Spatial and temporal variation of edge effects in coastal fragmented communities

FACULTAD DE CIENCIAS DEL MAR

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA

Estudiante: Alejandro Espada Pastor

Titulación: Grado en Ciencias del Mar

Supervisor: Dr. Rodrigo Riera Elena

Grupo de Biodiversidad y Conservación (BIOCON) IU-ECOAQUA.

Departamento de Biología, Facultad de Ciencias del Mar

Universidad de Las Palmas de Gran Canaria

ULPGC

Acknowledgements

I would like to thank all my colleagues and friends who have accompanied and supported me throughout my career. Especially to my supervisor, Dr Rodrigo Riera, for motivating me and showing me part of the world of marine ecology. Also for supporting me and allowing me to do this work with his help. Secondly to Fco. Javier Suárez Santana together with my lab mates, Adrián Torres, Juan Carlos de la Rosa and Olatz Peñalver for giving me their help when I needed it and for making my stay in the lab very comfortable. And finally to my family for keeping me on my feet and being with me in both good and bad times. For all this and more I thank you for being by my side.

Index

Abstract

Fragmentation is a phenomenon that produces the rupture of the continuity of a habitat. These can be in marine, aquatic or terrestrial environments. Habitats may be considered isolated patches with their particular communities. Each patch has an edge zone, edge fence and inner zone. The ecotone is found at the edges of two patches. There is a mobility of species due to the connectivity between patches, and variations of univariate descriptors, i.e. species richness and individual abundances, is expected. This study shows differences in species richness and individual abundance of the epifauna community inhabiting intertidal macroalgae. For this purpose, samples were collected in different months from the coastal locations where fragmented habitats were found. It allows us to evaluate the differences in communities that are affected by the edge effect and also by the spatial and temporal differences. As a result there is a tendency for abundance to be higher in the inner of the patch zone while species richness remains similar among the patch zones, i.e. edge, near edge and inner areas. There is also a greater difference between communities at Roque Tortuga between March and May while Rincón de los Castellanos showed greater similarity in its epifauna community. And it is observed that the patch effect is not the main impact that generates a difference between epifaunal communities. For a more precise understanding of fragmentation and the edge effect, it should be studied how it affects other substrates, in other locations or even in other marine ecosystems.

Keywords: Fragmentation, Edge Effects, Epifauna, Macroalgae, Patch, Spatial scale, Temporal scale.

INTRODUCTION

Changes in seascape are steadily increasing all over the globe (Halpern et al., 2019) . The coral reef bleaching (Morais et al., 2018) and the loss of seagrass (Waycott et al., 2009) are clear examples regarding the importance of these modifications. Human-driven and natural perturbations are the main responsible of these shifts (Vitousek et al., 2008), but also environmental factors, e.g. hydrodynamics, produce alterations of the ecosystem (Reed & Hovel, 2006). Perturbations and environmental factors are able to underpin the fragmentation of habitats, affecting the entire ecosystem (Hovel & Lipcius, 2001). These stressors may underpin fragmentation of the habitat, being divided in several patches (Gross et al., 2018); hence, the features and associated communities may vary. The most recent studies about the effects of fragmentation and formation of patches belong to the terrestrial realm (Chu et al., 2022; Fitz et al., 2022; Zambrano et al., 2019). Seagrasses are the best studied fragmented ecosystems in the coastal environment (Carroll et al., 2012; Mills & Berkenbusch, 2009; Vega Fernández et al., 2005), due to the fact that they have an important ecological role. A wide variety of species shelter, mate, breed, and feed in these ecosystems (Ettinger et al., 2017). Even so, macroalgae such as kelp forests (Deza & Anderson, 2010) are overlooked when compared to seagrass studies.

Marine ecosystems could be fragmented in several patches by stressors (Abadie et al., 2019). Patches generate edges that have particular features among them, such as the variation of vegetation, animal communities and substrate (Gross et al., 2018). These patches may be divided into the patch edge, the proximity of this edge and the inner area (Moore & Hovel, 2010). This differentiation creates a gradient of richness and abundance within the patch, and also between the patch and their surrounding habitat (Fahrig, 2003; Gross et al., 2018). The species from different patches coexist in this area, in the ecological term of ecotone (Du et al., 2022). The ecotones usually have the highest biodiversity, sharing species from both habitats they delimitate (Fahrig, 2003). However, this trend has some exceptions, for example, biodiversity is low in an edge in contact with an unvegetated area (Gross et al., 2018). Current environmental scenarios increase the edge effect due to their high fragmentation rate by anthropogenic activity (Abadie et al., 2019). The effect is not only limited to the impact on the ecosystem but also the associated fauna and flora (Vega Fernández et al., 2005). These concomitant consequences have been observed in insects of terrestrial plants or marine benthic invertebrates in macroalgae (Grez et al., 2004; Johnson & Heck, 2006).

Macroalgae allow the development of associated communities composed of small organisms (Kelaher & Castilla, 2005). The morphological complexity enables for a great variety of species to take refuge from predation, establish a great place for reproduction and feed (Hovel et al., 2021). The macroalga provide an important source of study of the relationship that they form with the associated epifauna. The epifauna is composed of different phyla such as echinoderms, arthropods, annelids and mollusks. These species have the features to be associated with a benthic ecosystem and are integers of coastal food nets (Gagnon et al., 2021). Epifauna are characterized by having a short life span. All stages of their life cycle can be observed in a short period of time such as months. Hence, the epifauna community is considered as an excellent indicator of variations to biodiversity and abundance (Healey & Hovel, 2004; Moore & Hovel, 2010; Pierri-Daunt & Tanaka, 2014) when perturbations occur.

The main objective of the study is to analyze the edge effect in patched macroalgae assemblages through the variation of the associated epifaunal community. Also observe if there is a spatial and temporal variability that may affect living organisms in the populations. Macroalgae form complex ecosystems in which a great diversity of organisms live. These ecosystems are sensitive to human and natural disturbances, making them a key community for study. These disturbances generate phenomena that modify the landscape e.g. fragmentation; hence, may affect associated communities. Due to the consequences produced such as isolation by the distance between patches, change in the optimal conditions for the growth of the algae that form the population, modification of the substrate where the organisms develop. It is therefore important to evaluate the changes caused by the edge effect and fragmentation on ecosystems and consequently to be able to manage the disturbances that affect them. The initial hypothesis is that the edge effect of the macroalgae underpins a drastic shift between the associated epifauna communities of the different zones of the patch. Complementarily, spatial (study locations) and temporal (different time periods) variability affect the range of the edge effect in the epifaunal community.

MATERIAL AND METHODS

Study area and sampling design

A preliminary survey was carried out in the coastline of the island of Gran Canaria to find locations with fragmented algae populations. These macroalgae should have a complex morphology to harbour a rich epifaunal community. As a result of this survey, we found an inlet at Roque Tortuga and another inlet at Rincón de los Castellanos, both of which met the above requirements.

Figure 1. Map of the island of Gran Canaria, showing the study locations.

The sampling was carried out according to the patches' disposition at each zone. The objective was to collect 18 samples from Roque Tortuga and 18 samples from Rincón de los Castellanos in March and the same amount of samples in May. In order to observe the evolution at temporal and spatial scale of epifaunal communities and to evaluate the edge effect to various factors. From each patch, 3 replicates were collected from each of the three zones (edge, near edge and inner area), with a total of 9 epifauna samples from each sample patch. Each of the sampling localities consists of 2 patches, resulting in 18 samples in each locality (2 patches x 9 samples per patch), and therefore, 36 samples between the two localities selected for the present study (2 time periods x 18 samples per period at each locality). A temporal variation study was conducted, collecting a total of 36 samples in March and another 36 in May, with an overall number of samples of 72. The sampling procedures were destructive, because all the material is collected by scraping with a spatula the area delimited by the quadrant (25 x 25 cm), conventionally used in ecological studies. And the sample obtained was stored in zip bags, which are conveniently labeled to identify them. For its preservation it was frozen directly with sea water or with a 70% alcohol solution.

Figure 2. Photograph of the sampling site in Roque Tortuga (NE of Gran Canaria) showing patch distribution.

In the area of Roque Tortuga, two patches were defined by the growth of Corallinaceae algae. Both patches were separated *ca.* 2-3 m, due a rock formation that prevented the connection between them. The algae *Corallina elongata* dominated in the area during March. In May, a reduction of this alga was observed. In one patch (Fig. 2, red patch) the substrate is sandy in the other (Fig. 2, blue patch) is rocky. The beach is sheltered to waves because it is located between two cliffs.

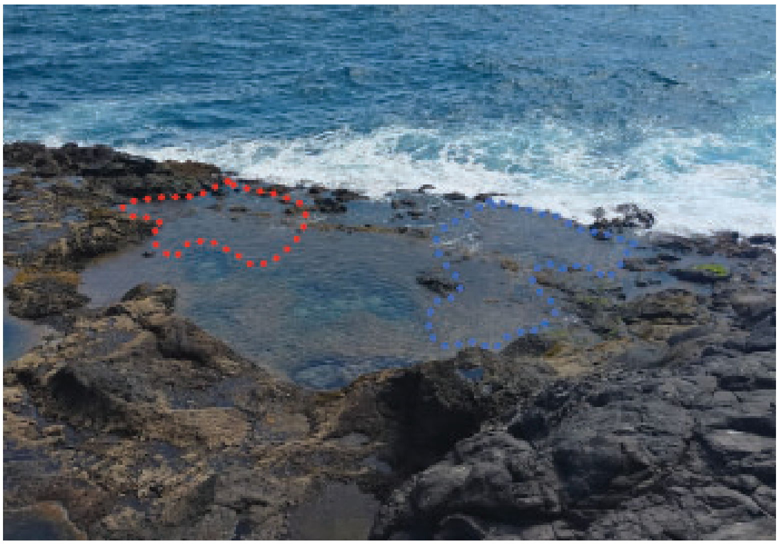

Figure 3. Photograph of the sampling site, Rincón de los Castellanos (East of Gran Canaria), showing patch distribution.

In the area of Rincón de los Castellanos, two patches were defined according to the distribution of populations of *Corallina elongata*. separated by *ca*. 7 m. Initially in March the patches were dominated by *Corallina elongata* but in May we observed a drastic shift as they were substituted by cespitose algae. This area is defined by a rocky and hard substrate, affected by a high exposure to waves, with no natural protection.

Identification of epifauna

Prior to identification, a sorting of the collected samples is performed. In which all observable species are extracted, the minimum required size of these is the one visible to the eye. The species found are initially separated into vials according to phylum to facilitate subsequent identification to species level. By visualizing them under a binocular stereo microscope, a thorough identification and a count of individuals of each species was conducted. This required the use of taxonomic identification guides of the represented groups collected in samples (e.g. Lincoln, 1979; Day, 1968). Once the data from all the samples were collected, we created a database in Excel to perform statistical analysis.

Data analysis

Statistical data analysis was performed using the R software. Boxplot graphs were used to represent the data distribution of species richness and individual abundances. In addition, it shows the median or second quartile, the distance between the third quartile and the first quartile and extreme values that cannot be explained by the distribution. The first quartile indicates that 25% of the values are equal to or less than this and the third quartile with 75% of the values.

Subsequently, the realization of the non-metric multidimensional scaling (n-MDS) that allows an analysis based on the ordination of the sampling points in a two-dimensional spatial system where the disparity or similarity of the points is observable. To conduct this, a code was created for the automatic selection of the lowest stress in a total of 20 trials. Three n-MDS were performed with different factors of interest to the study. The first one shows the distribution considering spatial (location) and temporal (time) variables. Thus, the differences of the epifaunal communities at temporal and spatial scales were observable. The second shows the difference in the communities comparing the different patch sites at the temporal level. And the third one at the spatial level.

Permutational Multivariate Analysis of Variance (PERMANOVA) allows an analysis of a group of objects that are distributed or dispersed according to the factors taken into account. PERMANOVA is performed taking into account the following factors: location, time, location and time at the same time, fragmentation (according to patch sites), fragmentation with time and finally fragmentation with location. As results we obtain the F value and the probability of F. The latter to be significant must have a value <0.05.

The abovementioned statistical analyses were carried out using a set of R packages. Mainly the *vegan* package contains the codes to perform the NMDS and PERMANOVA, *ggplot2* allows to perform graphs, among them the box_plot. Other packages such as *tidyverse*, *janitor, flextable* and *readxl* are also used in order to read the data and make graphs and tables with higher quality.

RESULTS

A total of 18,773 individuals were collected, belonging to 99 morphospecies. Three amphipod species stand out because of their dominance, i.e. *Ampithoe rubricata* (30%), *Apohyale perieri* (20%) and *Elasmopus rapax* (13%). There are also species with a very low percentage such as *Porcellana platycheles, Platynereis dumerilii, Lepadogaster candollei, Pinctada radiata* and *Ophiolepis paucispina* (0.005%) .

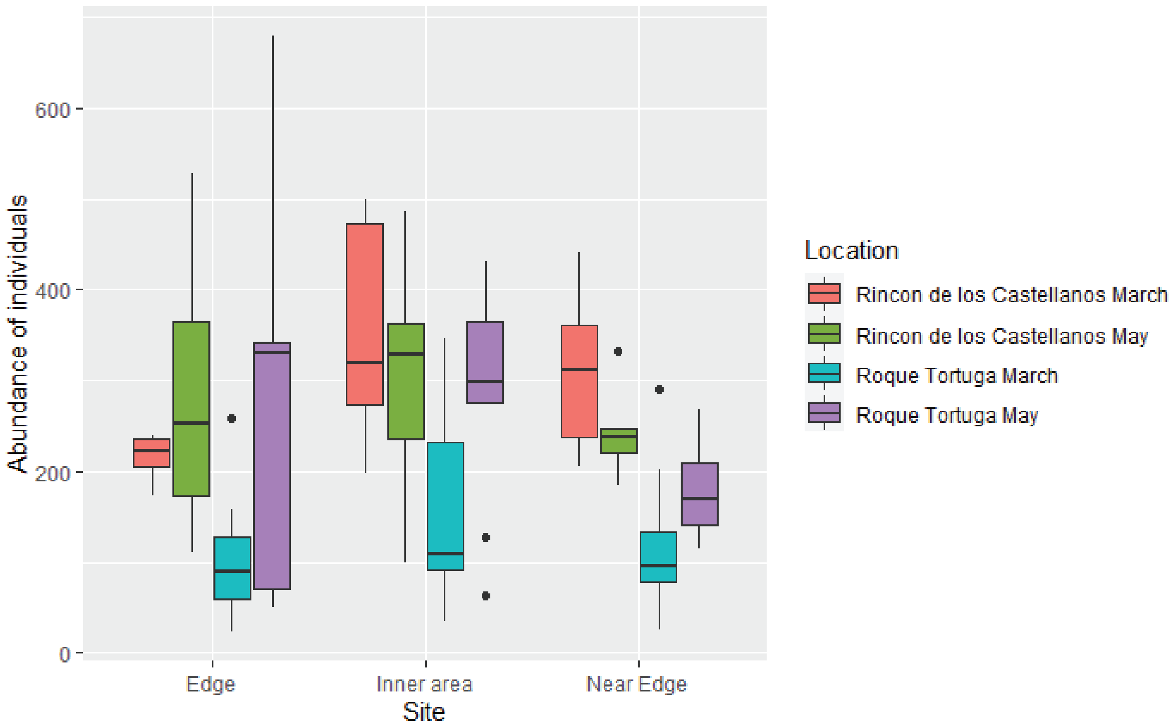

Figure 4. Abundance of epifauna at both sites during March and May.

Generally in the inner zone the abundances was higher (Roque Tortuga March, mean ± SD, 239.8 ± 0.4, Roque Tortuga May, 293.8 ± 0.63, Rincón de los Castellanos March, 306,7 ± 0.71, Rincón de los Castellanos, 221.2 ± 0.52), the edge zone preceded it in terms of abundance (Roque Tortuga March, 66.2 ± 0.13, Roque Tortuga May, 143.9 ± 0.33, Rincón de los Castellanos March, 78.7 ± 0.25, Rincón de los Castellanos, 76.43 ± 0.25) and the zone near the edge had the minimum abundances (Roque Tortuga March, 106.2 ± 0.25, Roque Tortuga May, 113.1 ± 0.33, Rincón de los Castellanos March, 249.7 ± 0.48, Rincón de los Castellanos= 239.8 ± 0.63). This trend was not observed in all cases, in Roque Tortuga and Rincón de los Castellanos during March the minimum abundance was found at the edge instead of the area near the edge. Although there was a disparity between the abundances of the edge and inner zone replicates, in the near edge zone the number of organisms tended to be more similar between replicates. The inner zone of the patch accumulated a large number of organisms as it was more centered. In terms of location, the difference was notable, with a tendency to be greater in Rincón de los Castellanos than Roque Tortuga. The differences between periods of time (March-May) were also notorious, especially accentuated in May (Fig. 4).

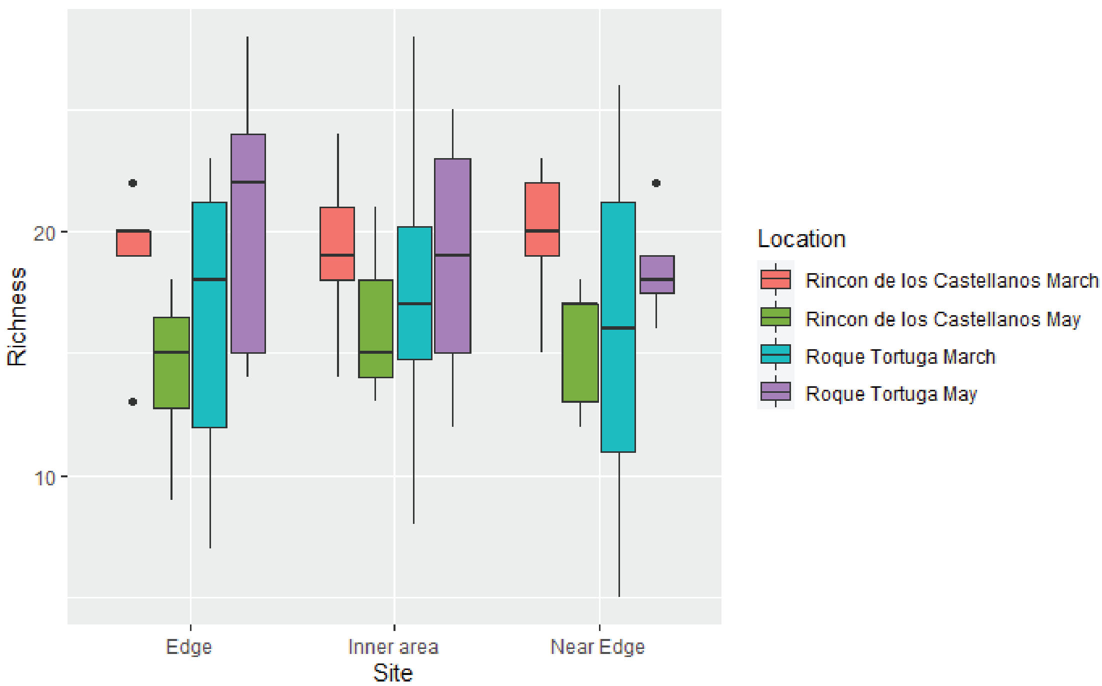

Figure 5. Species richness of epifaunal community at both sites during March and May.

Generally the number of species was similar, mostly comprising 15 and 20 taxa. The similarity of the replicates of the edge zone, near edge and inner zone at Rincón de los Castellanos was greater than at Roque Tortuga. No temporal trends (March-May) were observed regarding variations of species richness at both sites. More consistent differences were observed when considering the abundance of individuals according to location and time, whilst the species richness tended to be similar spatially and temporally (Fig. 5).

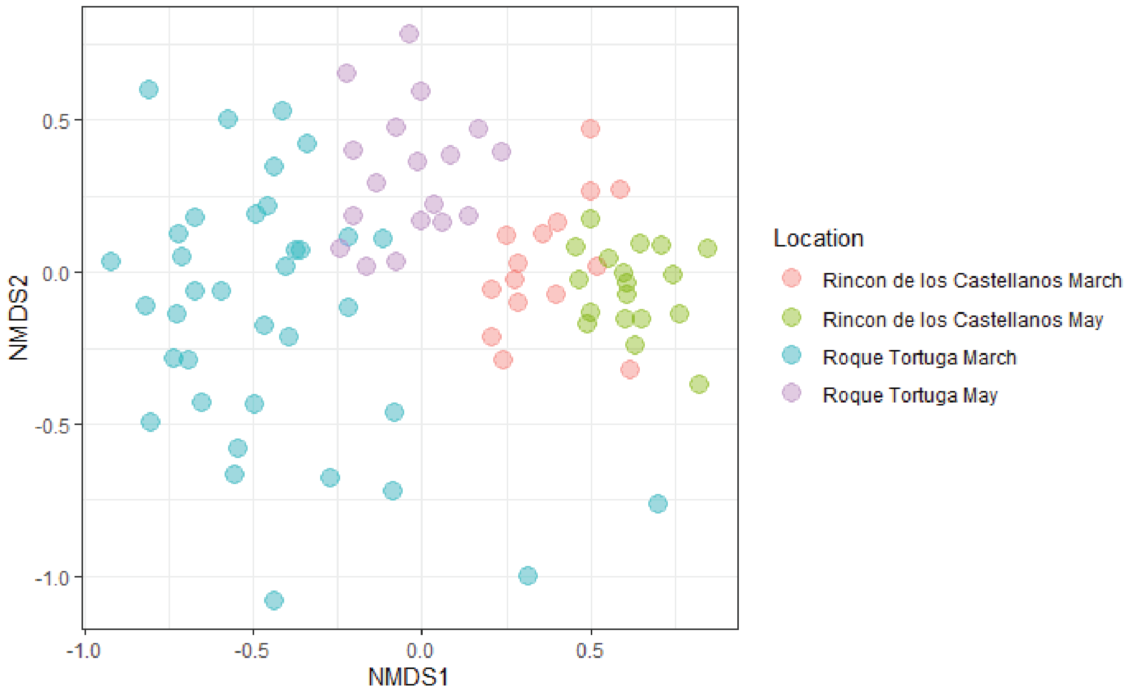

Figure 6. NMDS showing sampling sites and both time periods (March and May).

According to the two localities there was a great difference between the community composition, since a low overlap of dots is observed in Figure 3. A great disparity among the samples from Roque Tortuga was observed whilst a high similarity was found in samples from Rincón de Los Castellanos (Fig. 6).

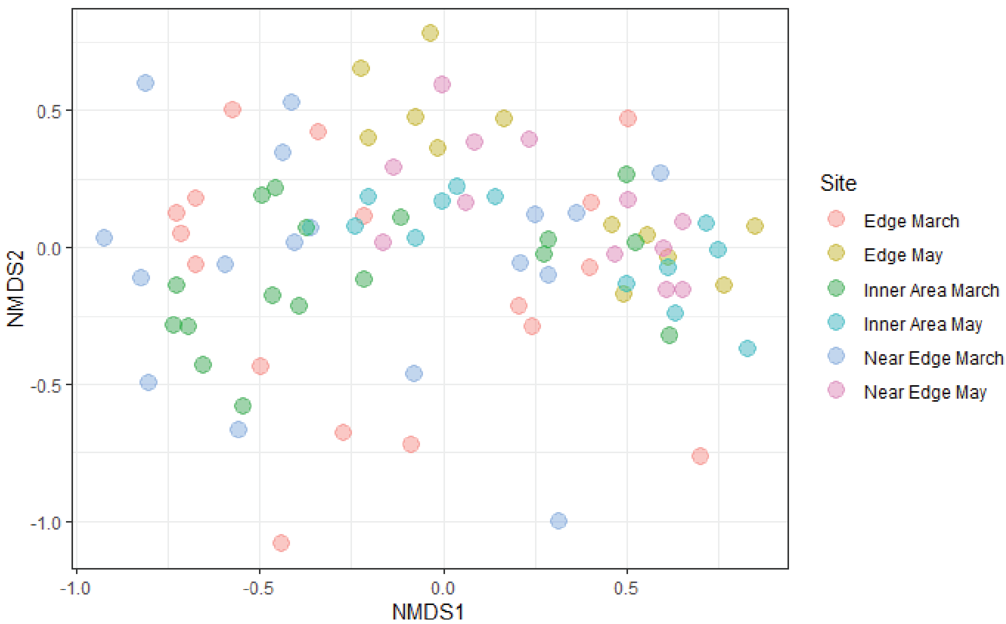

Figure 7. NMDS showing patch areas (Ege, Near Edge and Inner area) during both time periods (March and May).

Spatial and temporal disparity was observed in the sampling sites when considering the patch areas (edge, near edge and inner area) during both time periods. The samples were mostly distributed in the two-dimensional plane without any trend of grouping, though a high similarity is observed in near edge samples. There was a difference between the epifaunal communities of both sites (Rincón de los Castellanos and Roque Tortuga) in the different months (March and May) (Fig. 7).

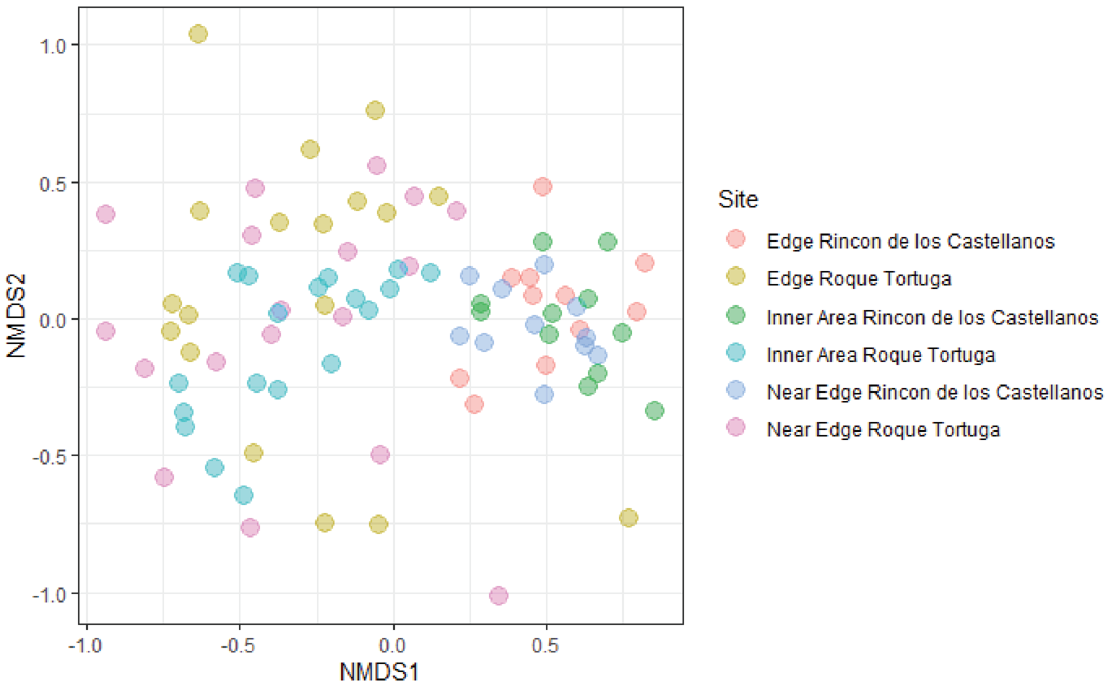

Figure 8. NMDS showing patch areas (Ege, Near Edge and Inner area) at both sampling sites (Roque Tortuga and Rincón de Los Castellanos)

A disparity of the epifaunal communities was observed when considering the spatial variability using the patch areas. Although in the samples from Rincón de los Castellanos, the samples showed a tendency to grouping. On the contrary, in the location of Roque Tortuga there was a higher dispersion of samples (Fig. 8).

Factores	F	Pr..F.
Location	19.10	0.0001
Time	8.14	0.0001
Location(T)	11.70	0.0001
Fragmentation	1.47	0.1108
Fragmentation(L)	4.92	0.0001
Fragmentation(T)	2.32	0.0009
Fragmentation(T,L)	3.89	0.0001

Table 1. Results of the PERMANOVAs carried out with their respective factors. p values < 0.001 denote significant differences.

The value obtained when performing the PERMANOVA taking into account the fragmentation factor (F = 1.47, p = 0.1108) showed no significance among the three patch areas (edge, near edge and inner area). When grouping all species from edge zone samples regardless temporal variability (March and May) or spatial variability (Roque Tortuga or Rincón de los Castellanos) the probability that most of the identified species appear is high, as well as the probability that they are repeated in the rest of the patch sites (near edge zone and inner zone). However, when considering the fragmentation factor taking into account location (F = 4.92, p = 0.0001), time (F = 2.32, p = 0.0009) and both factors (F = 3.89, p = 0.0001), the values obtained show highly significant differences. The values obtained from the PERMANOVA when considering location and time showed highly significant differences (F = 11.70, p = 0.0001). The same was true for the analysis considering location (F = 19.10, p = 0.0001) and time (F = 8.14, p = 0.0001) separately. (Table 1)The significant values imply that the epifaunal communities of the studied patches vary temporally (March and May) and spatially (Roque Tortuga and Rincón de los Castellanos). Obtaining a non-significant value for the edge effect shows that the epifaunal difference is not mainly due to this phenomenon.

DISCUSSION

The edge effects of fragmented habitat in the intertidal depend on local (study locations) and temporal (March and May) factors. The univariate descriptors show contrasting values for abundance in the different zones, being highest in the inner zone. The zone near the edge and the edge have an alternation in the abundance at the temporal level, that is, in March is greater in the zone near the edge than in the edge. The opposite occurs in

May. The species richness is similar at the temporal and spatial level. When observing the epifaunal communities at local and temporal scales, Roque Tortuga showed a greater monthly disparity while Rincón de los Castellanos presented a greater similarity. Considering fragmentation and the temporal factor, a disparity is observed in the edge and inner zones while there is a higher similarity between samples from the near edge zone. The fragmentation and the difference in location imply a difference between the communities of Roque Tortuga, but a similarity in Rincón de los Castellanos. Finally, we obtained a significant value in the edge effect of PERMANOVA, the similarity between species in different areas is higher when they are not differentiated by location or time. When observing the temporal and spatial evolution of the edge effect, the obtained values are significant. Significant values show a difference between habitat communities. This indicates that fragmentation does not cause a great difference between the epifaunal communities of the studied macroalgae assemblages.

The most drastic effects of fragmentation have been shown in terrestrial environments (Zambrano et al., 2019). For example, extensive studies have been conducted on grasslands affected by fragmentation due to anthropogenic perturbations (Bruun, 2000). This fragmentation greatly affects the renewal of pastures and affects the species that depend on them (Cousins et al. 2003). Managing grazing on a rotational basis, giving a temporary margin, decreases the edge effect of fragmentation (Chu et al., 2022). However, edge effects and fragmentation are not only limited to the terrestrial realm, but also to their marine and freshwater counterparts (Deza & Anderson, 2010; Healey & Hovel, 2004; Pierri-Daunt & Tanaka, 2014; Rielly-Carroll & Freestone, 2017). It results in the separation of algal populations or seagrass beds into isolated patches; and the communities inhabiting these habitats are affected. Former studies show a higher density in the edge zone due to the advantage given by the spatial distribution of seagrass habitats (Warry et al., 2009). Considering that this study observes the epifauna, it shows this tendency in March, but not in May. Most studies on the edge effect are conducted in seagrass meadows (Carroll et al., 2012; Mills & Berkenbusch, 2009; Gross et al., 2018). If we compare an area where the *Zostera muelleri* population is fragmented with a continuous one, we observe a difference in the epifaunal communities, with a higher density in the continuous one (Mills & Berkenbusch, 2009). This trend is not shown for all organisms inhabiting the fragmented population (Vega Fernández et al., 2005).

Fragmentation has repercussions on ecosystems and the species that coexist in them (Gagnon et al., 2021). Loss of biodiversity, connectivity, reduction of ecosystem functions, increased predation are some of the main consequences of various processes (Fahrig, 2003; Hovel et al., 2021; Laurel et al., 2003). This phenomenon can be caused by environmental factors such as temperature, change of substrate, waves, etc. For example, temperature is a delimiting factor in the growth of species and shows an increase in the abundance and richness in the univariate parameters of biodiversity in response to an increase in temperature (Duffy et al., 2016). In addition, temperature is a factor that affects algal growth and can lead to habitat fragmentation (Singh & Singh, 2015). It produces a change in the algal structures due to a limitation of nutrients by the stratification of waters produced by temperature changes (Geppi & Riera, 2022). The change in the structure of the algae produces a change in their spatial distribution and can become fragmented (Moore & Hovel, 2010). The epifaunal communities of the ecosystems can be modified before habitat disruption (Vega Fernández et al., 2005). Former works that study the consequences of fragmentation focused on different ecological aspects, such as survival or predation (Hovel et al., 2021; Hovel & Lipcius, 2001) For example, it is observed that the survival rate decreases with increasing patchiness of the area (Hovel & Lipcius, 2001). It is extensively known that the local extinction of algae assemblages reduces the refuge and shelter of a wide range of organisms (Fahrig, 2003) Predation is greater the smaller the patch, but the distribution of predators should be taken into account when focusing on the edge effects on epifaunal communities (Laurel et al., 2003).

CONCLUSIONS

The present results need to be taken with caution since only two study locations (Rincón de los Castellanos and Roque Tortuga) and two time periods (March and May) were considered. Also the low level of fragmentation observed at both sites is a limiting factor to scale up our results in other environments and study regions. By changing the conditions or the factors to be taken into account, the results may be different. Therefore, it is proposed to study the edge effect and fragmented habitats by varying or extending the factors to be taken into account, such as the variability of the hydrodynamics affecting the coast, the geographical variability (studying other islands of the Canary archipelago or adjacent archipelagos such as, Madeira, Azores and Cape Verde, or even other ecoregions (NE Atlantic Ocean, Mediterranean Sea, etc.)) or focusing on other organisms. Nowadays, fragmentation and the edge effect are of great importance because they are extensive and affect ecosystems and all trophic levels of organisms associated with these ecosystems. They are also partly due to human-driven disturbances and might be used as a tool to measure anthropic actions.

REFERENCES

Abadie, A., Richir, J., Lejeune, P., Leduc, M., & Gobert, S. (2019). Structural changes of seagrass seascapes driven by natural and anthropogenic factors: A multidisciplinary approach. *Frontiers in Ecology and Evolution*, *7*(May). https://doi.org/10.3389/fevo.2019.00190

Bruun, H.H. 2000. Patterns of species richness in dry grassland patches in an agricultural landscape.Ecography 23: 641–650.

Carroll, J. M., Furman, B. T., Tettelbach, S. T., & Peterson, B. J. (2012). Balancing the edge effects budget: bay scallop settlement and loss along a seagrass edge. In *Ecology* (Vol. 93, Issue 7).

Chu, L., Hou, M., & Jiang, Z. (2022). How does the fragmentation of pasture affect grassland ecology?——Evidence from typical pastoral areas in China. *Ecological Indicators*, *136*. https://doi.org/10.1016/j.ecolind.2022.108701

Cousins, S.A.O., Lavorel, S. & Davies, I. 2003. Modeling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden.Landscape Ecology 18: 315–332

Day, J., & P. (1968). A Monograph on the Polychaeta of Southern Africa Part 1, Errantia: Part 2, Sedentaria Published by the Trustees of the British Museum (Natural History), London, 1967 Publication no. 656. Pp. viii 878. Price £15. Journal of the Marine Biological Association of the United Kingdom, 48(3), 836-836. doi:10.1017/S0025315400019299

Deza, A. A., & Anderson, T. W. (2010). Habitat fragmentation, patch size, and the recruitment and abundance of kelp forest fishes. *Marine Ecology Progress Series*, *416*, 229–240. https://doi.org/10.3354/meps08784

Du, X.-F., Liu, H.-W., Li, Y.-B., Li, B., Han, X., Li, Y.-H., Mahamood, M., & Li, Q. (2022). Soil community richness and composition jointly influence the multifunctionality of soil along the forest-steppe ecotone. *Ecological Indicators*, *139*, 108900. https://doi.org/10.1016/j.ecolind.2022.108900

Duffy, J. E., Lefcheck, J. S., Stuart-Smith, R. D., Navarrete, S. A., & Edgar, G. J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. Proceedings of the National Academy of Sciences of the United States of America, 113(22), 6230–6235. https://doi.org/10.1073/pnas.1524465113

Eros, E. :, & Geppi, F. (n.d.). Herbarium data reveal the long-term effects of ocean warming on the morphology of fucoid seaweeds from the Canary Islands (NE Atlantic Ocean).

Ettinger, C. L., Voerman, S. E., Lang, J. M., Stachowicz, J. J., & Eisen, J. A. (2017). Microbial communities in sediment from Zostera marina patches, but not the Z. marina leaf or root microbiomes, vary in relation to distance from patch edge. *PeerJ*, *2017*(4). https://doi.org/10.7717/peerj.3246

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. In *Annual Review of Ecology, Evolution, and Systematics* (Vol. 34, pp. 487–515). Annual Reviews Inc. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fitz, J., Adenle, Ademola. A., & Ifejika Speranza, C. (2022). Increasing signs of forest fragmentation in the Cross River National Park in Nigeria: Underlying drivers and need for sustainable responses. *Ecological Indicators*, *139*, 108943. https://doi.org/10.1016/j.ecolind.2022.108943

Gagnon, K., Gustafsson, C., Salo, T., Rossi, F., Gunell, S., Richardson, J. P., Reynolds, P. L., Duffy, J. E., & Boström, C. (2021). Role of food web interactions in promoting resilience to nutrient enrichment in a brackish water eelgrass (Zostera marina) ecosystem. *Limnology and Oceanography*, *66*(7), 2810–2826. https://doi.org/10.1002/lno.11792

Grez, A., Zaviezo, T., Tischendorf, L., Fahrig, L. (2004). A transient, positive effect of habitat fragmentation on insect population densities. *Oecologia*, *141*(3), 444–451. https://doi.org/10.1007/s00442-004-1670-8

Gross, C., Donoghue, C., Pruitt, C., & Ruesink, J. L. (2018). Habitat use patterns and edge effects across a seagrass-unvegetated ecotone depend on species-specific behaviors and sampling methods. *Source: Marine Ecology Progress Series*, *598*, 21–33. https://doi.org/10.2307/26503078

Halpern, B. S., Frazier, M., Afflerbach, J., Lowndes, J. S., Micheli, F., O'Hara, C., Scarborough, C., & Selkoe, K. A. (2019). Recent pace of change in human impact on the world's ocean. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-47201-9

Healey, D., & Hovel, K. A. (2004). Seagrass bed patchiness: Effects on epifaunal communities in San Diego Bay, USA. *Journal of Experimental Marine Biology and Ecology*, *313*(1), 155–174. https://doi.org/10.1016/j.jembe.2004.08.002

Hovel, K. A., Duffy, J. E., Stachowicz, J. J., Reynolds, P., Boström, C., Boyer, K. E., Cimon, S., Cusson, M., Fodrie, F. J., Gagnon, K., Hereu, C. M., Hori, M., Jorgensen, P., Kruschel, C., Lee, K. S., Nakaoka, M., O'Connor, N. E., Rossi, F., Ruesink, J., … Ziegler, S. (2021). Joint effects of patch edges and habitat degradation on faunal predation risk in a widespread marine foundation species. *Ecology*, *102*(5). https://doi.org/10.1002/ecy.3316

Hovel, K. A., & Lipcius, R. N. (2001). Habitat fragmentation in a seagrass landscape: Patch size and complexity control blue crab survival. *Ecology*, *82*(7), 1814–1829. https://doi.org/10.1890/0012-9658(2001)082[1814:HFIASL]2.0.CO;2

Johnson, M. W., & Heck, K. L. (2006). Effects of habitat fragmentation per se on decapods and fishes inhabiting seagrass meadows in the northern Gulf of Mexico. *Marine Ecology Progress Series*, *306*, 233–246. https://doi.org/10.3354/meps306233

Kelaher, B. P., & Carlos Castilla, J. (2005). Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale coastal upwelling on the coast of Northern Chile. *Estuarine, Coastal and Shelf Science*, *63*(1–2), 155–165. https://doi.org/10.1016/j.ecss.2004.10.017

Laurel, B. J., Gregory, R. S., & Brown, J. A. (2003). Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod Gadus spp. *Marine Ecology Progress Series*, *251*, 245–254. https://doi.org/10.3354/meps251245

Lincoln, R. J. (1979). British marine amphipoda: Gammaridea. London: British Museum (Natural History.

Mills, V. S., & Berkenbusch, K. (2009). Seagrass (Zostera muelleri) patch size and spatial location influence infaunal macroinvertebrate assemblages. *Estuarine, Coastal and Shelf Science*, *81*(1), 123–129. https://doi.org/10.1016/j.ecss.2008.10.005

Moore, E. C., & Hovel, K. A. (2010). Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities. *Oikos*, *119*(8), 1299–1311. https://doi.org/10.1111/j.1600-0706.2009.17909.x

Morais, J., Medeiros, A. P. M., & Santos, B. A. (2018). Research gaps of coral ecology in a changing world. In *Marine Environmental Research* (Vol. 140, pp. 243–250). Elsevier Ltd. https://doi.org/10.1016/j.marenvres.2018.06.021

Pierri-Daunt, A. B., & Tanaka, M. O. (2014). Assessing habitat fragmentation on marine epifaunal macroinvertebrate communities: An experimental approach. *Landscape Ecology*, *29*(1), 17–28. https://doi.org/10.1007/s10980-013-9970-1

Reed, B. J., & Hovel, K. A. (2006). Seagrass habitat disturbance: *Source: Marine Ecology Progress Series*, *326*, 133–143. https://doi.org/10.2307/24870697

Rielly-Carroll, E., & Freestone, A. L. (2017). Habitat fragmentation differentially affects trophic levels and alters behavior in a multi-trophic marine system. Oecologia, 183(3), 899–908. https://doi.org/10.1007/s00442-016-3791-2

Singh, S. P., & Singh, P. (2015). Effect of temperature and light on the growth of algae species: A review. In Renewable and Sustainable Energy Reviews (Vol. 50, pp. 431–444). Elsevier Ltd. https://doi.org/10.1016/j.rser.2015.05.024

Vega Fernández, T., Milazzo, M., Badalamenti, F., & D'Anna, G. (2005). Comparison of the fish assemblages associated with Posidonia oceanica after the partial loss and consequent fragmentation of the meadow. *Estuarine, Coastal and Shelf Science*, *65*(4), 645–653. https://doi.org/10.1016/j.ecss.2005.07.010

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (2008). Human domination of Earth's ecosystems. In *Urban Ecology: An International Perspective on the*

Interaction Between Humans and Nature (pp. 3–13). Springer US. https://doi.org/10.1007/978-0-387-73412-5_1

Warry, F. Y., Hindell, J. S., Macreadie, P. I., Jenkins, G. P., & Connolly, R. M. (2009). Integrating edge effects into studies of habitat fragmentation: A test using meiofauna in seagrass. *Oecologia*, *159*(4), 883–892. https://doi.org/10.1007/s00442-008-1258-9

Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(30), 12377–12381. https://doi.org/10.1073/pnas.0905620106

Zambrano, L., Aronson, M. F. J., & Fernandez, T. (2019). The Consequences of Landscape Fragmentation on Socio-Ecological Patterns in a Rapidly Developing Urban Area: A Case Study of the National Autonomous University of Mexico. *Frontiers in Environmental Science*, *7*. https://doi.org/10.3389/fenvs.2019.00152