

cases, are primarily used by humans for bathing (Luengo Barreto, 2018). However, their functionality can vary significantly according to their typology and the degree of human intervention involved; for example, artificial tide pools are often designed with features that facilitate human access and use, while natural tide pools generally lack such structures. Artificial tide pools are increasingly being created as part of coastal infrastructure projects to mitigate biodiversity loss associated with shoreline armouring, with a growing body of work demonstrating their ecological value and potential role in ecological engineering (Firth et al., 2014, 2016; Evans et al., 2019). Natural tide pools, by contrast, remain more exposed to hydrodynamic forces, often with restricted access and fewer safety features (Luengo Barreto, 2018).

Moreover, regardless of their specific type, all tide pools share the characteristic that, when isolated from the open sea during low tide, they undergo gradual changes in key physical parameters such as salinity, pH, and dissolved oxygen levels (Casado-Abellán and Riera, 2024; González-Aragón et al., 2024). This creates conditions that make survival difficult for the species residing within them, prompting a diverse range of organisms worldwide to develop various morphological and biological adaptations to thrive in these ever-changing environments (Reese, 1969; Neumann, 1976; Richards, 2011). For this reason, we can find novel morphologies not observed in other subtidal areas, while at the same time, morphological diversity remains limited, centred around very specific optima. Moreover, this acts as an environmental filter, as species lacking these specific adaptations are unable to establish themselves in this environment (Boyle and Horn, 2006).

Among these species, in the tide pools we can find all kinds of organisms, from a large quantity of algae covering both the surface and the most inaccessible crevices of the pool, to arthropods, echinoderms, molluscs, and fish (Fairchild et al., 2018). For this study, we focused on the ichthyofauna, since these pools play a unique role for this particular group by serving as feeding areas, offering protection, and providing hiding places for the larval and juvenile stages of different species, as well as for adult individuals from nearby zones (Beckley, 1985; Dias et al., 2016; Andrades et al., 2023).

The fish found in tide pools can be classified into three main categories:

- (i) Residents, which are those that have developed specific anatomical, morphological, and physiological adaptations to inhabit these environments. They mainly belong to the families Blenniidae and Gobiidae (Mahon and Mahon, 1994; Arakaki and Tokeshi, 2005);
- (ii) Partial residents or transitory individuals, who spend part of their life cycle in tide pools and the remainder in open waters. An example is seen in families such as Scaridae or Pomacentridae, which spend their juvenile stages in pools and leave once they reach

- maturity (Gibson, 1982; Mahon and Mahon, 1994);
- (iii) Visitors are those that become trapped in pools after entering during high tide and are unable to exit when the tide goes out, or because they attempt to escape the pressure of a predator. Families such as Carangidae are known to appear as accidental visitors in tide pools (Mahon and Mahon, 1994).

Furthermore, depending on their classification, totally different behaviours can be observed among these fish, clearly evidencing which have developed specific adaptations for the environment and which have not (Brown et al., 2011). Residents are adapted to remain close to the substrate and navigate easily among the rocks on the pool floor, tolerating extremely shallow waters with ease. In contrast, visitors struggle to move effectively in these shallow zones and tend to remain in the central areas of the tide pool, where the water is deeper and the conditions more closely resemble those of the surrounding intertidal zone (Faria and Almada, 2006). Tidal cycles also interact with pool type to influence assemblage structure: resident species may remain relatively constant across tides, while visitors and partial residents fluctuate strongly depending on water connectivity and tidal stage (White et al., 2020; Andrades et al., 2023).

The remarkable biodiversity of species associated with tide pools, together with their widespread occurrence across global coastlines and the ecological variability they encompass, underscores the scientific relevance of studying these environments (Denny and Gaines, 2007). Nevertheless, artificial tide pools remain underexplored compared to natural ones, despite their increasing prevalence as a result of ocean sprawl and coastal engineering (Firth et al., 2016; Pérez-Hernández et al., 2020). Studying both natural and artificial pools in parallel therefore provides an opportunity to assess their relative ecological roles, while also examining how tidal cycles mediate fish assemblages within them.

The main objective of this study is to analyse the different species found in both natural and artificial tide pools throughout the day, at low and high tide. The hypothesis is that species present at both tides will be found with a constant number of individuals—these would be the residents—whereas there will be more notable variations in the number of individuals and even in the diversity of other species, evidencing a flux of incoming and outgoing visiting species. Furthermore, to analyse the hypothesis more precisely and to determine whether external factors can generate variations, this study will pursue the following specific objectives: (i) to compare differences in diversity or number of individuals between natural and artificial tide pools; (ii) to observe behavioural differences in the tide pool between resident and visiting species; (iii) to maintain a more refined record of the fish species found in the tide pools of the Canary Islands.

To this end, five natural tide pools and five artificial tide pools on the island of Gran Canaria were selected.

Gran Canaria is a key location for global maritime traffic, connecting more than 180 ports around the world, linking Europe, Africa, and America (Castro et al., 2022). In contrast to areas further north in Europe, whose tide pools have been widely studied, such as in Ireland (Baer and Stengel, 2010) or Iceland (Steinarsdóttir et al., 2003), southern regions like Macaronesia have not received as much attention. Therefore, this study also offers the opportunity to investigate these little-known tide pools in an environment that suffers from significant anthropogenic impact in the marine realm due to ocean sprawl (Pérez-Hernández et al., 2020), and to compare the results obtained with those from other, more extensively studied tide pools in Europe and around the world.

MATERIALS AND METHODS

Study area

The study area is in the northern sector of Gran Canaria (27°N, 15°W), particularly in the municipalities of Gáldar and Arucas, where most the island's tide pools are concentrated (Luengo-Barreto, 2018) (Fig. 1). Gran Canaria, one of the central islands of the Canary archipelago, covers an area of approximately 1,560 km² and has a coastline of about 243 km (Luengo-Barreto, 2018). The high density of tide pools in the northern region is largely due to its rugged volcanic coastline, shaped by historical lava flows that cooled into irregular platforms and depressions. This northern coastline is exposed to persistent Atlantic swells, resulting in high-energy wave action that intensifies coastal erosion and sculpts the basaltic rock, promoting the formation of natural cavities that retain seawater at low tide (Romero-Martín and García-Romero, 2017). These characteristics make the area particularly suitable for the development of tide pools of varying sizes and depths. Furthermore, many of these pools become isolated during low tide, generating microhabitats with steep environmental gradients that favour the presence of highly adapted intertidal species (Riera and Delgado, 2019). This combination of geological structure, wave exposure, and tidal isolation explains the unusually high number and ecological importance of tide pools in this region.

Two distinct types of tide pools are present in the study area: natural and artificial. Natural tide pools are volcanic depressions formed by geological and erosive processes, characterized by irregular shapes, variable depths, and direct exposure to wave action. In contrast, artificial tide pools are purpose-built structures created as part of coastal infrastructure to facilitate bathing and recreational activities (Luengo-Barreto, 2018). These pools are generally reinforced with concrete walls and have more regular morphologies, often incorporating access steps and protective barriers to improve human use. All tide pools in this study were located in the mid-intertidal zone, with seawater input during high tide

and isolation from the sea during low tide. Their tidal elevation was approximately 1–1.5 m above the lowest tidal level. The Canary Islands experience a semidiurnal tidal regime with an average range of about 2 m (Riera and Delgado, 2019), which determines the frequency and extent of water exchange in these habitats. Specifically, 10 tide pools were sampled, with 5 being artificial and the other 5 natural. The artificial ones are: El

Puertillo, Agaete, El Altillio, La Laja, and El Agujero, while the natural ones are: El Sombrero, El Estrecho, Sobradillo 1, Sobradillo 2, and Los Espejos (Fig. 1). Artificial tide pools are generally larger than natural ones, largely due to their design for recreational bathing. For this study, pools of similar size were selected, ranging from 20–30 m in length and 0.5–2 m in depth to ensure comparability (see Table 1).

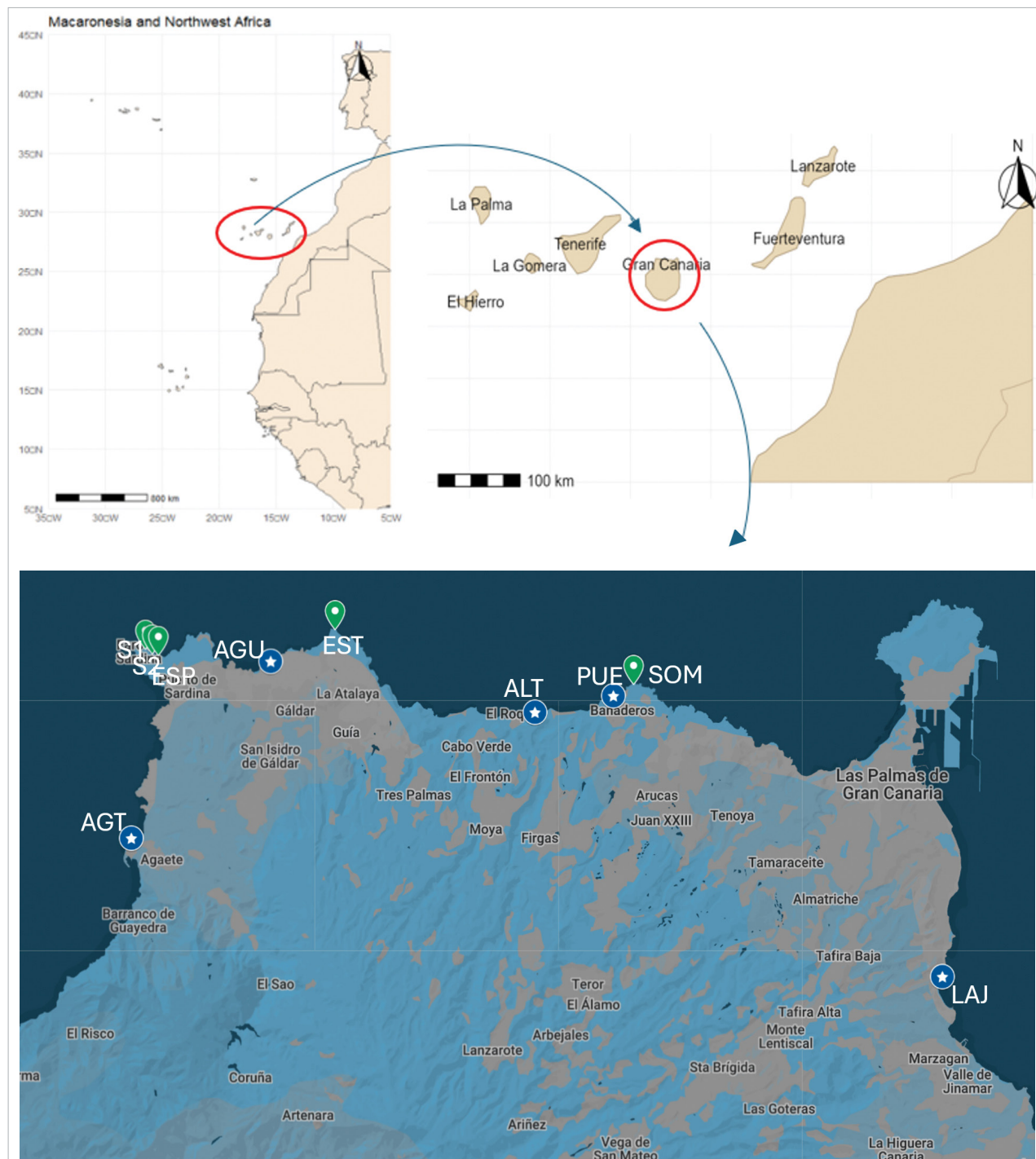


Fig 1. Map of the study area showing the biogeographical region of Macaronesia, the location of the island of Gran Canaria, and the study sites (natural pools (green) and artificial pools (blue) on the northern coast of Gran Canaria). AGT, Agaete; ESP, Espejos, S1, Sobradillo 1, S2, Sobradillo 2; AGU, Agujero; EST, Estrecho; ALT, Altillio; PUE, Puertillo; SOM, Sombreo; LAJ, Laja

Table 1. Surveyed intertidal pools in Gran Canaria, including type, area, average depth, and coordinates

Pool	Type	Area (m ²)	Depth (m)	Coordinates
Charcones del Puertillo	Artificial	7,800	1.4	28° 09' 04'' N 15° 32' 15'' W
Charco del Altillo	Artificial	800	1.4	28° 08' 46'' N 15° 33' 55'' W
Charcos de La Laja (1 & 2)	Artificial	500 & 600	1.2 & 1.5	28° 03' 50'' N 15° 25' 06'' W
Charco del Agujero	Artificial	1,000	1.4	28° 09' 41'' N 15° 39' 38'' W
Charco de las Salinas (Agaete)	Artificial	2,000	2.0	28° 06' 23'' N 15° 42' 39'' W
Charco del Sombrero	Natural	250	1.8	28° 09' 15'' N 15° 31' 49'' W
Charco del Estrecho	Natural	500	1.0	28° 10' 17'' N 15° 38' 15'' W
Charco de los Espejos	Natural	300	1.6	28° 09' 55'' N 15° 42' 20'' W
Charco del Sobradillo "1"	Natural	500	1.2	28° 09' 53'' N 15° 41' 43'' W
Charco del Sobradillo "2"	Natural	350	1.5	28° 09' 53'' N 15° 41' 43'' W

Additionally, the tidal elevation of each pool was also considered, and all selected pools were located in the mid- to lower-intertidal zone, ensuring that they experienced complete immersion at high tide and full isolation at low tide.

This criterion ensures greater accuracy when detecting differences related to tidal changes. Artificial tide pools are defined as those that include human-made structures, such as ramps, walkways, or stairs. In contrast, natural tide pools are those that remain unmodified since their original formation. Furthermore, for the preliminary selection of tide pools to be sampled and to determine which met the requirements, both Google Earth (Google Earth, 2025) and Luengo Barreto (2018) were employed to obtain detailed information and classifications of the different tide pools. Field visits prior to sampling confirmed accessibility, tidal behaviour, and pool suitability for fish censuses. To ensure a more accurate census, each tide pool was subdivided into two distinct sections (M1 and M2) to cover the pool's surface more effectively.

Data collection

Fish assemblages were recorded through standardized visual censuses conducted by a snorkeler during daylight hours. The observer moved slowly across each pool at a consistent pace, covering the entire surface and depth while avoiding disturbance of the fish. To ensure systematic coverage, every pool was subdivided into two sections (M1 and M2), with a 15-minute census carried

out in each section. During each census, all individuals were identified to the lowest taxonomic level possible and counted directly *in situ*, allowing for the non-destructive detection of both resident and transient species across tidal stages. Each tide pool was surveyed twice within a single day—once at low tide and once at high tide, or vice versa—to capture short-term differences in species richness and abundance attributable solely to tidal state. This protocol was repeated in March and April to provide a preliminary assessment of temporal variation, acknowledging that while replication was limited, it allowed for the detection of potential short-term fluctuations associated with species mobility, seasonal habitat use, or life cycle transitions occurring in early spring.

For species identification, a record was kept of the most likely species to be encountered, enabling the majority to be identified on the spot. For those that could not be immediately identified, a species identification guide was used as a reference (Brito et al., 2002; Espino et al., 2018). To achieve the highest level of precision, each fish was identified to the species level to facilitate a better comparison with other studies and to capture the biodiversity of the tide pools of Gran Canaria as accurately as possible. In addition, the World Register of Marine Species (WoRMS, 2025) was used to verify taxonomic names. In total, five natural and five artificial tide pool sites were sampled, and where sites such as La Laja contained more than one pool, each was counted separately to ensure maximum precision. All

observations were entered into an Excel spreadsheet, forming a database organized by locality, tidal phase, species, and specific zones within each pool. This dataset was later used for statistical analysis.

Data analysis

Data analysis was performed using RStudio v4.2.3 (R Core Team, 2023). Initial data processing included the calculation of univariate descriptors such as total fish abundance, species richness, means, and standard deviations for each tide pool. Differences between groups were assessed with Kruskal–Wallis non-parametric tests, given that normality assumptions were not met. In these tests, “groups” refer to pool type (natural vs. artificial), tidal stage (high vs. low), and sampling month (March vs. April). Community composition patterns were explored through Non-metric Multidimensional Scaling (nMDS) based on Bray–Curtis dissimilarities to visualize similarities and differences in fish assemblages across sites and conditions. The dissimilarities were based explicitly on the counts of each species recorded in each tide pool at high and low tide. The data were not transformed prior to analysis. This approach was chosen because the raw count data, which included many low values and zeros, preserved the ecological interpretability of relative abundances. For community composition analyses, the focus was specifically on whether pools differed, without treating repeated sampling of the same pool as a separate factor. The significance of these patterns was formally tested using Permutational Multivariate Analysis of Variance (PERMANOVA), which evaluated the effects of month, tidal stage, and pool type on community structure. Additionally, Similarity Percentage (SIMPER) analysis was applied to identify the species contributing most to the dissimilarities observed between natural and artificial pools and between tidal stages. All multivariate analyses were conducted with the *vegan* package (Oksanen et al., 2022), while *ggplot2* (Wickham, 2016) was used for graphical outputs summarizing abundance, richness, and ordination results.

RESULTS

Fish composition

A total of 8,015 individual fish belonging to 25 species were recorded across the ten surveyed tide pools. In March, a total of 3,987 individuals were counted, and in April 4,028, with 23 species detected in each month. The average abundance per pool ($\pm$ standard deviation throughout) was 397.8 ± 398.0 individuals in March and 403.3 ± 359.3 in April, while the average species richness was 12.4 ± 4.1 species per pool in March and 13.8 ± 3.8 in April. The pool with the highest abundance was La Laja, an artificial pool, with 1,318 individuals recorded in March, whereas the lowest abundance was found at Charco del Estrecho, a natural pool, with 102 individuals

in the same month. Regarding species richness, the pools in Agaete showed the highest diversity in both sampling periods, with 20 species, while the lowest richness was also recorded at Charco del Estrecho, with just 7 species in March. The most abundant species overall were *Chelon labrosus*, *Sarpa salpa*, and *Thalassoma pavo*. Artificial pools were dominated by *C. labrosus* and *S. salpa*, while natural pools showed greater representation of species such as *Thalassoma pavo*, *Parablennius parvicornis*, and *Gnatholepis thompsoni* (Fig. 2). Regarding the tide, a higher overall abundance was recorded during low tide (4,679 individuals) compared to high tide (3,230 individuals). However, species richness remained identical between tides, with 23 species recorded under both conditions, suggesting a relatively stable species composition regardless of tidal fluctuations.

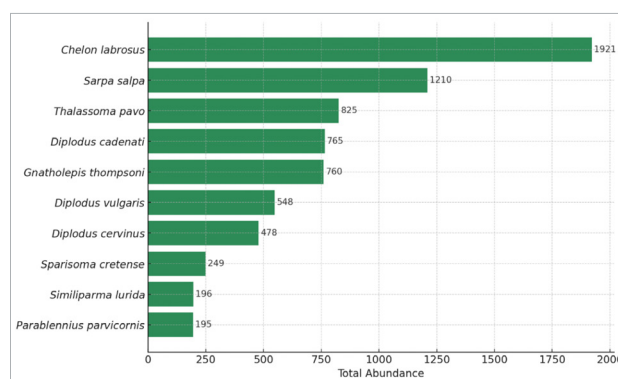


Fig 2. Total abundance of the 10 most frequently observed fish species across all sampled tidal pools. *Chelon labrosus* and *Sarpa salpa* were the most dominant species, with over 1,000 individuals each, highlighting their ecological prevalence in these environments.

Total fish abundances showed marked variations depending on the type of tide pool, tidal stage, and sampling month. In general, artificial pools exhibited a higher number of individuals than natural ones. In March, artificial pools accounted for 3,372 individuals (1,436 during high tide and 1,936 during low tide), compared to 690 individuals recorded in natural pools (293 during high tide and 397 during low tide). The same pattern was observed in April, with 3,266 fish in artificial pools (1,478 during high tide and 1,788 during low tide), versus 762 individuals in natural pools (365 during high tide and 397 during low tide). Regarding tidal stage, low tide consistently yielded higher fish abundance than high tide in both months. In March, 2,333 individuals were observed during low tide and 1,729 during high tide. In April, the difference was even more pronounced, with 2,185 fish during low tide vs. 1,843 during high tide. This trend was particularly evident in artificial pools, where low tide consistently surpassed high tide in total counts. At the site level, La Laja and Agaete stood out as the pools with the highest overall abundances, especially during low tide in March. In contrast, natural pools such

as Estrecho and Espejos exhibited the lowest abundances in both months and tidal stages, reflecting consistent differences in the capacity of pools to retain or attract fish depending on their structural characteristics (Fig. 3).

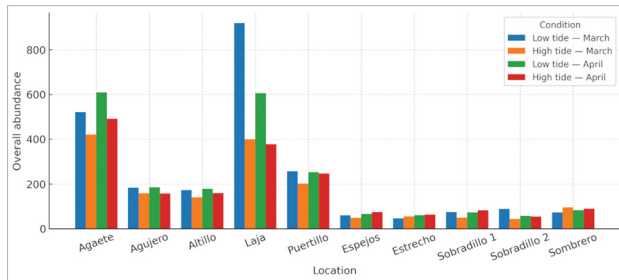


Fig 3. Overall fish abundance at each tidal pool location under four conditions combining tidal state and month. 'LT' refers to low tide and 'HT' to high tide. Data were collected during March and April 2024. Values represent the total number of individuals recorded per site under each condition. Sites are arranged in alphabetical order; the first five correspond to artificial pools, and the last four to natural ones.

Fish abundance showed consistent patterns across both months and tidal stages (Fig. 3). Artificial pools generally hosted a greater number of individuals than natural ones, with particularly high counts during low tide. This suggests that artificial pools—possibly due to their structural characteristics such as larger size, greater depth, and reduced exposure—offer more favourable conditions for fish aggregation. Natural pools, although less populated overall, maintained steady numbers across tides, pointing to their stability as microhabitats. Statistical analysis confirmed that pool type had a significant effect on abundance (Kruskal-Wallis, $H = 57.072$, $p < 0.001$), highlighting the importance of habitat structure over short-term temporal or tidal variations. No significant differences were found between months (March - April) ($H = 0.361$, $p = 0.547$) nor between tidal stages, i.e. low and high tide ($H = 2.792$, $p = 0.094$) (Fig. 4).

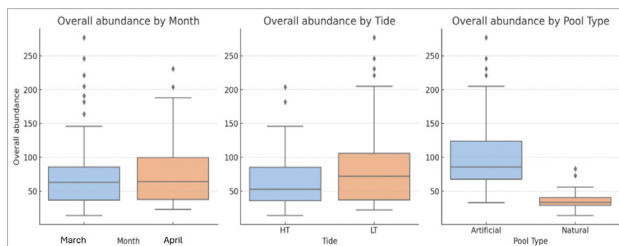


Fig 4. Boxplots showing total fish abundance across different factors: month (March vs. April), tidal condition (High Tide vs. Low Tide), and pool type (natural vs. artificial)

A total of 25 fish species were recorded across the sampled tide pools. Species richness varied considerably depending on pool type, tidal condition, and sampling month. Artificial pools generally hosted slightly more species than natural ones, particularly during low tide.

In March, artificial pools recorded 20 species during low tide and 15 during high tide, while natural pools reached 21 species at low tide and 15 at high tide. In April, artificial pools hosted 21 species during low tide and 20 during high tide, whereas natural pools showed consistent values of 20 species under both tidal conditions. At the site level, the pool at Agaete reached a maximum of 17 species during low tide in both March and April. Alttillo and Puertillo also exhibited high richness, with up to 17 and 14 species, respectively, depending on the condition. In contrast, pools such as Estrecho, Espejos, and Sombrero consistently recorded lower richness, with maximum values of 9–10 species and minimums as low as 5 or 6 under certain conditions (Fig. 5). Overall, species richness tended to be slightly higher during low tide, especially in artificial pools. April also showed marginally higher richness than March, although the trend was not consistent across all locations. These findings suggest that short-term patterns in species presence and detectability may be influenced by both tidal stage and habitat structure.

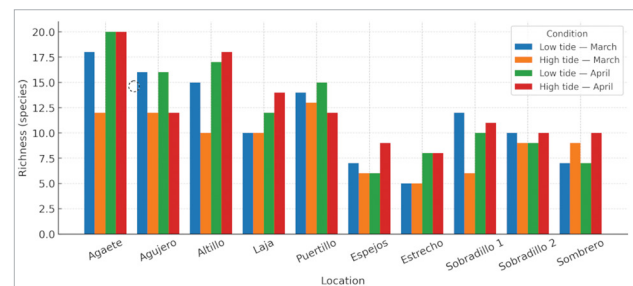


Fig 5. Species richness, across tidal pools, separated by site, tidal condition, and sampling month. Sites are arranged in alphabetical order; the first five correspond to artificial pools, and the last four to natural ones.

Species richness varied moderately between sites but overall followed a pattern similar to abundance. Artificial pools, i.e. Agaete, Agujero, Alttillo, Laja and Puertillo, consistently supported a higher number of species, with the Agaete site showing the greatest richness. In contrast, natural pools, i.e. Espejos, Estrecho, Sobradillo 1, Sobradillo 2 and Sombrero, hosted fewer species, often limited to more specialized intertidal taxa (Fig. 6).

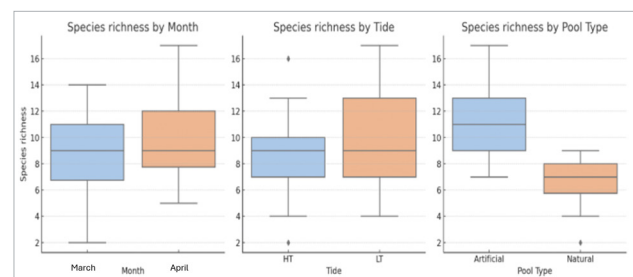


Fig 6. Boxplots showing species richness across different factors: month (March vs. April), tidal condition (High vs. Low tide), and pool type (natural vs. artificial)

Richness did not change significantly between months ($H = 2.725$, $p = 0.098$) or tidal stages ($H = 2.514$, $p = 0.112$), suggesting that fish community composition is relatively stable over short timeframes and tidal conditions. As with abundance, only the type of pool significantly influenced richness ($H = 62.185$, $p < 0.001$), reinforcing the ecological relevance of artificial vs. natural pool environments in shaping community diversity.

Multivariate analysis

The non-metric multidimensional scaling (nMDS) analysis was performed separately for March and April to explore patterns in fish community composition in relation to pool type (natural vs. artificial) and tidal stage (high vs. low tide). In both months, the assemblages recorded in different pools under varying tidal conditions and months were widely dispersed in the ordination space, without forming distinct clusters by pool type or tidal stage. Although low tide samples tended to cluster slightly in certain areas of the plots, this pattern was neither strong nor consistent between months. The general similarity observed between March and April suggests that the overall structure of fish communities remained relatively stable over the sampling period. These results are consistent with previous univariate analyses, which also detected no significant differences in total abundance or species richness between months or tidal stages. Together, the nMDS supports the idea that the most substantial differences in community structure are more closely related to pool type than to temporal or tidal variation (Fig. 7).

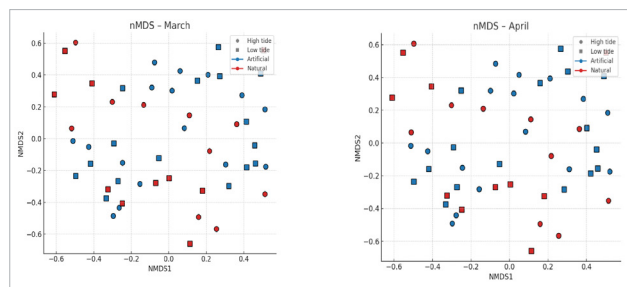


Fig 7. nMDS plots showing fish assemblage structure in intertidal pools during March (stress = 0.12) and April (stress 0.14). Symbols indicate tide (low tide (square) and high tide (circle)) and colours indicate pool type (natural= red & artificial = blue).

The PERMANOVA model, which included the factors *pool type*, *tidal stage*, and *sampling month*, as well as the interaction between pool type and tide, revealed that pool type was the main driver of differences in fish community composition ($F = 74.91$; $p = 0.001$), explaining 42.01% of the total variation. A significant, though much smaller, effect of tidal stage was also detected ($F = 2.95$; $p = 0.029$). In contrast, sampling month had no significant effect ($F = 1.00$; $p = 0.361$), suggesting temporal stability in community structure over the study period. On the other

hand, the interaction between pool type and tide was not significant ($F = 0.46$; $p = 0.737$), indicating that the effect of tide on species composition was similar across natural and artificial pools (Table 2). That is, although differences were observed between tidal stages and between pool types independently, there was no combined pattern indicating that the effect of one factor depended on the other.

Table 2. Results of PERMANOVA testing the effects of pool type, tide, month, and their interaction on fish assemblage structure. Significant effects ($p < 0.05$) are highlighted. R^2 (%): percentage of the total variation in fish assemblage structure explained by each factor in the model.

Factor	df	F	p-value	R^2 (%)
Pool type	1	74.91	0.001	42.01
Tide	1	2.95	0.029	1.65
Month	1	1.00	0.361	0.56
Pool $\times$ Tide	1	0.46	0.737	0.26

The SIMPER analysis revealed that differences in species composition between groups were mainly driven by a small number of dominant species. In the comparison between artificial and natural pools, *Chelon labrosus*—classified as a partial resident that frequently uses pools for feeding but also moves between adjacent habitats—contributed most to dissimilarity, accounting for 16.63% of the total difference. This was followed by *Sarpa salpa* (12.43%), another partial resident that typically occurs in schools and exploits tide pools opportunistically, *Gnatholepis thompsoni* (6.97%), considered a resident species closely associated with pool substrates, and *Diplodus cadenati* (6.92%), also a resident that relies heavily on these habitats. The ten most influential species collectively accounted for over 63% of the accumulated dissimilarity, indicating a marked distinction between the two pool types—likely related to the greater capacity of artificial pools to host mobile or gregarious coastal species (Table 3a).

In the case of the tidal comparison, the pattern was similar but with a lower cumulative contribution: *Chelon labrosus* again topped the list with a 13.5% contribution, followed by *Sarpa salpa* (8.68%) and other species with similar habits. Notably, most of the species driving these differences were either residents or partial residents, suggesting that behavioural use of the pools is tied to their residency status. Visitor species contributed little to the dissimilarities. The ten most important species explained approximately 50% of the total dissimilarity between high and low tide, suggesting that while tidal stage does influence community composition, its effect is less pronounced and more evenly distributed across species compared to the stronger effect of pool type (Table 3b).

Table 3a and 3b. SIMPER analysis showing the species contributing most to differences in fish assemblages between (a) artificial and natural pools, and (b) high tide (HT) and low tide (LT). The top 6 contributing species are listed with their individual and cumulative contributions to dissimilarity.

a) Artificial vs. Natural

Species	Mean abundance (Artificial)	Mean abundance (Natural)	Contribution (%)	Cumulative dissimilarity (%)
<i>Chelon labrosus</i>	35.38	1.95	31.31	31.31
<i>Sarpa salpa</i>	17.13	1.45	14.72	46.03
<i>Diplodus cadenati</i>	10.66	1.20	9.19	55.22
<i>Gnatholepsis thompsoni</i>	4.53	10.75	7.88	63.10
<i>Diplodus vulgaris</i>	7.47	0.65	6.53	69.63
<i>Diplodus cervinus</i>	6.72	0.95	5.68	75.31

b) High tide vs. Low tide

Species	Mean abundance (HT)	Mean abundance (LT)	Contribution (%)	Cumulative dissimilarity (%)
<i>Chelon labrosus</i>	15.04	30.00	33.68	33.68
<i>Sarpa salpa</i>	10.50	11.69	13.04	46.72
<i>Diplodus cadenati</i>	5.58	8.46	8.20	54.92
<i>Gnatholepsis thompsoni</i>	5.96	7.88	7.43	62.36
<i>Diplodus vulgaris</i>	3.73	5.96	6.20	68.56
<i>Diplodus cervinus</i>	3.54	5.46	5.66	74.22

DISCUSSION

This study reveals clear patterns in the distribution of intertidal fish according to pool type and tidal stage. During low tide, a higher abundance of individuals was observed, largely driven by the presence of juveniles seeking shelter in the shallow, isolated waters of the pools (Iglesias, 2012). Despite this increase in numbers, species diversity remained relatively stable across tidal phases, suggesting a consistent taxonomic composition. In terms of habitat, artificial pools supported both greater abundance and higher diversity, likely due to their larger size, more stable physical conditions, and reduced exposure to wave action (Ostálé-Valderramas et al., 2018). Nevertheless, natural pools more frequently hosted species typically associated with tide pool environments, such as gobies and blennies, which are known for their adaptations to fluctuating and harsh intertidal conditions (White et al., 2015). These differences highlight the distinct ecological roles that natural and artificial tide pools may play within the coastal mosaic. The patterns observed here align with those reported in other intertidal systems, where habitat characteristics strongly influence community structure. The patterns observed in the intertidal pools of Gran

Canaria are consistent with findings from other coastal systems with similar environmental conditions. For instance, Faria and Almada (2006) documented higher fish abundance during low tide along the Atlantic coast of Portugal, with a relatively stable species composition between tidal stages, aligning well with the results of this study. Fernández-Martín et al. (2024) emphasized the crucial role of substrate characteristics in shaping intertidal organism distribution in the Canary Islands, highlighting that less disturbed habitats support the persistence of species adapted to environmental stress. Dias et al. (2016) also demonstrated that intertidal pools serve as alternative nursery habitats for coastal fish, reporting high concentrations of larvae and juveniles of species such as *Diplodus sargus*, which underscores the ecological importance of these habitats during early life stages. Further supporting these findings, research from other regions highlights how habitat complexity and connectivity significantly influence the composition and abundance of intertidal fish communities. Francour et al. (2009) showed that structural complexity in Mediterranean intertidal pools enhances juvenile fish diversity and abundance, emphasizing the role of refuges and microhabitats in juvenile survival.

Additionally, Bezerra et al. (2017) revealed that seasonal variations in temperature and algal cover modulate fish community distribution and behaviour in intertidal pools, suggesting that variable environmental factors also contribute to community structure differences. Together, these studies, alongside the current results, highlight the importance of considering both physical habitat features and environmental conditions when interpreting intertidal fish community dynamics.

While the findings of this study are robust, it is essential to consider certain limitations—particularly those related to the sampling design—when evaluating the generalizability of the conclusions. Acknowledging these constraints is important for accurately interpreting the broader implications of the results. Firstly, the sampling was carried out over a relatively short period of time, which limits the ability to assess potential seasonal or interannual variations in community structure. Moreover, since data collection relied on surface visual censuses, some species with more cryptic behaviour or benthic habits may have gone undetected, particularly in pools with greater structural complexity. Although efforts were made to select pools of similar size and depth, a degree of natural variability remains, which could influence the observed composition. For future research, it would be advisable to extend the temporal scope through year-round monitoring to identify seasonal patterns in juvenile presence and determine whether their concentration during low tide reflects a consistent or episodic phenomenon. It would also be beneficial to incorporate complementary methods, such as underwater cameras or nighttime surveys, and to explore additional environmental variables—such as temperature, dissolved oxygen concentration, or algal cover—that may modulate the presence and abundance of certain fish species.

The results of this study provide valuable insights for the conservation of intertidal coastal ecosystems, particularly on islands such as Gran Canaria, where human pressure on the coastline continues to increase (Delgado and Riera, 2020). The differences observed between natural and artificial pools suggest that both habitat types serve complementary ecological functions: while artificial pools can act as accessible nurseries for generalist species or juvenile coastal fish, natural pools support more specialized faunal components that are sensitive to habitat alteration. This duality highlights the importance of preserving natural pools as reservoirs of native biodiversity, while also highlighting the potential to optimize the design and management of artificial pools to enhance their ecological functionality. Furthermore, given that artificial pools support high abundance and diversity, they could be considered valuable components in active conservation strategies, serving as reinforcement habitats or refuges for threatened intertidal species that appear to adapt well to the dynamics and structure of these modified systems. In this context, the data obtained here may serve as a foundation for the development of

monitoring programs, restoration strategies, or coastal management policies that integrate these habitats as key elements within the coastal landscape and as sensitive indicators of intertidal ecosystem health.

CONCLUSIONS

This study demonstrates that the tide pools of Gran Canaria host diverse ichthyofaunal communities, with community structure strongly influenced by pool type—natural or artificial—while temporal variation (March vs. April) and tidal stage (high vs. low tide) show comparatively weaker effects. Artificial pools supported higher fish abundances, likely due to their greater size, depth, and structural stability. However, natural pools harboured a higher proportion of native species, such as gobies and blennies, which are specifically adapted to the harsh intertidal conditions, underscoring their ecological importance. Moreover, the higher number of individuals observed at low tide—particularly juveniles—suggests that these habitats may serve as refuges and recruitment areas. The stable species richness observed between tidal stages and months indicates that tide pools act as temporally consistent microhabitats, offering essential environments for resident species. This work highlights the importance of considering both abundance and taxonomic composition when evaluating the ecological value of coastal systems, especially under increasing anthropogenic pressure. The results suggest that natural pools, despite lower total abundances, play a key role in conserving specialized and native intertidal species.

TIP PLIMNOG BAZENA KAO DOMINANTAN ČIMBENIK U ODNOSU NA UTJECAJ PLIME I OSEKE NA ZAJEDNICE RIBA U LITORALNOJ ZONI SUPTROPSKOG OTOKA

SAŽETAK

Plimni bazeni dinamična su međuplimna staništa koja su domaćini specijaliziranim ribljim zajednicama prilagođenim ekstremnim i promjenjivim uvjetima okoliša. Ova studija istražuje kako ciklusi plime utječu na raznolikost i brojnost ihtiofaune u prirodnim i umjetnim plimnim bazenima duž obale Gran Canarije, Kanarski otoci. Deset bazena (pet svakog tipa) uzorkovano je tijekom plime i oseke tijekom dvomjesečnog razdoblja. Vrste riba identificirane su i kvantificirane pomoću vizualnih tehnika, a podaci su analizirani pomoću multivarijantne statistike. Rezultati su pokazali da, iako je bogatstvo vrsta ostalo relativno stabilno tijekom plimnih faza, brojnost riba općenito je bila veća tijekom oseke (uglavnom zbog povećane prisutnosti mladih jedinki). Nadalje, pronađene su jasne razlike u strukturi zajednice između prirodnih i umjetnih bazena: umjetni bazeni podržavali su veću

brojnost riba, dok su prirodni bazeni bili domaćini većem udjelu domaćih, specijaliziranih vrsta poput glavoča i babica. Ovi nalazi ističu ekološku ulogu plimnih bazena kao područja za razmnožavanje i utočišta te naglašavaju važnost razmatranja tipa staništa i dinamike plime i oseke pri procjeni obalne bioraznolikosti u suptropskim morskim ekosustavima.

Ključne riječi: plimni bazeni, ihtiofauna, bogatstvo vrsta, brojnost riba, Kanarski otoci, Sjeveroistočni Atlantski ocean

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DECLARATION OF COMPETING INTEREST

The authors declare no conflict of interest.

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SUPPLEMENTARY MATERIAL

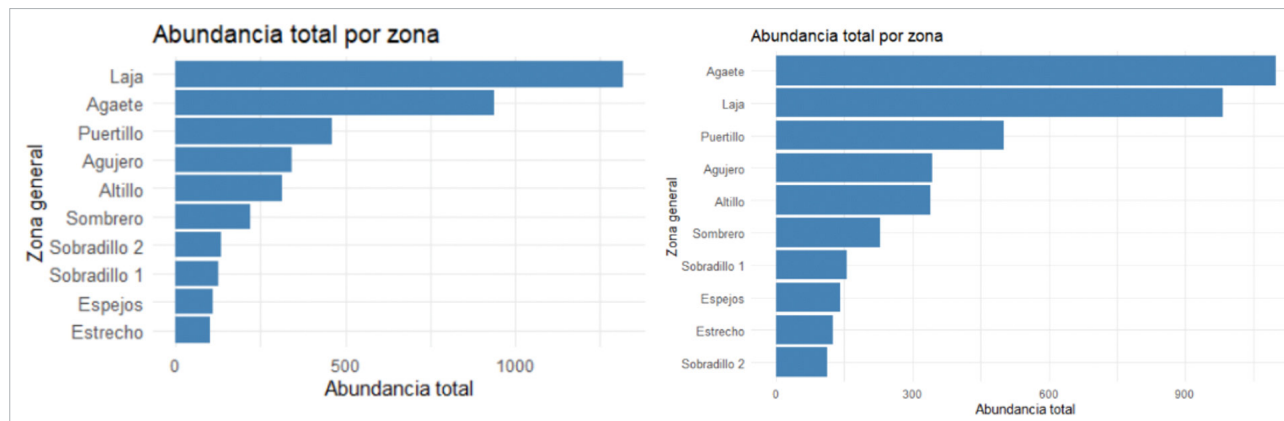


Fig S1. Total fish abundance by general sampling zone in March and April. Artificial pools such as La Laja and Agaete showed the highest abundances in both months, while natural pools like Estrecho and Espejos exhibited the lowest values. The abundance pattern was consistent, with minor differences in ranking between months.

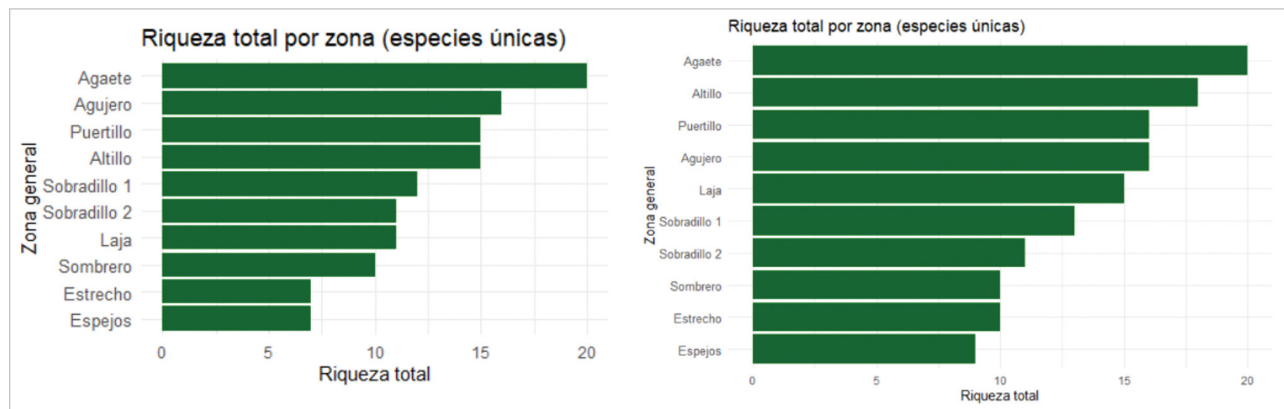


Fig S2. Species richness (unique species) by general sampling zone in March and April. Artificial pools (e.g. Agaete, Puertillo, Altillo) consistently supported a greater number of species, whereas natural pools such as Estrecho and Espejos showed the lowest richness values. Overall patterns remained stable between sampling months.

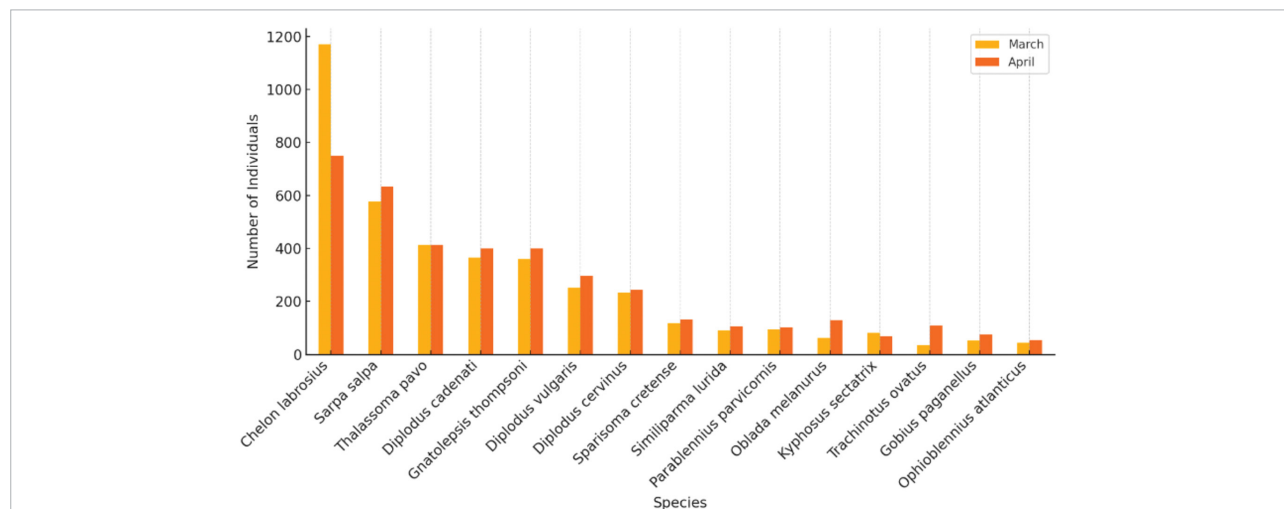


Fig S3. Total number of individuals per species recorded in March and April. *Chelon labrosus* was the most abundant species in both months, followed by *Sarpa salpa*, *Thalassoma pavo*, and *Diplodus* spp. Moderate seasonal shifts were observed in the relative abundance of several species.