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Are invasive barnacles displacing native species? Patterns of settlement and co-occurrence in the southwestern Gulf of Mexico

¿Los balanos invasores están desplazando a las especies nativas? Patrones de asentamiento y coexistencia en el suroeste del golfo de México

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ABSTRACT

Background: Barnacles are among the most successful invasive invertebrates worldwide. In the Gulf of Mexico, invasive barnacle species coexist with native species. In Laguna de Términos, Campeche, previous studies have recorded two invasive species: *Amphibalanus amphitrite* and *A. reticulatus*. However, native populations typically dominated on natural substrates. **Goals**: This study provides the first evidence of the dominance of invasive barnacles on artificial substrates in the region. This research was part of a broader investigation on the diversity and spatial distribution of invertebrate recruitment in seagrass meadows, using collectors not specifically designed for sessile organisms. **Methods:** Three seagrass meadow sites, each over 7 km apart and varying degrees of wave exposure, were selected to assess spatial variability in meadow-associated organism community. Artificial seagrass units made of plastic straps were strategically deployed at the center, edge, and outside of each meadow during the summer. Upon retrieval, a significant abundance of barnacles prompted a detailed analysis of this community. **Results:** Invasive species dominated all three sites, comprising 55% of total barnacle settlements, while native species accounted for 45%. Among invasive species, *A. amphitrite* was the most abundant (94%), followed by *A. reticulatus* (6%). Among native species, *A. eburneus* was the most abundant (74%), followed by *A. venustus* (18%) and *A. improvisus* (8%). Significant differences were found by site ($p<0.01$) and by meadow zone between invasive and native ($p<0.05$). **Conclusions:** We observed a possible displacement of native barnacles by the invasive barnacles, based on previous studies concerning natural substrates in Laguna de Términos. However, our study focused on artificial substrates, where ecological dynamics may differ. There is no conclusive evidence of displacement, and the potential impact remains uncertain, whether temporary or permanent.

Key words: *Amphibalanus*, coastal lagoon, Gulf of Mexico, marine invasions, settlement

RESUMEN

Antecedentes: Los balanos se encuentran entre los invertebrados invasores más exitosos del mundo. En el golfo de México, especies de balanos invasores coexisten con especies nativas. En la Laguna de Términos, Campeche, estudios previos habían registrado la presencia de dos especies invasoras, *Amphibalanus amphitrite* y *A. reticulatus*. Sin embargo, las poblaciones nativas típicamente dominaban en sustratos naturales. **Objetivos:** Nuestro estudio proporciona la primera evidencia del dominio de balanos invasores en sustratos artificiales. Este estudio formó parte de una investigación más amplia sobre la diversidad y distribución espacial del reclutamiento de invertebrados en praderas de pastos marinos, usando colectores no específicamente diseñados exclusivamente para organismos sésiles. **Métodos**: Tres sitios de praderas de pastos marinos, separados entre sí por más de 7 km, con distintos grados de exposición al oleaje, fueron seleccionados para examinar la variabilidad espacial de la comunidad de organismos asociados a las praderas. Se colocaron estratégicamente unidades de pasto marino artificial, hechas de cintas plásticas, en el centro, borde y exterior de cada pradera durante el verano. Al recuperar los colectores, se observó una abundante presencia de balanos, lo que motivó un análisis más detallado de esta comunidad. **Resultados:** Las especies invasoras dominaron en los tres sitios, representando el 55% de los asentamientos totales, mientras que las especies nativas representaron el 45%. Entre las especies invasoras, *A. amphitrite* fue la más abundante (94%), seguida de *A. reticulatus* (6%). Entre las especies nativas, *A. eburneus* fue la más abundante (74%), seguida de *A. venustus* (18%) y *A. improvisus* (8%). Se encontraron diferencias significativas entre sitios ($p<0.01$) y entre zonas de la pradera entre especies invasoras y nativas ($p<0.05$). **Conclusiones:** Observamos un posible desplazamiento de balanos nativos por balanos invasores, basándonos en estudios previos sobre sustratos naturales en la Laguna de Términos. Sin embargo, nuestro estudio se centró en sustratos artificiales, donde la dinámica ecológica puede diferir. No hay evidencia concluyente de desplazamiento y el impacto potencial, ya sea temporal o permanente, sigue siendo incierto.

Palabras clave: *Amphibalanus*, asentamiento, golfo de México, invasión marina, laguna costera

INTRODUCTION

Crustaceans are considered among the most common invasive organisms in marine environments (Carlton *et al.*, 2011). Among them, barnacles (Cirripedia) stand out for their remarkable ability to adapt to different environments and attach to nearly any hard substrate, often facilitating their successful introduction in new areas (Torres *et al.*, 2011). The main ecological effects of these organisms include competition for space and food with native species, habitat alteration, and negative impacts on the settlement, growth, and survival of other sessile organisms (Boudreaux *et al.*, 2009). However, in many areas where they are introduced, information about their population dynamics remains scarce. This is crucial because not all non-native species become invasive in their introduced environments (Katsanevakis *et al.*, 2014). Some species fail to thrive, while others may persist at low abundances without causing negative effects until a change in environmental conditions triggers population growth, allowing them to outcompete native species (Katsanevakis *et al.*, 2014).

The species *Amphibalanus amphitrite* (Darwin, 1854) and *A. reticulatus* (Utinomi, 1967) are native to the Indo-Pacific region, were introduced to the western Atlantic in the mid-20th century, coinciding with the intensification of maritime traffic and the role of vessels as dispersal vectors (Carlton *et al.*, 2011). Since then, numerous reports have documented their presence along the Atlantic coast of the Americas, from the United States to Argentina, including the Gulf of Mexico and Caribbean islands (Henry & McLaughlin, 1975; Ferreira *et al.*, 2009), as well as the Eastern Pacific for *A. amphitrite* (Henry & McLaughlin, 1975; Carlton *et al.*, 2011; Ramos-Morales *et al.*, 2024).

In the Gulf of Mexico, *A. amphitrite* was first recorded in 1931 in Dry Tortugas, Florida, possibly as a result of ship-mediated transport (Carlton *et al.*, 2011). However, its establishment in other areas was not documented until the 1950s and 1960s, with reports from several bays in Florida (Tampa, Boca Ciega, St. Marks, and St. Andrews) and later in Texas (Corpus Christi in 1971 and Port Mansfield). In Mexico, the species was reported as early as 1965 in the state of Veracruz (Wells, 1966; Zullo, 1966; Henry & McLaughlin, 1975; Gittings, 1985; Gittings *et al.*, 1986). *Amphibalanus reticulatus* was first detected in 1972 on platforms and pilings in Louisiana, and by 1986 it was common along the north-central Gulf coast, from Louisiana to Texas (Gittings *et al.*, 1986). It has been suggested that in turbid waters of this region, *A. reticulatus* may have partially displaced *A. amphitrite* (Gittings *et al.*, 1986).

In the Mexican coast of the Gulf of Mexico, both species have been reported in the states of Tamaulipas, Veracruz, and Campeche (Henry & McLaughlin, 1975; Celis *et al.*, 2007; Winfield *et al.*, 2010; Ávila *et al.*, 2018). Specifically, in Laguna de Términos, Campeche, one of the largest coastal estuarine lagoons of Mexico, Ávila *et al.* (2018) conducted the first study to examine the presence and behavior of invasive barnacles in the region. Their research focused on the population dynamics of *A. amphitrite* settled on two native oyster species, which served as natural substrates. The authors reported that the abundance of this invasive barnacle was comparable to that of native species, highlighting the need for continued monitoring to detect potential structural shifts in the benthic community.

The most visible morphological characteristic of these invasive species is the vertical magenta line pattern that starts at the base of each plate and extends to the apex, distinguishing them from the neutral and whitish tones of native Gulf of Mexico species (Fig. 1). In its native range, *A. amphitrite* demonstrates strong competitive abilities by forming dense beds capable of excluding competitors from rocky reef habitats (Pochai *et al.*, 2017). However, in the Gulf of Mexico, no prior references had documented invasive species displacing native organisms.

This study aimed to contribute to the understanding of the spatial distribution of recruitment of the invasive barnacles *A. reticulatus* and *A. amphitrite* within seagrass meadows in the southern Gulf of Mexico. Using artificial seagrass units, we quantified and compared the abundance of recruits with that of native species. Furthermore, we evaluated the distribution of recruits within and among seagrass meadows (at small and landscape scales, respectively) with relation to environmental factors.

MATERIAL AND METHODS

Study area and sampling design: The study was conducted in the Laguna de Términos system, Campeche, located in the southern Gulf of Mexico (Fig. 2). Within this system, three sampling sites were selected, each characterized by monospecific meadows of *Thalassia testudinum* Banks ex Koenig. These sites were distributed along the inner coast of Carmen Island and were named based on their proximity to an urban area (Ciudad del Carmen) and varying degrees of wind-driven wave exposure: Undisturbed and Protected Site (UPS), Undisturbed and Semi-Exposed Site (USES), and Disturbed and Exposed Site (DES) (Fig. 3).

To examine the spatial distribution of barnacle recruitment among and within seagrass meadows, Artificial Seagrass Units (ASUs) were used. These consisted of a rigid plastic mesh base (20 x 20 cm) to which green polypropylene straps (1.2 x 30 cm) were attached . The density (80 straps/ASU) and length (30 cm) of the plastic straps were based on the density and blade length previously reported for *T. testudinum* meadows in the study area (Hernández-Peña, 2018). At each study site, nine ASUs were simultaneously deployed for 80 days (from late June to early September 2022): three in the central part of the meadow, three at the edge, and three outside the seagrass meadow. ASUs were anchored to the seafloor using 0.5x40 cm steel rods and arranged in parallel alignment with the seagrass meadow edge, with a separation of 2 m between each one. The distance between each ASU group (central, edge, and outside) was 20 m.

To characterize the environment in each sampling zone, sedimentation rate (g dry weight/m²/day), hydrodynamics (% dissolution), depth (m), temperature (°C), and salinity (UPS) were measured at the beginning and end of the study. To measure sedimentation rate in each experimental area, three PVC sediment traps with an internal opening of 2.5 cm and a height of 15 cm were deployed (vertically and 1 m apart) at the start of the experiment and removed at the end. Hydrodynamics were calculated based on the weight loss (g) of gypsum cylinders due to water movement over a specific period. Three pre-weighed (dry weight, g) gypsum cylinders (5 cm in diameter) were placed in each experimental area, anchored to vertical PVC supports with plastic straps near the seabed. Water temperature and salinity were measured using a YSI-EXO2 multiparameter probe.

This study is part of a broader project about the spatial distribution of sessile invertebrate recruitment in seagrass meadows. Since water temperature is a key factor stimulating the reproductive stage of many shallow-water marine invertebrates, the study was conducted during the summer season (May-September), when this factor increases seasonally.

Laboratory work: Barnacles and other sessile invertebrates were carefully detached from each side of the straps and placed in labeled containers with 70% alcohol. To determine density, the strap area of each ASU was calculated, considering both sides of the straps, resulting in a total area of 0.576 m² per ASU.

At the USES site, where a sample of 1,393 g was collected, subsampling was necessary due to the high abundance of specimens that made counting difficult. A 100 g subsample was used to count the specimens from that ASU and estimate the total abundance collected. Using stereoscopic and optical microscopes and following Henry & McLaughlin (1975), specimens were identified, measured, and sorted by species. Given the difficulty in accurately identifying tiny specimens to the species level, only individuals larger than 5 mm in diameter were identified accordingly. Smaller specimens were classified according to their distinctive coloration, either as invasive (pink stripes) or native (white).

Sediment collected in the traps was washed with distilled water to remove salts and then dried in a Terlab oven to obtain dry weight. The average sedimentation rate was expressed in g/m²/day for each site and zone. Gypsum cylinders used to measure hydrodynamics were retrieved after five days, dried in an oven at 50°C for 48 hours, and weighed to determine dry weight. Based on weight loss due to material dissolution, the average dissolution rate (% dissolution/day) was calculated for each zone (Maldonado & Young, 1996).

Statistical analysis: All data on barnacle sizes and abundances were tested for normality and homoscedasticity using Shapiro-Wilk and Levene tests, respectively. Depending on the results, one-way or two-way ANOVA were used for parametric data, while Kruskal-Wallis and Mann-Whitney U tests were applied for nonparametric data. Post hoc comparisons included Tukey and Dunn tests. To determine spatial variability (among sites and meadow zones) in environmental and biological variables, one-way and two-way ANOVAs were conducted, followed by the Student-Newman-Keuls post hoc test when normality and homoscedasticity assumptions were met. Nonparametric Kruskal-Wallis ANOVA and Tukey's post hoc test were used when assumptions were violated. For water temperature data, nonparametric Kruskal-Wallis ANOVAs were applied. For salinity, sedimentation rate, and hydrodynamics data, two-way ANOVAs were conducted.

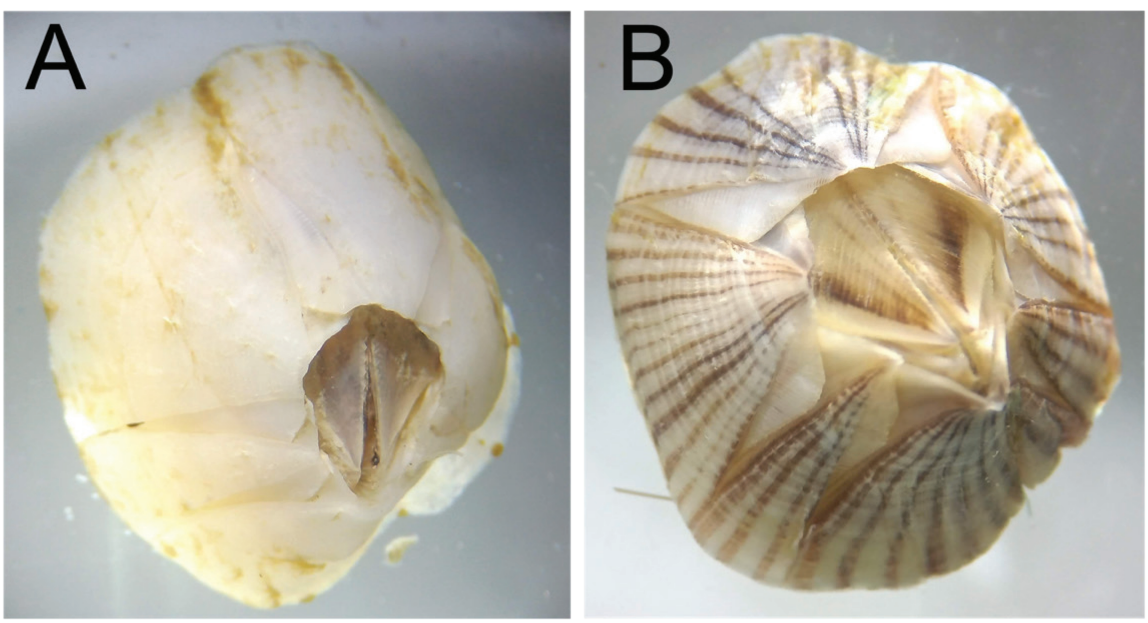

Figure 1. Comparison of external coloration patterns between native and invasive barnacles in Laguna de Términos. The native barnacle on the left (A) represents the typical white coloration observed across native species, while the invasive barnacle on the right (B) exhibits the characteristic purple striping found in invasive species. Although morphological differences among native species (*A. eburneus, A. venustus*, and *A. improvisus*) and invasive species (*A. amphitrite*, *A. reticulatus*) require microscopic examination, the images depict the most abundant and visually distinguishable representatives of each group.

Analysis of precursor diatoms. To evaluate differences in precursor diatoms in barnacle ecological succession, we randomly selected five ASUs straps from sites where native barnacles were abundant and five from sites dominated by invasive barnacles. Diatoms were collected from each ASU strap by scraping them with a blade and using distilled water. A composite sample was created for each category, resulting in two composite samples. To clean diatoms and remove organic matter, samples were placed in porcelain crucibles and dried at 100°C in a convection oven. The crucibles were then heated in a muffle furnace at 550°C for two hours. The diatom powder was recovered from the crucibles and suspended in 10 mL of distilled water. A 20 µL subsample was placed on a coverslip and dried in a convection oven for 24 hours. Two coverslips were prepared for each sample. For each site, two permanent diatom slides were created using high-refractive-index mounting resin (Pleurax= 1.7 I.R.). Diatom observations were made at 100X magnification and identified using specialized literature. Sample size for diatom counting was set at 300 frustules per site.

RESULTS AND DISCUSSION

Twenty-seven Artificial Seagrass Units (ASUs) were processed and analyzed, nine per site, with three in each area (center, edge, and outside of seagrass meadow). The estimated total surface area for the settlement was 15,552 m², calculated by considering both sides of all artificial seagrass leaves. It was observed that invasive species dominated at all three sites, representing 55% of the total barnacle settlements on the ASUs, while the remaining 45% consisted of native species. Among the invasive specimens, *A. amphitrite* was the most abundant, comprising 94% of the organisms, followed by *A. reticulatus* with 6%. Among the native species, *A. eburneus* (Gould, 1841) was the most abundant at 74%, followed by *A. venustus* (Darwin, 1854) at 18%, and *A. improvisus* (Darwin, 1854) at 8%.

There were significant differences in average abundance between sites for both invasive and native species ($p<0.01$, Fig. 3), with the USES site showing the highest abundance for both groups. These variations can be attributed to the different recruitment intensity of organisms on the ASUs at each site. The UPS site had a few tens of specimens, the DES site had hundreds, and the USES site had thousands.

The variation in abundance among sites can be explained by several factors, including competition with other species, predators, and seagrass density. For example, the UPS site is more influenced by marine environments due to its proximity to the entrance from the Gulf of Mexico into Laguna de Términos. This site had a higher settlement of marine organisms. Polycitoridae ascidians totaling 6 kg across the nine ASUs. The presence of a large number of ascidians can influence barnacle settlement, as they compete for space. The UPS site is a protected area with low water movement but constant circulation, and seagrass density here was 300 leaves per m². Additionally, the presence of *Menippe mercenaria* Say, 1818 (stone crab), a known barnacle predator, was observed at this site.

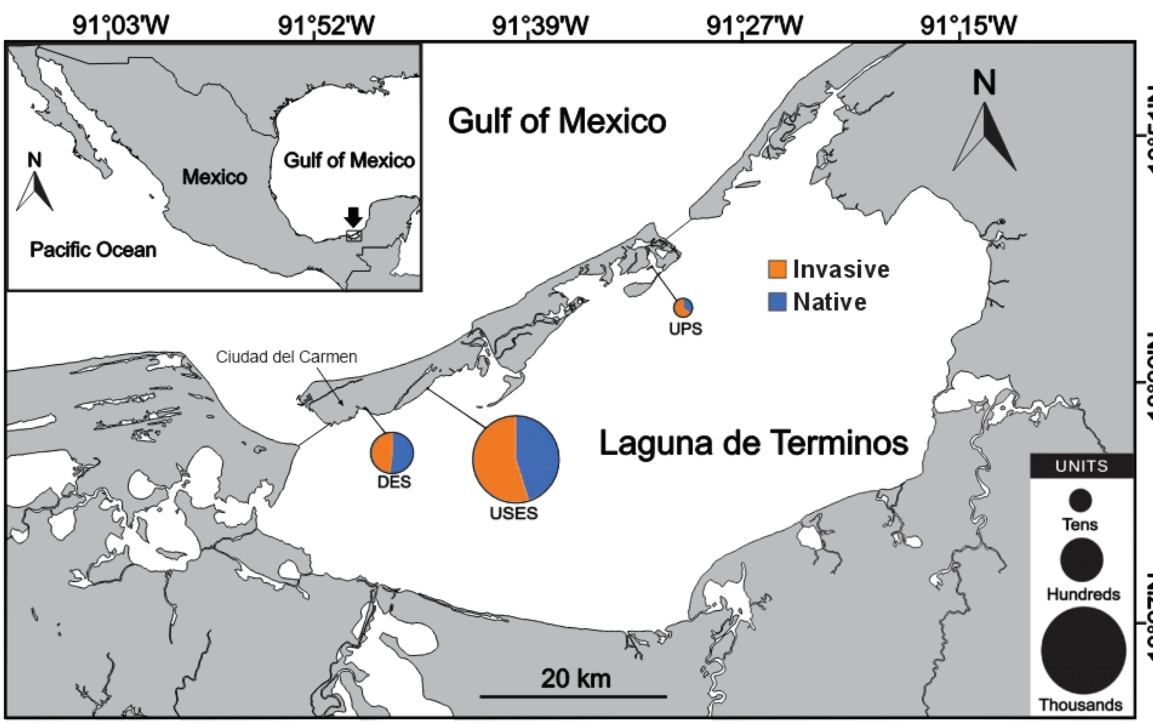

Figure 2. Map of sampling sites and proportions of native and invasive barnacle abundances. Sites are shown from left to right in order of exposure to anthropogenic disturbances: Site 1: Disturbed and exposed site (DES), Site 2: Undisturbed and semi-exposed site (USES), and Site 3: Undisturbed and protected site (UPS). Additionally, each site displays the relative proportion of barnacles found at each location.

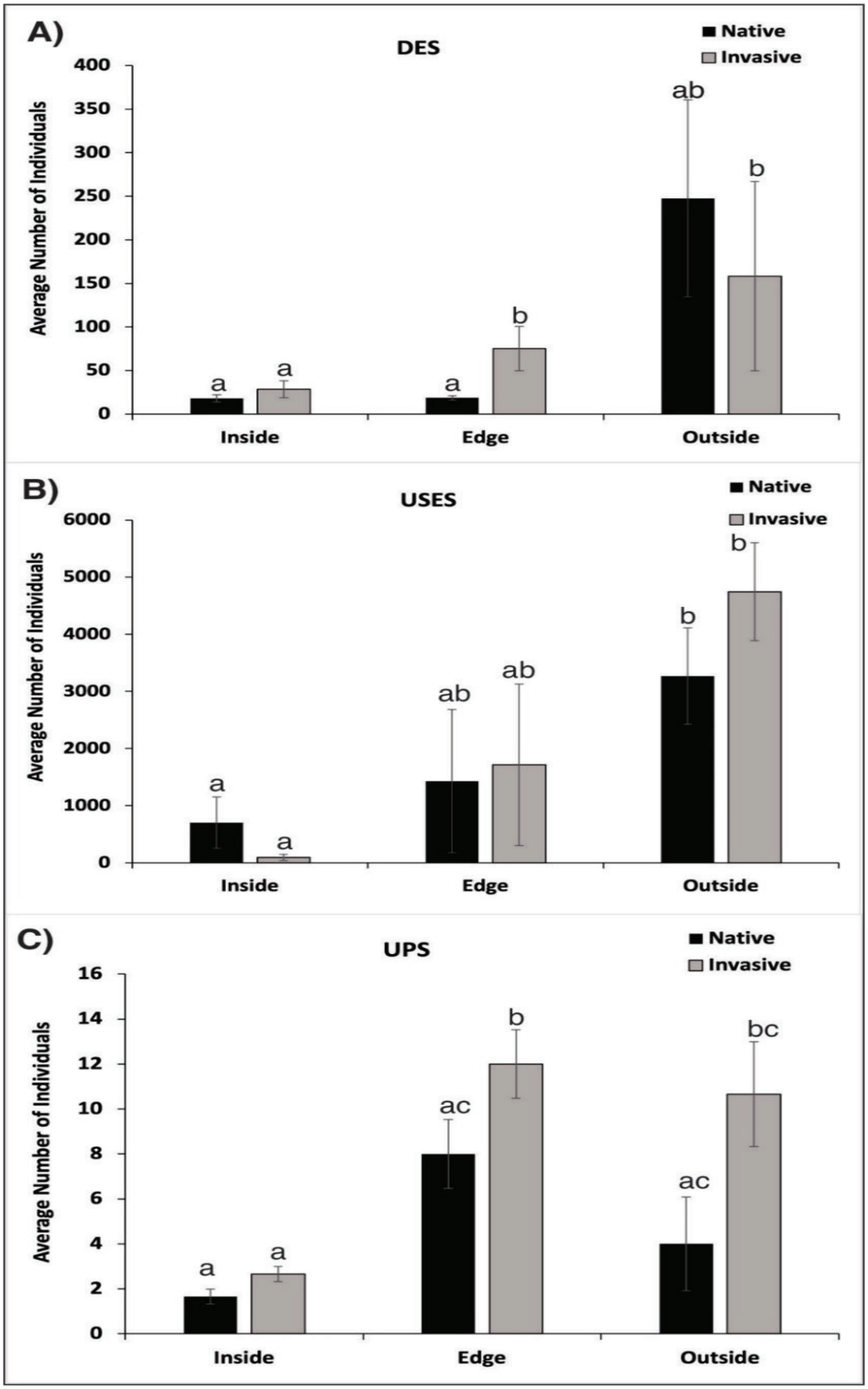

Figure 3. Average abundance by zone within, at the edge, and outside the seagrass bed at each site: A) DES, B) USES, C) UPS. *Different letters indicate significant differences (p<0.05).

The USES site had the highest barnacle settlement, with the total sample from the nine collectors weighing 1,393 grams. A homogeneous and representative subsample of 100 grams was needed to estimate abundance. This semi-protected site has the largest seagrass meadows among the three collection sites, with the highest leaf density at 508 leaves per m². This site showed the highest abundance of both native and invasive barnacles. Due to its location in the middle of the barrier island, there was less space competition from marine organisms, and no predators were present. Furthermore, this site is far from urban areas and is surrounded by mangroves that have been undergoing restoration since 2017 (Canales-Delgadillo *et al.*, 2019). This site has constant water flow, making conditions more similar to a pristine area, potentially allowing for the development of certain species compared to the other two sites.

The DES site is located very close to urban areas and is an exposed site with higher turbidity. Its water is a mix of seawater and river water flowing into the mouth of Laguna de T**é**rminos (Ramos-Miranda *et al.*, 2005), including organic matter from urban wastewater and a nearby municipal slaughterhouse (Briceño-Vera *et al.*, 2021). The seagrass density at this site was 358 leaves per m². The most abundant organism associated with barnacles was *Neritina virginea* (Linnaeus, 1758) (nerite snail), a grazer snail, and no barnacle predators were observed at this site.

Differences in barnacle abundance were observed depending on the location of the collector (inside, edge, or outside the seagrass meadow) (Fig. 3). Thus, information was selected to compare native and invasive abundances in each zone: inside the meadow, at the edge, and outside the meadow. Barnacle abundance was significantly higher outside the meadow compared to inside ($p<0.05$). The general trend showed a greater presence of barnacles outside the meadow, decreasing toward the center of the meadow at all sites.

It is noteworthy that the analysis of environmental parameters in these zones (inside, edge, and outside) revealed similar environmental characteristics in terms of hydrodynamics and temperature, with significant differences in sedimentation rates. In this regard, seagrass meadows modify water current speeds and particle settling, influencing sedimentation from the water column to the seafloor (Reidenbach & Timmerman, 2019).

A possible explanation for the higher number of organisms outside the meadow could be related to food availability, which is crucial for the proliferation of sessile species such as barnacles, which prefer areas with continuous current flow and higher food availability (Phillips, 2005). Additionally, there may be more competition between different species inside the meadow (Janiak & Branson, 2021).

However, it is interesting to note that both the USES and DES sites exhibited a greater proportion of native barnacles compared to invasive barnacles in specific areas. At the USES site, this proportion was observed inside the seagrass meadow, while at the DES site, it was found outside the meadow. Yet, in this site, according to the analysis, all zones did not reveal significant differences between natives and invaders (Fig. 3). As mentioned earlier, these two sites cannot be directly compared due to the different scales of abundance observed. Furthermore, although the USES site is semi-protected, denser seagrass meadows alter water currents and promote the settlement of suspended particles, leading to clearer water and constant flows. Settlement was consistent on each ASU for both native and invasive species across all sites.

Specific studies on the barnacle *A. amphitrite* (Pochai *et al.*, 2017) mention its preference for substrates such as exposed rocks, bivalve shells, and artificial structures. It is known to tolerate disturbed environments, such as pollution from direct sewage discharge, where other barnacle species are no longer found. On the other hand, *A. reticulatus* tends to prefer natural substrates like oyster and clam shells, showing less preference for artificial substrates. Although both species have similar biological characteristics, differences in abundance observed in this study can be attributed to their ecology. *Amphibalanus amphitrite* has a high reproductive capacity, lacks natural predators in invasion sites, and has documented invasion records in all the world's oceans (Chen *et al.*, 2014). Additionally, *A. reticulatus* has been identified as an invasive species in Hawaii, Brazil, and the northern United States, thriving in temperate waters in these regions (Carlton *et al.*, 2011), suggesting a greater preference for temperate waters and possible inability to compete in waters as warm as those recorded in Laguna de Términos.

It is also known that introduced species are more common in artificial structures; the collectors simulating seagrass provided the suitable substrate for barnacles to develop persistent communities (Janiak & Branson, 2021). Considering that *A. reticulatus* prefers natural substrates, our study may be biased due to the materials used for the collectors being entirely plastic.

Additionally, we must consider that settlement is strongly influenced by the ecological succession of early colonizers (bacteria, protozoa, diatoms), which can modify colonization patterns (Marimuthu *et al.*, 2023). Settlement on artificial substrates can vary depending on factors such as space availability, seasonality, microbiota, reproductive rates of each species, etc. (Pirtle *et al.*, 2019).

Given the interest in finding evidence that could explain the atypical dominance of natives in the outer collectors of DES (Fig. 3A) and the inner collectors of USES (Fig. 3B), we examined whether these results were related to differences in diatom communities—precursors to barnacles in the ecological succession of the collectors, since the collectors were completely new. Consequently, these collectors were analyzed afterward. This analysis revealed notable differences in diatom community composition between the two conditions. The collectors dominated by natives exhibited a richness of 17 species, of which only five species represented 80% of the abundance: *Cocconeis scutellum* Ehrenberg, 1838 (26%), *Grammatophora oceanica* Ehrenberg, 1840 (19%), *Achnanthes longipes* C. Agardh, 1824 (12%), *Amphora coffeiformis* (C. Agardh) Kützing, 1844 (12%), and *Navicula platyventris* Meister, 1935 (11%) (Fig. 4). The collectors dominated by invaders showed a richness of 29 species, with seven species representing 80% of the abundance: *Grammatophora oceanica* (29%), *Rhopalodia acuminata* Krammer, 1987 (22%), *Navicula perrhombus* Hustedt ex Simonsen, 1967 (10%), *Mastogloia binotata* Grunow Cleve, 1895 (6%), *Planothidium* sp. (5%), *Navicula platyventris* (5%), and *Bacillaria paxillifera* (O.F. Müller) T. Marsson, 1901 (3%). Differences in diatom richness and abundance lead us to question: Did the peculiar development and growth of the biofilm influence the settlement of native or invasive barnacles? This question requires a more in-depth experimental study with controlled environments and succession analysis. At this point, all we can say is that differences in diatom richness and abundance played a role in barnacle settlement, though we cannot determine to what extent or whether randomness is the reason for the difference.

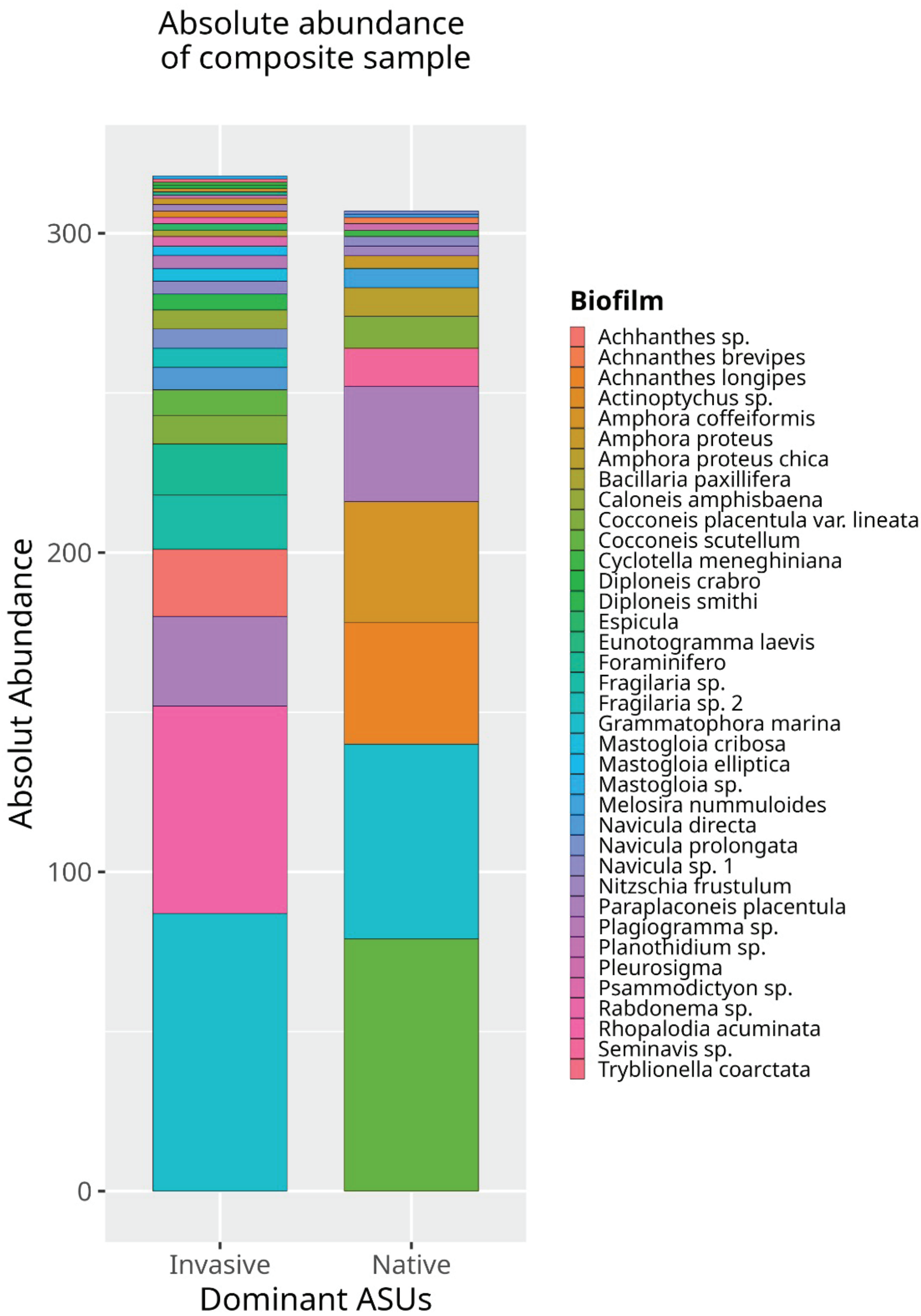

Figure 4. Comparison of biofilm population structure between Artificial Seagrass Units (ASUs) with abundant invasive barnacles and ASUs where native barnacles predominate.

Once established and self-sufficient in invasive systems, potentially invasive species can produce effects that vary in magnitude and scale (Mrnak *et al.*, 2023). Therefore, we consider that we observed a displacement of native barnacles by the invasive barnacle *A. amphitrite* on artificial substrates in Laguna de T**é**rminos. However, we still do not know the potential impact of the displacement of native barnacles or whether we are witnessing a structural change, either temporary or permanent, which could be subject to reproductive processes or fluctuations in population abundance due to climatic phenomena or global warming, among other factors. Additionally, we cannot rule out the possibility that the presence of artificial substrates has facilitated the opportunistic settlement of the invasive species, increasing its colonization when suitable substrates are available. This could result in an apparent dominance of invasive species on artificial substrates, though such patterns may be seasonal. In this regard, our results contrast with that of a previous study carried out in this same study area reporting that the frequency of occurrence, density and coverage of *A. amphitrite* in shells of live specimens of *Crassostrea rhizophorae* Guilding, 1828 and *C. virginica* Gmelin, 1791 were within the range recorded in other native barnacles such as *A. eburneus*, *A. venustus* and *A. improvisus* with which it coexists (**Ávila** *et al.,* 2018).

Currently, the only inference we can make is that native barnacle populations may be affected by the presence of invasive barnacles in the area. However, the magnitude of the effects and the significance of the event remain unknown. We are interested in conducting further studies on barnacle settlement using both natural and artificial substrates over longer exposure periods to determine whether we are observing a shift in barnacle community structure or merely temporary fluctuations in barnacle populations in the Laguna de Términos. These findings are preliminary and highlight the need for continued monitoring and long-term studies.

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