



Spatio-temporal variability of amphipod assemblages associated with rhodolith seabeds

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Trabajo Fin de Título para la obtención del Máster Interuniversitario en Oceanografía Spatio-temporal variability of amphipod assemblages associated with rhodolith seabeds



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Abstract

Maërl (rhodolithic) beds are habitats underpinned by rhodoliths, which are distributed worldwide within the photic zone, from the intertidal down to 200 m depth. The morphology of individual rhodoliths is directly affected by physical processes, such as the degree of hydrodnamism and light availability, which typically change with depth. Concurrently, epiflora attached on rhodoliths can experience both seasonal and depth variation; consequently, epifauna living associated with rhodoliths can respond to such changes. In this study, we partitioned the relevance of scales of temporal (four seasons through two years) and spatial (three depth strata: 18, 25 and 40 m) variation on the diversity, structure and abundances of amphipod assemblages living in maërl beds of Gran Canaria Island (eastern Atlantic). . A total of 3,996 individuals, belonging to 32 taxa, were here identified. Multivariate analysis of the amphipod assemblage structure revealed consistent differences between depths; more diverse and abundant amphipod assemblages were observed at 18 and 25 m depth relative to 40 m. This pattern was particularly related to the epiphytic algal biomass, which was also greater at 18 and 25 m depth. Six species dominated the assemblage, accounting for ca. 75.5% of the total abundance, including: Gammaropsis ostroumowi, Ampithoe ramondi, Dexamine spinosa, Pardia punctata, Pseudoprotella phasma and Ampithoe helleri; these species showed larger abundances at 18 and 25 m than at 40 m. Among these species, G. ostroumowi and A. ramondi dominated the assemblage. For both species, ovigerous females were observed throughout the entire study, with larger abundances at 18 and 25 m for G. ostroumowi and A. ramondi. Juveniles of both species were exclusively recorded at 18 and 25 m, being absent at 40 m. A peak of juveniles of both species occurred in spring, most likely linked with the larger biomass of epiphytic algae. In summary, this study has demonstrated that the assemblage of amphipods associated with rhodolith seabeds can greatly vary across scales of both spatial (depth) and time (seasons), in particular due to variation in the amount of epiphytic algae attached to rhodoliths, which therefore seem to provide key resources for associated amphipods.

Keywords: Amphipoda, population structure, rhodolith seabeds, algal biomass, bathymetric gradient.

1. Introduction

1.1. Ecology, structure and conservation of rhodolith beds

In the marine environment, biological assemblages are conditioned by abiotic and biotic processes, which influence the reproduction, settlement and mobility of marine organisms (Jones *et al.*, 1994; Fernandez-Gonzalez, 2017; Otero-Ferrer *et al.*, 2019). Habitats can be structured upon the so-called ecosystem "bioengineers", such as seagrasses, macroalgae or corals (Jankowski *et al.*, 2015). Because their relevance, these "bioengineers" have been deeply studied, e.g. how environmental changes dictate their composition, structure and functioning (O'Connor, 1991; Rowley, 2018; Tuya *et al.*, 2018).

Rhodoliths, nodules of branching and unattached coralline red algae creating extensive beds, which are collectively known as maërl, have been described worldwide as ecosystem bioengineers (Teichert, 2014). Rhodoliths are mainly composed by nongeniculate, free-living, calcareous macroalgae, belonging to the Rhodophyta, which present a rugged appearance and diverse morphology (Figueiredo et al., 2007). In particular, in the temperate waters of the Atlantic Ocean, the main algal species of rhodoliths are those corresponding to the genus Lithothamnion and Phymatolithon (Konar et al., 2006). The ecological relevance of maërl habitats is because the branched and intertwined nature of these red algae provide relatively stable three-dimensional habitats for associated fauna (Riosmena-Rodríguez, 2017). At the same time, rhodoliths are colonised by epiflora, which provide a secondary habitat, increasing the spatial heterogeneity of maërl beds (Nelson et al., 2012; Riosmena-Rodríguez, 2017). Therefore, rhodoliths and attached epiflora facilitate associated epi- and infauna, since they provide a large number of available ecological niches and protection against predators as well (Jones et al., 1994; De Grave, 1999; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Amado-Filho et al., 2010; Thomsen, 2010). For these reasons, maërl beds are considered "hot spots" of biodiversity (Sciberras et al., 2009). For example, rhodoliths support a higher diversity and abundance compared to surrounding sedimentary habitats (Neill et al., 2015). As a result, they are considered within the list of European priority conservation habitats (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora) and also in the Annex V of the OSPAR convention (Hall-Spencer et al., 2010). Despite their importance, the ecology of these complex habitats has received little attention, relative to communities supported by, for example, kelps or seagrasses (Nelson et al., 2012).

These biogenic habitats are distributed worldwide within the photic zone, from the intertidal zone down to 200 m depth (Foster, 2001; Konar *et al.*, 2006; Sciberras *et al.*, 2009; Riosmena-Rodríguez *et al.*, 2017), mainly in environments characterized by a high light penetration and moderate levels of hydrodynamism (Foster, 2001). Maërl beds are vertically distributed across abrupt environmental gradients, which may occur through narrow vertical scales (i.e. from 0 to 50 m depth), influencing the distributional and abundance patterns of associated organisms (Tuya *et al.*, 2007; Brokovich *et al.*, 2008). In turn, variations in depth directly affects physical processes, such as hydrodynamism, light attenuation, sedimentation, temperature and salinity (Fulton *et al.*, 2005; Bridge *et al.*, 2016; Mindel *et al.*, 2016), which alter the distribution and structure of mäerl beds (Steller *et al.*, 2007; Sciberras *et al.*, 2009), including the size, morphology and physiology of individual rhodoliths, and consequently of associated epiflora and fauna (Steneck, 1986; Grall and Hall-Spencer, 2003; Peña and Bárbara, 2007). In addition, the epiflora that grows on rhodoliths can experience pronounced seasonal trends in response, for example, to seasonal variation in light availability (Otero-Ferrer *et al.*, 2019).

1.2. Amphipod assemblages living in rhodoliths

Epifauna living associated with "bioengineer" species respond to changes experienced by the habitats where they live (Thomsen *et al.*, 2010); this is an important aspect, for example, to assess the ecological relevance of rhodoliths for associated epifauna. However, fauna associated with maërl beds has received relatively little attention compared with other habitats, such as those dominated by seagrasses or corals. Invertebrates, such as echinoderms, polychaetes, bivalves, molluscs and crustaceans, have been widely found associated with rhodoliths, being amphipods one of the most abundant groups (Teichert, 2014), which often present high abundances and diversity (Ortíz and Lemaitre, 1994). For example, De Grave (1999) showed that the order Amphipoda dominated the fauna of crustaceans, accounting for more than 95% in terms of total numerical abundance. The distribution and abundance of amphipods living in rhodoliths depend on the availability of resources, which may differ between species and even within the phases of their life cycles (De Grave, 1999; Teichert, 2014).

The order Amphipoda, peracarid crustaceans belonging to the Phylum Arthropoda, includes 9,900 described species (Horton *et al.*, 2016). Most amphipods are usually associated with benthic habitats, despite some members of the suborder Hyperiidea are planktonic (Fernandez-Gonzalez, 2017). Amphipods present sexual dimorphism; the external physiognomy allows to differentiate between males and females. These marine invertebrates are annual iteroparous, reproducing several times throughout the year and

reaching sexual maturity at approximately 30 days (Cunha *et al.*, 2000). In addition, they undergo a direct development; juveniles are born fully developed from the marsupium of the mother, where they are transported until the moment of hatching (Thiel, 1998).

Amphipods have different trophic strategies, including detritivores, omnivores, carnivores and herbivores, which take advantage of available resources (Guerra-García *et al.*, 2014). In addition, they constitute an important link in the trophic web, being the main prey for other crustaceans, polychaetes and many species of fish (Jiménez Prada *et al.*, 2015). Their ability to adapt to different environments, including resistance to extreme situations, a wide spectrum of trophic strategies, in conjunction with their dispersal capacity through passive drifting (e.g. currents) or rafting (individuals adhering to various types of materials such as fragments of algae), promote amphipods to have a wide geographic distribution, occupying a great diversity of ecological niches (Highsmith, 1985; Thiel and Gutow, 2005). In the field of ecology, amphipods are very useful as bioindicators of environmental conditions, since they are highly sensitive to impacts on the environment, compared to other groups of macroinvertebrates (Sanchez-Jerez, 1997; Guerra-García and García -Gomez, 2001).

In the last decades, rhodoliths seabeds have been studied from several points of view, including patterns of faunal diversity according to the complexity of rhodoliths (Riosmena-Rodríguez, 2017). However, there are few studies addressing variation in the diversity and assemblage structure of fauna across bathymetric gradients, through varying annual seasons. Depth can affect the structure of rhodolith beds, and therefore the diversity and distribution of associated epiflora and epifauna (Thomsen *et al.*, 2010; Otero-Ferrer *et al.*, 2019). In particular, rhodolith beds in the Canary Islands occupy extensive areas across a large bathymetric gradient, from ca. 15 m to 150 m depth (Riera *et al.*, 2013). Under this premise, there are very few studies on spatio-temporal changes in the diversity and structure of amphipod assemblages living in rhodolith beds throughout such a broad bathymetric range. Therefore, the present study aims to partition the relevance of temporal (seasons) and spatial (varying depth strata) variation in the diversity, structure and abundance of amphipod assemblages living in maërl beds.

The specific objectives of the present study are the following:

- 1. To describe changes in the richness, assemblage structure and abundance of amphipods associated with rhodolithic bottoms at different depths and seasons on the island of Gran Canaria.
- 2. To analyse the relationship between the richness, structure and abundance of amphipod assemblages and the epiflora attached on rhodoliths, due to seasonal and bathymetric effects.

3. To analyse temporal (seasonal) patterns in the population structure of the two most abundant species of amphipods, *Gammaropsis ostroumowi* and *Amphitoe ramondi*, including the abundance of ovigerous females and juveniles, across the bathymetric gradient.

2. Material and methods

2.1. Study Area

The study was carried out at the east coast of Gran Canaria Island (Canary Islands, eastern Atlantic Ocean) (Fig. 1) on a rhodolith bed near Gando Bay $(27^{\circ}55'54''N, 15^{\circ}21'11''W)$, during two successive years (2015 - 2017) (Fig. 1). In this area, the NE trade winds notably determine the local oceanographic patterns. Wind waves, with higher prevalence during summer seasons, generate near-bottom turbulence at lower depths, affecting shallow subtidal habitats, e.g. the presence of seagrass meadows (Pavón-Salas *et al.*, 2000). Rhodolith beds appear locally distributed as mosaics of neighbouring habitat patches, between 15 and 50 meters depth (Fig. 1). The study took place at three different depths (18 m, 25 m and 40 m), which somehow encompass the local bathymetric range in the vertical distribution of rhodolitic beds, while keeping SCUBA security standards at all times. The rhodolith beds are mainly composed by several genus of red calcareous algae, such as *Lithothamnion* sp and *Phymatolithon* sp (Fig 2b) (Haroun *et al.*, 2002; Pardo *et al.*, 2014).



Figure 1. Location of the study area on the island of Gran Canaria (Northeast Atlantic Ocean), including the three sampling sites at 18 m (triangle), 25 m (square) and 40 m (circle). The cartography was carried out, from side scan sonar technologies.

2.2. Sampling design and collection of samples

Sampling was carried out during two years (2015 and 2016), including four seasonal sampling campaigns in autumn (December), winter (March), spring (July), and december (October). Samples were taken using SCUBA at each of the three depth strata (Fig 2a). On each stratum, n=5 random replicates ($25 \times 25 \text{ cm}$) were taken each time, by collecting all rhodolithic nodules up to 5 cm inside the bottom. SCUBA divers collected the samples by hand, which were enclosed within cloth bags. Samples were preserved in a freezer at -20° C until sorting.



Figure 2. Collection of samples (a) and rhodoliths formed by red calcareous algae (*Lithothamnion* sp and *Phymatolithon* sp) (b). Source: Francisco Otero-Ferrer.

2.3. Identification and counting of amphipods

Each sample was defrosted, and filtered through a 0.5 mm sieve, to remove sand and debris from the rhodoliths. All organisms retained by the mesh sieve were identified under a stereomicroscope (Leica, EZ4W, Germany) to the lowest possible taxonomic level. In particular, the identification of the organisms belonging to the order Amphipoda was carried out, in most of the cases, to the level of species. However, certain individuals were identified at the level of genus or family, due to their taxonomic complexity. Determination of the species was carried out initially using a binocular microscope; an optical microscope was employed for certain taxonomic characters, which are relatively small. Identifications were based upon the mainly taxonomic guide by Hayward and Ryland (1990) and references from the Macaronesian area (Biernbowm, 1996; Guerra-García, 2001; Sciberras *et al.*, 2009; García-Sanz *et al.*, 2015; Fernández-Gonzalez, 2017; Otero-Ferrer *et al.*, 2019). For the two most abundant species, *G. ostroumowi* and *A. ramondi* (Fig 3a y 3b, respectively), the abundances were partitioned according to ovigerous females and juveniles.



Figure 3. Image of the two dominant species, G. ostroumowi (a) and A. ramondi (b) of this study.

2.4. Data analysis

Multivariate analysis

Generalized Linear Models (GLMs), using a negative binomial family due to over dispersion of abundance data, were fitted to the multivariate abundance data matrix using the R-package 'mvabund ' (Wang et al., 2012). We tested the multivariate hypothesis of whether the amphipod assemblage structure (composition and abundances) varied between depths (18, 25 and 40 m), months (i.e. seasons) and years. The importance of these multivariate differences was tested by the 'Anova' function using the factors: "Depth" (fixed factor with 3 levels: 18 m, 25 m and 40 m), "Month" (fixed factor with 4 levels: December, March, July and October) and "Year" (random factor with two levels), which provided an analysis of the deviance. P-values were then calculated using 999 resampling iterations via a PIT-trap resampling procedure. The relative contribution of each of the three factors to explain the overall multivariate variance was estimated via the 'best.r.sq' function. In order to apply the model with greater parsimony, the AIC was obtained for the null model and models containing only the covariate (the algal biomass) and the entire set of predictors (full model including the tree factors). Ordination bidimensional (nm-MDS) plots were obtained, separately for each of the two years, to observe dissimilarities in the assemblage structure of amphipods according to depths and months. Data was initially square-root transformed to down weight the prevalence of abundant species; resemblances between each pair of samples were calculated from Bray-Curtis dissimilarities.

Univariate analysis

Mixed GLMs were fitted to univariate responses, including the richness and total abundance of amphipods, as well as the abundances of the most abundant species (*Gammaropsis ostroumowi, Ampithoe ramondi, Pardia punctate, Dexamine spinosa, Pseudoprotella phasma* and *Ampithoe helleri*), and the abundance of ovigerous females and juveniles of *G. ostroumowi* and *A. ramondi*, by means of the R-packages 'lme4' (Bates *et al.,* 2007) and 'lmerTest' (Kuznetsova *et al.,* 2017). Models were fitted using a Poisson, or a negative binomial, family distribution of residuals. For all fitted GLMs, diagnosis plots of residuals were visually inspected to check the appropriateness of fitted models. A linear regression analysis tested if the richness and total abundance of amphipods was predicted by the total epiphytic algal biomass; I used the R 'ggplot2' package (Wickham, 2010). The homogeneity of variances was checked visually from a graphical inspection of residuals; if homogeneity was not fulfilled, the data were square-root-transformed.

3. Results

3.1. Multivariate responses

A total of 3,996 individuals within the order Amphipoda were counted, including a richness of 32 taxa (25 determined at the species level, 4 at the genus level and 3 at the family level) (Suppl. Fig. 2). Six species dominated the assemblage, accounting for ca. 75.5% of the total abundance, including: *G. ostroumowi* (Fig. 3a), *A. ramondi* (Fig. 3b), *D. spinosa, P. punctata, P. phasma* and *A. helleri*. The structure of the amphipod assemblages differed between depths, months and years (Fig. 4, Deviation analysis, P <0.001, Table 1). In general, the factors 'year' and 'depth' explained a larger amount of variation of the multivariate dataset (ca. 10 and 12%, respectively) relative to 'month' (ca. 6%). In fact, the ordination plots (nm-MDS) showed a dispersion of the amphipod assemblages corresponding to different depths and months across the entire bidimensional space, for each of the two years (Fig. 4). In the case of the first year, there was not a clear segregation of samples according to the three depth strata (Fig. 4a). On the other hand, in the case of the second year, samples from 40 m depth majorly clustered on the left side of the ordination space (Fig. 4b).



Figure 4. Two-dimensional nm-MDS diagram showing similarities in the structure of amphipod assemblages between months and depths in 2016 (a) and 2017 (b). Each symbol corresponds to a depth and a month. \blacktriangle : 18 m, \blacktriangledown : 25 m, \bullet : 40 m. Black coloured: December, light grey: July, dark grey: October, unfilled symbols: March.

 Table 1. Analysis of deviance of the multivariate abundance data, including Deviance values and associated P-values.

| | Res. df | df | Dev | Р |
|---------------------------|---------|----|-------|----------|
| (Intercept) | 119 | | | |
| Covariable= Biomass algae | 118 | 1 | 84.2 | 0.003** |
| Depth | 116 | 2 | 223.3 | 0.002** |
| Year | 115 | 1 | 124.0 | 0.001*** |
| Month | 112 | 3 | 334.3 | 0.001*** |
| Depth x Year | 110 | 2 | 101.3 | 0.001*** |
| Depth x Month | 104 | 6 | 215.4 | 0.001*** |
| Year x Month | 101 | 3 | 358.9 | 0.001*** |
| Depth x Year x Month | 95 | 8 | 698.9 | 0.001*** |

Table 2. AIC analysis for the multivariate abundance dataset for a null model (no factors included), a model with only the covariate (epiphytic algal biomass) and the complete model (all factors included). The smaller the value of the AIC, the better the model.

| | Df | AIC |
|---------------------------|-----|--------|
| None (null model) | 119 | 5305.8 |
| Covariable= Biomass algae | 32 | 5298.1 |
| Depth, Year, Month | 192 | 5009.1 |

3.2. Univariate responses

The richness of taxa at 40 m was significantly lower than at 18 and 25 m (Fig. 5; 'Depth (40m)', Table 3, P = 0.000283). In particular, in the month of July of the 2016, the highest number of taxa was recorded at 18 and 25 m depth (Fig. 5). There was a significant, positive, relationships between the richness of taxa and the epiphytic algal biomass (Fig. 6, P <0.001749, R^2 = 0.1185).



Figure 5. Temporal variation in the richness of amphipods (number of taxa) at 18, 25 and 40 m depth during two consecutive years. Error bars are \pm SE of means.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|-------------|
| (Intercept) | 1.86828 | 0.15299 | 12.212 | <2e-16*** |
| Depth (25m) | -0.34572 | 0.22565 | -1.532 | 0.125500 |
| Depth (40m) | -0.95486 | 0.26302 | -3.630 | 0.000283*** |
| Month (Jul) | 0.06697 | 0.20963 | 0.319 | 0.749380 |
| Month (Mar) | 0.14267 | 0.20619 | 0.692 | 0.488960 |
| Month (Oct) | 0.11767 | 0.20710 | 0.568 | 0.569908 |
| Depth (25m) x Month (Jul) | 0.35923 | 0.30577 | 1.175 | 0.240058 |
| Depth (40m) x Month (Jul) | 0.15096 | 0.36032 | 0.419 | 0.675240 |
| Depth (25m) x Month (Mar) | 0.20632 | 0.30578 | 0.675 | 0.499850 |
| Depth (40m) x Month (Mar) | 0.25016 | 0.35120 | 0.712 | 0.476280 |
| Depth (25m) x Month (Oct) | 0.11332 | 0.30932 | 0.366 | 0.714115 |
| Depth (40m) x Month (Oct) | 0.44615 | 0.34561 | 1.291 | 0.196744 |

Table 3. Results of the mixed GLMs testing for the effects of "depths" and "months" on the richness of amphipods. Significant difference at *p<0.05, **< 0.01, ***< 0.0001.



Figure 6. Relationship between of richness of amphipod and the epiphytic algal biomass.

In general, larger amounts of epiphytic algae attached to rhodoliths were collected at 18 and 25 m than at 40 m (Fig. 7; 'Depth (40m)', Table 4, P = 0.00013). Higher values of algal biomass were often observed in July and October of both years (Fig. 7); however, the highest algal biomass was recorded at 25 m in December of 2016 (1820.01 \pm 804.27 mg kg⁻¹). The algal biomass was significantly lower in March (Fig. 7; 'Month (Mar)', Table 4, P= 0.00206), in particular at 18 m in March of 2016 (2.784 \pm 2.091 mg kg⁻¹).



Figure 7. Temporal variation in the algae biomass at 18, 25 and 40 m depth during two consecutive years. Error bars are \pm SE of means.

Table 4. Results of the mixed GLMs for the effect of "depths" and "months" on the algal biomass. Significant differences at p<0.05, p<0.01, p<0.001.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|------------|
| (Intercept) | 6.63943 | 0.42671 | 15.560 | <2e-16*** |
| Depth (25m) | 0.21135 | 0.60344 | 0.350 | 0.72615 |
| Depth (40m) | -2.31311 | 0.60444 | -3.827 | 0.00013*** |
| Month (Jul) | 0.06014 | 0.60345 | 0.100 | 0.92062 |
| Month (Mar) | -1.86098 | 0.60405 | -3.081 | 0.00206** |
| Month (Oct) | 0.15243 | 0.60344 | 0.253 | 0.80058 |
| Depth (25m) x Month (Jul) | -0.38473 | 0.85341 | -0.451 | 0.65213 |
| Depth (40m) x Month (Jul) | 0.91614 | 0.85433 | 1.072 | 0.28356 |
| Depth (25m) x Month (Mar) | -0.15094 | 0.85421 | -0.177 | 0.85975 |
| Depth (40m) x Month (Mar) | 1.87590 | 0.85522 | 2.193 | 0.02827* |
| Depth (25m) x Month (Oct) | -0.53074 | 0.85341 | -0.622 | 0.53400 |
| Depth (40m) x Month (Oct) | 0.41172 | 0.85447 | 0.482 | 0.62992 |

The total abundance of amphipods decreased significantly with depth; higher abundances were observed at 18 and 25 m than at 40 m depth (Fig. 8; 'Depth (40 m)', Table 5, P = 0.0000143). A significant, positive, relationship was detected between the total abundance of amphipods and the epiphytic algal biomass (Fig. 9, P <0.0003148), despite the low coefficient of determination ($R^2 = 0.1046$).



Figure 8. Temporal variation of the total abundance of amphipods (ind x mg⁻¹ x kg⁻¹ \pm SE) at each depth (18, 25 and 40 m) during two consecutive years (2016-17). Error bars are \pm SE of means.

Table 5. Results of the mixed GLMs testing for the effects of "depths" and "months" on the total abundance of amphipods. Significant difference at *p<0.05, **< 0.01, ***< 0.0001.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|--------------|
| (Intercept) | 3.0670 | 0.4344 | 7.060 | 1.66e-12*** |
| Depth (25m) | -0.5174 | 0.3826 | -1.353 | 0.716 |
| Depth (40m) | -1.7770 | 0.4096 | -4.339 | 0.0000143*** |
| Month (Jul) | 0.2702 | 0.4146 | 0.652 | 0.515 |
| Month (Mar) | 0.1505 | 0.4210 | 0.358 | 0.721 |
| Month (Oct) | 0.3297 | 0.4256 | 0.775 | 0.438 |
| Depth (25m) x Month (Jul) | 0.8282 | 0.5291 | 1.565 | 0.117 |
| Depth (40m) x Month (Jul) | 0.7381 | 0.5533 | 1.334 | 0.182 |
| Depth (25m) x Month (Mar) | 0.5308 | 0.5297 | 1.002 | 0.316 |
| Depth (40m) x Month (Mar) | 0.4561 | 0.5590 | 0.816 | 0.415 |
| Depth (25m) x Month (Oct) | 0.2860 | 0.5351 | 0.534 | 0.593 |
| Depth (40m) x Month (Oct) | 1.3811 | 0.5560 | 2.484 | 0.013* |



Figure 9. Relationship between the total abundance of amphipods (log transformed) and the epiphytic algal biomass.

As mentioned above, six species accounted for 75.5% of the total abundance, including: *G. ostroumowi* (Fig. 3a), *A. ramondi* (Fig. 3b), *D. spinosa*, *P. punctata*, *P. phasma* and *A. helleri* (Fig. 10; Suppl. Fig. 2). In general, these species showed a remarkable bathymetric pattern in their abundances, with larger abundances at 18 and 25 m than at 40 m (Fig. 10; Tables 6, 7 and 10).

The species *G. ostroumowi* (Fig. 10a) and *A. ramondi* (Fig. 10b) dominated the assemblage, in terms of abundances, with a total of 1520 and 890 individuals, respectively (accounted for 60.3% of the total abundance). The highest abundance, for *G. ostroumowi*, was recorded at 18 m in July of 2016 (55.2 ± 15.7 ind kg⁻¹) (Fig. 10a; 'Month (Jul)', Table 6, P = 0.00342), while for *D. spinosa* we recorded the largest abundances at 25 (Fig. 10c, 'Depth (25m)', Table 8, P= 0.0358).



Figure 10. Abundances of the six dominant amphipod species (mean number of individuals $kg^{-1} \pm SE$) at each depth (18, 25 and 40m) during two consecutive years. Error bars are $\pm SE$ of means.

Table 6. Results of the mixed GLMs testing for the effects of "depths" and "months" on the abundance of *G. ostroumowi*. Significant differences at *p<0.05, **< 0.01, ***< 0.0001.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|-------------|
| (Intercept) | 1.7373 | 0.3699 | 4.697 | 2.64e-16*** |
| Depth (25m) | -0.8429 | 0.4349 | -1.938 | 0.05258. |
| Depth (40m) | -1.2402 | 0.4501 | -2.755 | 0.00587** |
| Month (Jul) | 1.2276 | 0.4194 | 2.927 | 0.00342** |
| Month (Mar) | 1.1013 | 0.4253 | 2.590 | 0.00961** |
| Month (Oct) | 0.4649 | 0.4292 | 1.082 | 0.27875 |
| Depth (25m) x Month (Jul) | 1.1996 | 0.5803 | 2.067 | 0.03870* |
| Depth (40m) x Month (Jul) | 0.4007 | 0.5953 | 0.673 | 0.50092 |
| Depth (25m) x Month (Mar) | 0.5082 | 0.5821 | 0.873 | 0.38270 |
| Depth (40m) x Month (Mar) | -0.3544 | 0.6110 | -0.580 | 0.56187 |
| Depth (25m) x Month (Oct) | 0.9939 | 0.5981 | 1.662 | 0.09656. |
| Depth (40m) x Month (Oct) | 0.6455 | 0.6139 | 1.051 | 0.29306 |

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|-------------|
| (Intercept) | 1.1675 | 0.6067 | 1.924 | 0.054327. |
| Depth (25m) | -0.1759 | 0.5393 | -0.326 | 0.744328 |
| Depth (40m) | -3.1676 | 0.9024 | -3.510 | 0.000448*** |
| Month (Jul) | 0.5169 | 0.5716 | 0.904 | 0.365798 |
| Month (Mar) | -0.4639 | 0.5843 | -0.794 | 0.427165 |
| Month (Oct) | 1.1093 | 0.5851 | 1.896 | 0.057950. |
| Depth (25m) x Month (Jul) | 0.4365 | 0.7169 | 0.609 | 0.542642 |
| Depth (40m) x Month (Jul) | 2.0054 | 1.0327 | 1.942 | 0.052153. |
| Depth (25m) x Month (Mar) | 1.2615 | 0.7287 | 1.731 | 0.083427. |
| Depth (40m) x Month (Mar) | 2.9177 | 1.0454 | 2.791 | 0.005257** |
| Depth (25m) x Month (Oct) | -0.3262 | 0.7196 | -0.453 | 0.650346 |
| Depth (40m) x Month (Oct) | 2.7979 | 1.0220 | 2.738 | 0.006187** |

Table 7. Results of the mixed GLMs testing for the effects of "depths" and "months" on the abundance of *A. ramondi.* Significant differences at *p<0.05, **< 0.01, ***< 0.0001.

Table 8. Results of the mixed GLMs testing for the effects of "depths" and "months" on the abundance of *D. spinosa.* Significant differences at *p<0.05, **< 0.01, ***< 0.0001.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|---------|
| (Intercept) | 0.1823 | 0.4318 | 0.422 | 0.6729 |
| Depth (25m) | 1.1718 | 0.5615 | 2.099 | 0.0358* |
| Depth (40m) | -1.0986 | 0.7346 | -1.496 | 0.1348 |
| Month (Jul) | -0.4055 | 0.6439 | -0.630 | 0.5289 |
| Month (Mar) | -0.4055 | 0.6349 | -0.630 | 0.5289 |
| Month (Oct) | 1.3437 | 0.5580 | 2.408 | 0.0160* |
| Depth (25m) x Month (Jul) | -1.3122 | 0.8885 | -1.477 | 0.1397 |
| Depth (40m) x Month (Jul) | 1.5841 | 0.9736 | 1.627 | 0.1037 |
| Depth (25m) x Month (Mar) | -0.1671 | 0.8319 | -0.201 | 0.8408 |
| Depth (40m) x Month (Mar) | 0.9651 | 1.0069 | 0.958 | 0.3378 |
| Depth (25m) x Month (Oct) | -1.4238 | 0.7557 | -1.884 | 0.0596. |
| Depth (40m) x Month (Oct) | -19.7300 | 298.9581 | -0.007 | 0.9947 |

Table 9. Results of the mixed GLMs testing for the effects of "depths" and "months" on the abundance of *P. punctata.* Significant differences at *p<0.05, **< 0.01, ***< 0.0001.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|-----------|
| (Intercept) | -1.6094 | 0.8257 | -1.888 | 0.05909. |
| Depth (25m) | -0.6931 | 1.3979 | -0.496 | 0.62000 |
| Depth (40m) | -0.6931 | 1.3979 | -0.496 | 0.62000 |
| Month (Jul) | 1.5041 | 1.0321 | 1.547 | 0.14503 |
| Month (Mar) | 3.2189 | 0.9870 | 3.261 | 0.00111** |
| Month (Oct) | 2.8034 | 0.9922 | 2.825 | 0.00472** |
| Depth (25m) x Month (Jul) | 0.5754 | 1.6261 | 0.354 | 0.72347 |
| Depth (40m) x Month (Jul) | -18.5041 | 298.9584 | -0.006 | 0.99505 |
| Depth (25m) x Month (Mar) | -0.5108 | 1.5795 | -0.323 | 0.74639 |
| Depth (40m) x Month (Mar) | -2.1203 | 1.6618 | -1.276 | 0.20200 |
| Depth (25m) x Month (Oct) | 0.4155 | 1.5743 | 0.264 | 0.79183 |
| Depth (40m) x Month (Oct) | 0.7802 | 1.5705 | 0.497 | 0.61935 |

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|-----------|
| (Intercept) | 1.5261 | 0.5146 | 2.966 | 0.00302** |
| Depth (25m) | -1.1206 | 0.7580 | -1.478 | 0.13931 |
| Depth (40m) | -2.7300 | 0.9172 | -2.977 | 0.00292** |
| Month (Jul) | -1.7492 | 0.7955 | -2.199 | 0.02790* |
| Month (Mar) | -3.1355 | 1.0039 | -3.123 | 0.00179** |
| Month (Oct) | -3.8286 | 1.2280 | -3.118 | 0.00182** |
| Depth (25m) x Month (Jul) | 2.2600 | 1.1071 | 2.041 | 0.04121** |
| Depth (40m) x Month (Jul) | 1.1347 | 1.3973 | 0.962 | 0.33621 |
| Depth (25m) x Month (Mar) | 2.2192 | 1.3143 | 1.689 | 0.09131. |
| Depth (40m) x Month (Mar) | 3.9828 | 1.4036 | 2.837 | 0.00455** |
| Depth (25m) x Month (Oct) | 3.3178 | 1.4737 | 2.251 | 0.02436* |
| Depth (40m) x Month (Oct) | 4.8095 | 1.5660 | 3.071 | 0.00213** |

Table 10. Results of the mixed GLMs testing for the effects of "depths" and "months" on the abundance of *P. phasma*. Significant differences at *p<0.05, **< 0.01, ***< 0.0001.

Juveniles of *G. ostroumowi* had larger abundances in July, particularly at 18 m in July of 2016 (16.4 \pm 5.5 ind kg⁻¹) (Fig. 11; 'Month (Jul)', Table 11, P = 0.0000142). Juveniles were only recorded at 18 and 25 m, while being absent at 40 m (Fig 11). Ovigerous females were observed throughout the entire study, including a peak, at 18 m in March of 2016 (6.6 \pm 1.9 ind kg⁻¹) (Fig. 11; 'Month (Mar) ', Table 10, P = 0.000125).



Figure 11. Temporal variation in the abundance of juveniles (a) and ovigerous females (b) of *G*. *ostroumowi* at 18, 25 and 40 m depth during two consecutive years. Error bars are \pm SE of means.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|-------------|
| (Intercept) | -0.5108 | 7.327 | -2.196 | 0.028056* |
| Depth (25m) | -19.7918 | 9.524 | 0.426 | 0.670313 |
| Depth (40m) | -19.7918 | 2.981 | -0.006 | 0.995264 |
| Month (Jul) | 2.7408 | 8.605 | 1.277 | 0.201700 |
| Month (Mar) | 2.1203 | 7.742 | 3.837 | 0.000125*** |
| Month (Oct) | 0.1542 | 1.036 | 0.000 | 1.000000 |
| Depth (25m) x Month (Jul) | 19.6030 | 1.102 | 0.464 | 0.642951 |
| Depth (40m) x Month (Jul) | -2.7408 | 2.981 | 0.005 | 0.995744 |
| Depth (25m) x Month (Mar) | 18.6523 | 1.034 | -1.254 | 0.209887 |
| Depth (40m) x Month (Mar) | -2.1202 | 2.981 | 0.005 | 0.995951 |
| Depth (25m) x Month (Oct) | 20.3308 | 1.575 | -0.697 | 0.485494 |
| Depth (40m) x Month (Oct) | -0.1542 | 2.981 | 0.006 | 0.995450 |

Table 11. Results of the mixed GLMs testing for the effects of "depths" and "months" on the abundance the ovigerous females of *G. ostroumowi*. Significant differences at *p<0.05, **< 0.01, ***< 0.001.

Table 12. Results of the mixed GLMs testing for the effects of "depths" and "months" on the abundance of juveniles of *G. ostroumowi*. Significant differences at *p<0.05, **< 0.01, ***< 0.0001.

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|--------------|
| (Intercept) | -0.5108 | 0.4893 | -1.044 | 0.296525 |
| Depth (25m) | -19.7918 | 4914.7687 | -0.004 | 0.996787 |
| Depth (40m) | -19.7918 | 4914.7689 | -0.004 | 0.996787 |
| Month (Jul) | 2.7408 | 0.5683 | 4.823 | 0.0000142*** |
| Month (Mar) | 2.1203 | 0.5764 | 3.678 | 0.000235*** |
| Month (Oct) | 0.1542 | 0.6746 | 0.229 | 0.819254 |
| Depth (25m) x Month (Jul) | 19.6030 | 4914.7684 | 0.004 | 0.996818 |
| Depth (40m) x Month (Jul) | -2.7408 | 6950.5328 | 0.000 | 0.999685 |
| Depth (25m) x Month (Mar) | 18.6523 | 4914.7688 | 0.004 | 0.996972 |
| Depth (40m) x Month (Mar) | -2.1202 | 6950.5328 | 0.001 | 0.999757 |
| Depth (25m) x Month (Oct) | 20.3308 | 4914.7688 | 0.004 | 0.996699 |
| Depth (40m) x Month (Oct) | -0.1542 | 6950.5328 | 0.000 | 0.999982 |

A similar temporal pattern, in terms of population structure, was observed for *A. ramondi*. Juveniles of *A. ramondi* had the largest abundances in July of 2016 (Fig. 12; 'Month (Jul)', Table 13, P = 0.0428). Also, ovigerous females reached the largest abundances in July of 2016, but at 25 m depth (Fig. 12), despite no statistically significant differences were observed.



Figure 12. Temporal variation in the abundance of juveniles (a) and ovigerous females (11) of *A. ramondi* at 18, 25 and 40 m depth during two consecutive years. Error bars are \pm SE of means.

Table 13. Results of the mixed GLMs testing for the effects of "depths" and "months" on the juveniles of *A. ramondi.* Significant differences at *p<0.05, **< 0.01, ***< 0.0001

| | Estimate | Std. Error | Z value | Р |
|---------------------------|----------|------------|---------|---------|
| (Intercept) | -0.9163 | 0.7300 | -1.255 | 0.2094 |
| Depth (25m) | -1.3863 | 1.3475 | -1.029 | 0.3036 |
| Depth (40m) | -19.3863 | 4914.7689 | -0.004 | 0.9969 |
| Month (Jul) | 1.8718 | 0.9243 | 2.025 | 0.0428* |
| Month (Mar) | 0.4055 | 0.9912 | 0.409 | 0.6825 |
| Month (Oct) | 1.0986 | 0.9482 | 1.159 | 0.2466 |
| Depth (25m) x Month (Jul) | 1.8418 | 1.5635 | 1.178 | 0.2388 |
| Depth (40m) x Month (Jul) | -1.8718 | 6950.5328 | 0.000 | 0.9998 |
| Depth (25m) x Month (Mar) | 1.3863 | 1.6477 | 0.841 | 0.4002 |
| Depth (40m) x Month (Mar) | -0.4055 | 6950.5329 | 0.000 | 1.0000 |
| Depth (25m) x Month (Oct) | -1.0986 | 1.8614 | -0.590 | 0.5551 |
| Depth (40m) x Month (Oct) | 18.9808 | 4914.7690 | 0.004 | 0.9969 |

4. Discussion

4.1. Effect of depth on amphipod assemblages

Our results showed differences in the multivariate structure of amphipod assemblages between the three depths, which were temporality consistent over time. In general, higher abundances were observed at 18 and 25 m than at 40 m deep.

The effect of environmental variation associated with depth on the size and shape of rhodoliths often suppose an increase in size with increasing depth, as well as a tendency towards more ellipsoid forms (Steller and Foster, 1995; Amado-Filho *et al.*, 2007; Otero-Ferrer *et al.*, 2019). Steller *et al.* (2003) showed, in the Gulf of California, that the morphology of rhodoliths changed with depth, influencing the diversity of the associated

species. In this sense, the amount of surface and shape provided by rhodoliths play a key role in maintaining the diversity of associated fauna (Hinojosa-Arango and Riosmena-Rodríguez, 2004; Sciberras *et al.*, 2009). In general, a greater number of epifaunal species was recorded in rhodoliths with greater branching (Hinojosa-Arango and Riosmena-Rodríguez, 2004; Sciberras *et al.*, 2009). This is because this type of morphology, in comparison to spherical forms, offers greater structural complexity and habitat heterogeneity (Otero-Ferrer *et al.*, 2019); such architectural habitat features play an important role in influencing the assemblage structure of epifauna (Vázquez-Luis *et al.*, 2009).

Most species of amphipods from the present study have been also found from other infralittoral and circalitoral habitats (Pérès, 1967; De Grave, 1999). Half of the amphipod species of this study were also reported in other coastal habitats from Gran Canaria Island (Png-González et al., 2014). In our case, the overall richness (32 taxa) was greater than in seagrass meadows constituted by Cymodocea nodosa (17 taxa) and beds dominated by the green algae Caulerpa prolifera (27 taxa) (Png-González et al., 2014). From the total of 32 species we here recorded, 16 species coincided in both studies; this appears to indicate that these species are well adapted to life under varying conditions provided by different habitats. This underwater vegetation facilitated crustaceans and polychaetes (Sánchez-Moyano et al., 2007), because, similar to rhodoliths, their structural complexity increases the amount of colonizable space, playing an important role for fauna (Taylor and Cole, 1994; Bologna, 1999). Nevertheless, there are differences in the species dominance of amphipods; species belonging to the family Caprellidae (e.g. Pseudoprotella phasma and Mantacaprella macaronensis) dominated in seagrass meadows (Png-González et al., 2014), whereas species of the families Photidae and Ampithoidae (e.g. Gammaropsis ostroumowi and Amphitoe ramondi, respectively) dominated in our study.

4.2. Influence of secondary habitat on amphipod assemblages

As expected from other studies in rhodoliths seabeds (Pascelli *et al.*, 2013), we found a marked bathymetric pattern in the amount of epiphytic algae attached to rhodoliths; larger biomasses were found at 18 and 25 m than at 40 m. This pattern seems to be linked with the larger availability of light at 18 and 25 m relative to 40 m, which is a key resource for the photosynthesis of epiphytic algae (Suppl. Fig. 1) (Connell, 2005; Cavalcanti *et al.*, 2014). The largest richness and abundances of amphipods, therefore, coincide with the largest epiphytic algal biomasses. The process by which a primary substrate (here, rhodoliths) supports a secondary habitat created by sessile organisms (here, epiphytic

algae), which concurrently facilitates abundances of invertebrates, is an example of an 'habitat cascade' (Thomsen et al., 2010). This processes by which a secondary habitat benefit multiple organisms has been studied from a wide variety of habitats (Thomsen et al., 2010; Cunha et al., 2000). The presence of vegetation (here, epiphytic algae on rhodoliths) enhances the heterogeneity and complexity of the habitat available for epifauna, increasing the abundance and species richness of amphipods compared to unvegetated habitats (Vázquez-Luis et al., 2009). The existence of epiphytic algae associated with rhodoliths alter local hydrodynamic regimes (Eckman, 1983), the availability of colonizable space, the quantity of food (Cunha et al., 2000), the intensity of predation, competition, as well as larval dispersal and further recruitment (Bosence 1976; Steller and Foster, 1995). The positive effect of epiphytic algae on associated epifauna has also been supported from other marine environments, such as those dominated by the seagrass Posidonia oceanica, where highest richness and abundances of epifauna were found with high epiphyte biomasses (Zakhama-Sraieb et al., 2011). Amphipods can actively select their habitat (Hay, 1996; Poore, 2005; Poore and Hill, 2006), which is related to food preferences, the quality of habitat for growth and the possibilities of survival in the face of predation (Poore and Hill, 2006; Vázquez-Luis et al., 2009). However, although active selection seems to be important, it is not sufficient to explain the different patterns in the distribution of epifauna (Virnstein and Howard, 1987). In turn, amphipods are widely consumed by decapods and fish, so amphipod require to avoid predation, looking for substrates with a large presence of algae (Gambi et al., 1992).

Amphipods have a wide trophic diversity, including herbivores, carnivores and omnivores (Guerra-García *et al.*, 2014). However, most species consume detritus (Sciberras *et al.*, 2009; Guerra-García *et al.*, 2014), which plays an important role as a trophic resource for marine invertebrates, being one of the main trophic pathways in the marine realm (Zimmerman *et al.*, 1979; Valiela, 1995), particularly in and around of vegetated habitats (Vázquez-Luis *et al.*, 2009; Michel *et al.*, 2015). The existence of a high number of species that feed on detritus can be attributed to the heterogeneity of the maërl beds (Sciberras *et al.*, 2009). The most abundant species of this study, *G. ostroumowi*, has been described from hard, detrital, algal and seagrass habitats (Zakhamasraieb *et al.*, 2011). The diet of *G. ostroumowi* consist of 99% of detritus (Guerra-García *et al.*, 2014), being able to take advantage of the heterogeneity of the rhodolith seabeds across a wide range of depths (Sciberras *et al.*, 2009). Individuals belonging to the family Ampithoidae (here, *A. ramondi* and *A. helleri*) have been found mainly at 18 and 25 m. This result was somehow expected, since Amphitoidae are mainly herbivores; these species are phyllophilic amphipods commonly associated with macroalgae (Vázquez-

Luis *et al.*, 2009). In particular, *A. ramondi* is a cosmopolitan species from tropical and warm temperate waters and prefers seaweeds (Vázquez-Luis *et al.*, 2009). The species *D. spinosa* showed a larger presence at 18 and 25 m than at 40 m, coinciding with the largest algal biomass. This is an herbivorous species, which is very common in algal canopies within the shallow subtidal (Ruffo, 1982; Guerra-García *et al.*, 2014).

4.3. Temporal dynamics of amphipod assemblages

Temporal variation in the richness and abundances of amphipods can be attributed to changes in habitat heterogeneity through timescales, particularly seasonal changes, which alter habitat complexity through increased epiphytes and associated algae (Sanchez-Jerez, 1997). In general, our study revealed that abundances of amphipods were higher during spring (July) and summer (October) relative to autumn (December) and winter (March). This agrees, for example, with Figueiredo *et al.* (2007), who observed larger abundances of amphipods in summer and autumn that were further reduced in winter. In our study, this may arise from seasonal changes in the epiphytic algal biomass on rhodoliths, which decreased during winter, as reported by Pascelli *et al.* (2013). In winter, reduced irradiance, low temperatures and strong waves, cause periodical disturbances in these habitats (Suppl. Fig. 1). For example, the suspension of sediments and the ripping off epiphytes due to the movement of rhodoliths affect associated epifauna (Steller and Foster, 1995; Amado-Filho *et al.*, 2007, 2010). These temporal changes tend to affect the population dynamics of the amphipod fauna, which even would explain the temporal variability we here found between both sampled years.

Iteroparity is a common reproduction strategy in invertebrates (Sainte-Maire, 1991). The population structure of the two most abundant species, *G. ostroumowi* and A. *ramondi*, was dominated by juveniles at all times. These results are consistent with studies conducted in rhodolith seabeds from the Gulf of California, in which juvenile individuals were consistently more abundant than adults (Riosmena-Rodríguez and Medina-Lopez, 2010). Colonization of substrates by amphipods is very fast due to its short life cycle. For example, Norderhaug *et al.* (2002) showed that amphipods associated with macrophytes in the Northeast Atlantic had high dispersion rates and rapid colonization by recruitment of juveniles. In our study, the two most abundant species, *G. ostromowi* and *A. ramondi*, only presented juveniles at 18 and 25 m depth. This results agrees with the study carried out by Sainte-Maire (1991), who postulated that the reproductive potential of the family Lysianassidae can be reduced at high depths. However, more exhaustive studies of the population structure of amphipods with depth are necessary, due to the little information that is available about them.

5. Conclusions

The present study is a first attempt to explore the bathymetrical and seasonal changes in the diversity and abundances of amphipods associated with rhodolith seabeds in the Canary Islands. Rhodolith seabeds are a "bioengineer" ecosystem, because of the refuge possibilities and resources they offer to associated epifauna. Significant variation through spatial (here, depth) and temporal scales (here, seasons), determining the diversity and abundances of amphipods, points to the presence of a secondary habitat generated by epiphytic algae on rhodolith nodules as a key mechanism driving such ecological patterns.

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6. Supplementary material

Suppl. Table. 1. Analysis of deviance of the multivariate abundance data, including Deviance values and associated P-values.

| | Wald value | Р |
|---------------------------|------------|-------------|
| (Intercept) | 3.328 | 0.06594. |
| Biomass algae | 6.137 | 0.189810 |
| Depth (25m) | 1.357 | 0.372627 |
| Depth (40m) | 1.327 | 1.96803 |
| Year | 3.329 | 0.065934. |
| Month (Jul) | 6.927 | 0.000999*** |
| Month (Mar) | 4.556 | 0.001998** |
| Month (Oct) | 3.388 | 0.035964* |
| Depth (25m) x Year | 1.357 | 0.372627 |
| Depth (40m) x Year | 1.327 | 0.196803 |
| Depth (25m) x Month (Jul) | 3.013 | 0.025974* |
| Depth (40m) x Month (Jul) | 0.125 | 0.961039 |
| Depth (25m) x Month (Mar) | 2.092 | 0.114885 |
| Depth (40m) x Month (Mar) | 0.583 | 0.585415 |
| Depth (25m)x Month (Oct) | 3.739 | 0.002997** |
| Depth (40m) x Month (Oct) | 0.444 | 0.803197 |
| Year x Month (Jul) | 6.925 | 0.000999*** |
| Year x Month (Mar) | 4.555 | 0.001998** |

| Year x Month (Oct) | 3.387 | 0.035964* |
|----------------------------------|-------|------------|
| Depth (25m) x Year x Month (Jul) | 3.013 | 0.025974* |
| Depth (40m) x Year x Month (Jul) | 0.125 | 0.961039 |
| Depth (25m) x Year x Month (Mar) | 2.091 | 0.114885 |
| Depth (40m) x Year x Month (Mar) | 0.584 | 0.585415 |
| Depth (25m) x Year x Month (Oct) | 3.739 | 0.002997** |
| Depth (40m) x Year x Month (Oct) | 0.443 | 0.804196 |



Suppl. Fig. 1. Temporal variation in the mean daily temperature (a), maximum daily light intensity (b) and maximum daily winter motion (c) at each depth (18, 25 and 40m) during two consecutive years (2016-17).



Suppl. Fig. 2. Temporal variation in the abundance of the different taxa of amphipods (ind x kg^{-1 \pm} SE) at each depth (18, 25 and 40m) during two consecutive years (2016-17).

Descripción detallada de las actividades desarrolladas durante la realización del TFT

Las actividades realizadas a lo largo del TFM se han centrado en la identificación y estudio de las diferentes poblaciones de anfípodos, así como en el análisis de diferentes tipos de datos, para determinar el efecto de la variación temporal y espacial en la diversidad y estructura de la comunidad de anfípodos asociados a fondos de maërl.

El análisis de las muestras de anfípodos ha constado de dos partes:

- Cuantificación e identificación al nivel taxonómico más bajo posible mediante un estereomicroscopio. En la mayoría de los casos, los especímenes se identificaron a nivel de especie.
- Cuantificación e identificación de juveniles y hembras ovígeras de las dos especies mayoritarias (*G. ostroumowi* y *A. ramondi*).

El análisis de los datos de la estructura de la comunidad de anfípodos consta de dos partes:

- Análisis multivariante de la estructura de la comunidad de anfípodos (composición y abundancia) mediante modelos lineales generalizados (GLM) para probar si varió entre las profundidades (18, 25 y 40 m), los meses (es decir, las estaciones) y los años.
- Análisis univariante mediante GLM mixtos y regresiones lineales, para observar las tendencias de riqueza, abundancia de anfípodos y estructura poblacional de las especies dominantes; además de probar la relación entre las abundancias de anfípodos y la biomasa de algas epífitas.

Durante el desarrollo del TFM se ha llevado a cabo una lectura de bibliografía relacionada con la materia de estudio, además del uso de diferentes guías taxonómicas del orden Amphipoda.

Formación recibida

Durante la realización del TFM realice el siguiente curso: "Diseño experimental y análisis estadístico: su aplicación en ciencias ambientales" impartido por mi director. Lo que me ha permitido profundizar de manera teórica y práctica, en conceptos estadísticos y en el análisis de datos mediante el software 'R'. Además, he obtenido una visión más holística de las posibilidades que otorga la estadística, como una herramienta con una gran aplicación en las ciencias marinas. Además, he adquirido conocimientos ecológicos previos al recibir una introducción en el laboratorio de mi hábitat de estudio, los fondos de rodolitos. Por otro lado, la colaboración de la Dra. Victoria Fernández (Universidad de Alicante) me ha permitido ampliar mis conocimientos taxonómicos y ecológicos de los anfípodos, que ha sido de gran utilidad a la hora del trabajo en el laboratorio.

Nivel de integración e implicación dentro del departamento y relaciones con el personal

Considero que he llegado a alcanzar una buena integración e implicación dentro del grupo en el que he desarrollado el TFM. El hecho de poder haber continuado la línea de trabajo que desarrolle durante el TFG me ha permitido obtener una mayor profundización y rendimiento de la temática en cuestión. Además, el hecho de que mi director haya realizado trabajos previos relacionados con el contenido del TFM, ha posibilitado un fácil entendimiento entre ambas partes.

Aspectos positivos y negativos más significativos relacionados con el desarrollo del TFT

Ha sido muy gratificante poder continuar estudiando la dinámica de los anfípodos como organismos modelo, en este caso a través de diferentes escalas temporales y gradientes batimétricos en los fondos de rodolitos. Esto me ha permitido entender el funcionamiento ecológico y fisiológico de otras poblaciones de anfípodos a las que estudié previamente en el mar Mediterráneo, ampliando mi visión sobre estos organismos en otras regiones biogeográficas, como son las Islas Canarias.

Las facilidades que me ha dado el grupo de investigación desde el primer día, han contribuido de forma significativa a sumergirme en el aprendizaje. No destacaría aspectos negativos relevantes; no obstante, la identificación de anfípodos ha sido un reto, ya que previamente no había trabajado con la mayoría de las especies presentes en nuestro estudio.

Valoración personal del aprendizaje conseguido a lo largo del TFT

En términos generales, considero que el aprendizaje adquirido en la realización del TFM será de utilidad en un futuro, ya que espero poder seguir profundizando en la macroecología y en la oceanografía. Por otro lado, en comparación al TFG, considero que he mejorado en cuestiones estadísticas, y con la ayuda de mi director he madurado en el desarrollo de la redacción de las diferentes partes de la memoria. Por ello, en términos generales, estimo que durante el TFM he experimentado un avance académico y estoy satisfecha con el trabajo.

7. References

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