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Small but key to nature conservation: Small packed communities in a small lagoon from a biodiversity hotspot

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ABSTRACT

1. Coastal lagoons are generally assumed to be naturally stressed environments. They are expected to be uniform ecosystems, dominated by r-strategist species.
2. There is increasing evidence that they are complex, with strong self-regulatory mechanisms and homeostatic capacity based on diversified trophic networks.
3. We here show a small coastal lagoon, with strong urban influences, yet with relatively complex communities enclosed in algal balls structured by *Valonia aegagropila* C. Agardh.
4. These balls were colonized by several algae and invertebrates living inside, constituting a biocenosis with a remarkable species richness and functional and structural diversity.
5. The results showed that the meiofaunal biomass from *Valonia* balls is not directly controlled by their size or total volume. Rather, the ability to produce its biomass and regulate its energy depends mainly on the characteristics of its diversity, either due to its species richness or the abundance of the fauna that inhabits this system.
6. Consequently, the biological productivity of the groups could be maintained in balance with the energy flow of the ecosystem in a context of a highly anthropized partially enclosed lagoon ecosystem.

1. Introduction

Within Earth's ecosystems, certain areas stand out as diversity hotspots because of their high concentration of representative species in a relatively small space (Walter, 1998). These hotspots exhibit exceptional biodiversity and are distributed worldwide. Although they cover only a fraction of the studied territory, they host significant associated diversity representing various biomes (Moreno et al., 2001; Moreno et al., 2001). Regions such as the Valdivian Forest, the Antilles, Australia's east coast, and the Macaronesian archipelagos are recognized as hotspots due to their abundant species richness (GEOG30, 2022). However, anthropogenic impacts pose a threat to the global importance and relevance of the biodiversity in these regions (Branquinho et al., 2019).

The high biodiversity and number of endemisms found in oceanic archipelagos are attributed, in part, to restricted connectivity (Pérez-Ruzafa, 2015). The barriers presented by island archipelagos create unique oceanographic conditions that diversify coastal environments.

Simultaneously, these barriers limit the movement of individuals between populations and the colonization of species, promoting diverse community structures and the emergence of endemism. This restricted connectivity is a shared characteristic with other ecosystems, including coastal lagoons (Ghezzi et al., 2015; Pérez-Ruzafa et al., 2019a).

Traditionally, coastal lagoons were perceived as environmentally stressed habitats dominated by opportunistic species (Elliott and Quintino, 2007). This perception led to the belief that lagoons were simple and uniform, as noted in benthic bionomics manuals (Peres and Picard, 1964; Augier, 1982), as well as in habitat conservation conventions such as EUNIS, the Barcelona Convention, and the Habitats Directive, among others. However, recent research has revealed that some lagoons, particularly those with limited connectivity to the open sea, exhibit complex food webs and an unexpected capacity for self-regulation in response to stress and eutrophication (Pérez-Ruzafa et al., 2011, 2019b, 2020a). Coastal lagoons play a vital ecological role, ranking among habitats with the highest biological and fishing production. They host

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rich biodiversity, serve as refuge and nursery grounds for numerous migratory marine species, and provide various ecosystem goods and services, underscoring their significant biological and socioeconomic importance (Marcos et al., 2019; Pérez-Ruzafa et al., 2020b). Despite their importance, coastal lagoons face numerous challenges, including contradictions, uncertainties, and a lack of planning that hinders effective protection against anthropic pressures (Pérez-Ruzafa et al., 2020b).

Among the well-known diversity hotspots, the Canary Islands emerge as a compelling focus for ecological research (Escáñez et al., 2021). This archipelago boasts one of Europe's most abundant and diverse faunal and floral populations (Whittaker and Fernández-Palacios, 2007; Hutsemékers et al., 2011). Nevertheless, the potential impacts it faces jeopardize the current ecological stability of the region, affecting the structure and functionality of its ecosystems (Branquinho et al., 2019). An intriguing potential diversity hotspot within the Canary Islands is the Charca de San Ginés coastal lagoon in Lanzarote (Riera et al., 2020). In this highly anthropized partially enclosed lagoon ecosystem, the seafloor is adorned with algal formations of *Valonia aegagropila* C. Agardh, commonly known as 'egagrópilas' (Pérez-Ruzafa et al., 2017). These formations are communities comprising numerous algae and invertebrate species, creating a biocenosis characterized by remarkable functional and structural diversity (Pérez-Ruzafa et al., 2017). This serves as an interesting example of fractal organization, with communities nested within communities and ecosystems, where the smallest unit is a self-sustaining community encapsulated within a small algae ball.

In this context, despite existing in a semi-enclosed anthropic setting, the Charca de San Ginés lagoon might seem like a relatively straightforward ecosystem, often dominated by opportunistic r-strategists (Odum, 1969, 1985; Dauvin, 2007; Elliott and Quintino, 2007). However, the *Valonia* structures cover most of the shallow areas in this habitat (Pérez-Ruzafa et al., 2017). Specifically, we seek to address the question of how numerous species associated with these structures manage to thrive and maintain stability within this anthropically-driven ecosystem.

Our primary objective is to provide insights into this question by analysing the biomass and production of various feeding groups of species inhabiting these 'balls'. Through this analysis, we aim to approximate an energy flow that could govern these communities. Consequently, we endeavour to comprehend how a closed lagoon environment within the Canary archipelago harbours a self-sustaining ecosystem boasting remarkable biodiversity.

2. Material and methods

2.1. Study area

The study area is the Charco de San Ginés, a 6.37ha coastal lagoon located on the north coast of Arrecife, Lanzarote (Canary archipelago) (Pérez Ruzafa et al., 2017). This coastal lagoon, bounded by artificial volcanic stone walls, is connected to the sea by a 29 m wide channel. With a maximum depth of 3 m, the tidal regime has an intense effect on the seabed of the lagoon, which is exposed during periods of low tide (Pérez-Ruzafa et al., 2017). The ecosystem is under a strong urban influence, which causes nutrient concentrations in the water column to be high, with concentrations of ammonium ($\text{NH}_4\text{-N}$) of $4.78 \pm 1.36 \mu\text{M}$, nitrate ($\text{NO}_3\text{-N}$) ($25.92 \pm 10.73 \mu\text{M}$), nitrite ($\text{NO}_2\text{-N}$) ($1.15 \pm 0.77 \mu\text{M}$), phosphate ($\text{PO}_4\text{-P}$) ($3.73 \pm 2.09 \mu\text{M}$), silicate ($15.47 \pm 2.29 \mu\text{M}$) and suspended solids ($110.6 \pm 71.45 \text{ mg/l}$). However, the water column maintains a high dissolved oxygen concentration ($8.36 \pm 0.18 \text{ mg/l}$), salinity ($34.67 \pm 0.09 \text{ PSU}$) and a low Chlorophyll *a* concentration ($0.51 \pm 0.15 \text{ mg/m}^3$) (Pérez-Ruzafa et al., 2017).

Despite its small size, the seabed has a variety of habitats. It is dominated by soft, muddy-sandy substrates, devoid of vegetation or covered by cyanophycean turfs, but it also has natural rocky outcrops, as well as artificial substrates. An important part of the lagoon, mainly in

the deeper areas, is covered by a biogenic formation made up of the green alga *Valonia aegagropila*, lying on the bottom not attached to the substrate, that forms easily movable balls or aggregates (Gil-Rodríguez et al., 2012; Machín-Sánchez et al., 2013) and which includes another series of closely related species, the whole behaving as a true ecological community.

2.2. Incubation experiments

To assess the effect of the *Valonia* balls community on water column characteristics and nutrient balance, incubations were carried out in separate glass cylinders of 66.5 cm height and 19.4 cm inner diameter. Two sets of experiments were carried out in January and March 2014, lasting 3 and 12 consecutive days, respectively. In each experiment, three tanks were used as controls, filled only with seawater, and three tanks in which a ball of *Valonia aegagropila* was placed. The balls were collected in the field by diving and transferred alive, cold and dark into individual containers with seawater just before the experiments were carried out. All test tubes were filled with 18 l of lagoon water from the same sample taken at the beginning of each experiment.

For the analysis of the environmental parameters, oxygen, temperature and pH, the measurements were taken by electrodes, in the middle zone of the water column of each tank, after very gentle agitation to homogenise it. Samples were taken once or twice a day, every day and at random times, during daylight hours (between 8 a.m. and 20 p.m.) (Fig. 1). For nutrient balance analysis, a daily sample was taken at random times during the day, using a syringe, first from the middle of the water column of each tank, after very gentle agitation to homogenise it, and then from the inside of the balls, which remained in the tank until the end of the experiment. Nutrients concentrations were determined using a continuous flow autoanalyzer (SYSTEA mMAC-1000 and SEAL AutoAnalyzer 3 with a JASCO Fluorescence detector FP-2020 Plus).

The differences between the controls and the treatments containing the balls from *Valonia* were analysed using PRIMER 7 package, by means of a Permanova analysis using 9999 permutations and the Montecarlo test performed on the Euclidean distance matrix. The data were previously square root transformed. For environmental parameters the design consisted of a single fixed factor with two levels (control vs. *Valonia*). In the case of nutrients, the fixed factors Treatment, with three levels (control, water column of the tank with *Valonia* and inside the ball of *Valonia*), and time (with 12 levels, from time 0 on the starting day to T11, the last day) were considered. In addition, the random factor Cylinder, nested in Treatment, was considered to control for between-tank/balls variability (Fig. 2).

2.3. Community sampling design

The San Ginés lagoon was sampled in two field surveys (October 2012 and May 2014). The collection of *Valonia* balls was conducted by hand, snorkelling at low tide, at a depth of ca. 1 m. Only permanently submerged pellets were collected. The samples were placed in individual bags with seawater and preserved in cold and dark for transfer to the laboratory. In the 2012 survey, 12 pellets were collected in four transects (T1-4), in two areas of the lagoon, 8 (four per transect) in zone 1 located in the most confined area, in the eastern part, and 4 (two in each transect) in zone 2 in the central area, which is more extensive and closer to the channel of communication with the open sea (Fig. 3). In the 2014 survey, 3 additional pellets were collected in May at zone 1.

2.4. Samples analysis

Once in the laboratory, the water retained inside the pellets, the largest and smallest diameter of the ellipsoid structure of the pellets (cm) and their total volume (cm^3) were measured. Subsequently, they were crushed and spread in a tray with seawater to estimate the percentage cover of each plant species (Cox, 1981) and to separate the

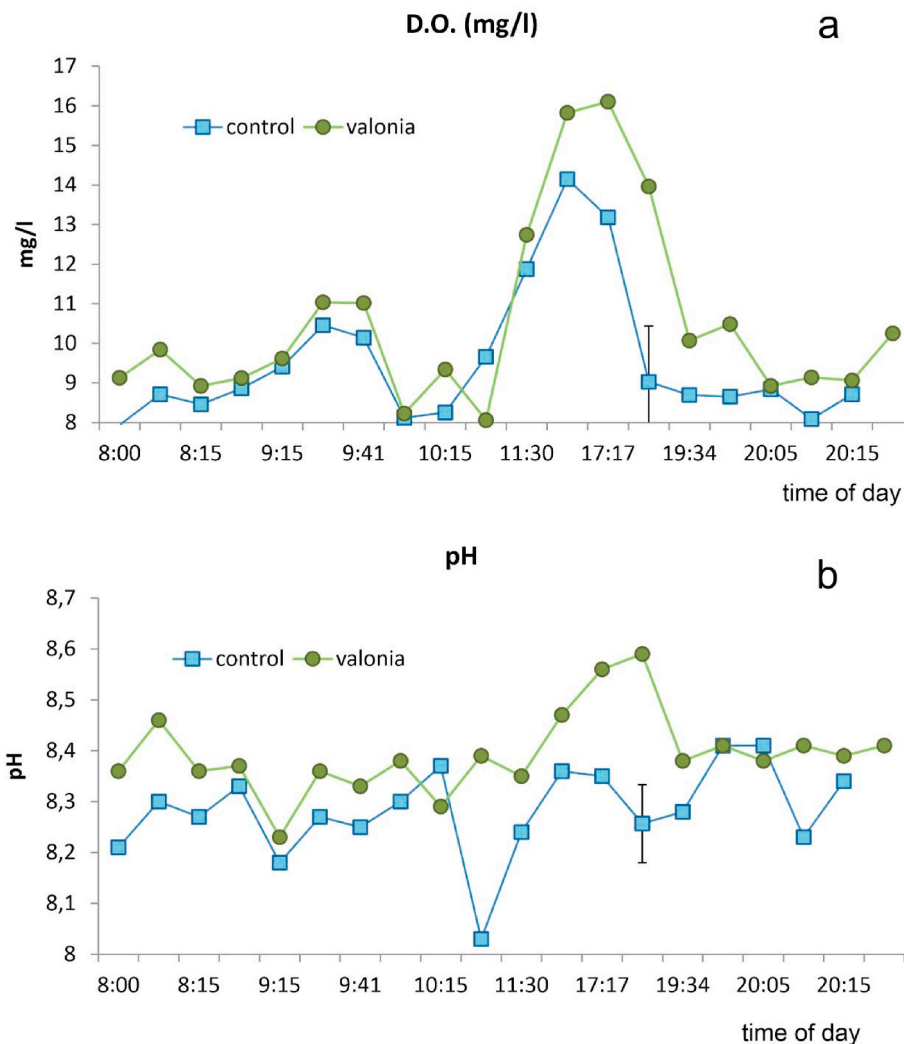


Fig. 1. Daily cycle [from 8:00 a.m. to 9:00 p.m.] of the evolution of dissolved Oxygen [a] DO (mg/l) and pH [b] in the water column present in the San Ginés lagoon. The logical cycle of phytoplankton production from control values (blue) and the production of the balls (green) is compared. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

faunal fraction. The algae samples, once separated, were preserved in seawater with 4% formalin and the fauna in 70° ethanol. Taxonomic identifications were made at species level or to the lower possible taxonomic level (Annex: Table VI). For taxonomic nomenclature, the records of the Algae Base (Guiry and Guiry, 2023, Algaebase. (s.f.)) and the World Register of Marine Species (WoRMS) (Costello et al., 2013) were followed.

The characterization of population structure within each *Valonia* ball involved an assessment of species richness (S), composition, and abundance (N). Abundance was quantified through measures such as percentage cover and the count of algal and faunal individuals. To determine the specific biomass of each species and their respective contributions to the overall pellet biomass, we employed the methods outlined by Edgar (1983, 1990). The first one calculates the ash-free dry weight (AFDW) based on the average size of identified species:

$$\text{Log}(B) = -1.01 + 2.64 \cdot \log(S) \quad (1)$$

Where B is faunal ash-free dry weight (mg) and S is sieving size(mm) (Edgar, 1983). For biomass calculations within each size category, we relied on previously published estimates of mean sizes across the taxonomic groups (Edgar, 1990). The mean biomass of animals in the various sieve size classes used in production calculations can be measured directly, or, providing that the faunal assemblage does not

contain many long flexible individuals or is dominated by a few very large animals (Edgar, 1990). To ascertain the productivity of individuals within each size category, we applied the general allometric equation developed by Edgar (1990):

$$P = (10^{((-2.31 + 0.8 \cdot \log_{10}(B \cdot 1000) + 0.89 \cdot \log_{10}(T)))/1000} \quad (2)$$

In this equation, P represents the daily productivity of an individual (mg AFDW/d), B denotes the biomass of an individual (mg AFDW), and T signifies the water temperature (°C) recorded at the time of sampling. Summation of the biomass and productivity estimates for individual animals (≤ 0.5 mm) yielded total biomass and total daily productivity estimates (mg AFDW/m² d) for each sample (Edgar, 1990).

2.5. Statistical analysis

Based on the analysis of the collected samples, we estimated various trends and distinctions in the ecological characteristics of the studied ecosystem. To achieve this, we conducted different comparisons and analyses using the R software (R Core Team, 2023). The initial step involved describing and comparing the apparent trends exhibited by various pellet characteristics in relation to the total biomass, which was calculated for both the fauna and the algae in the samples (see Fig. 4). To determine the final trends, we employed generalized linear models

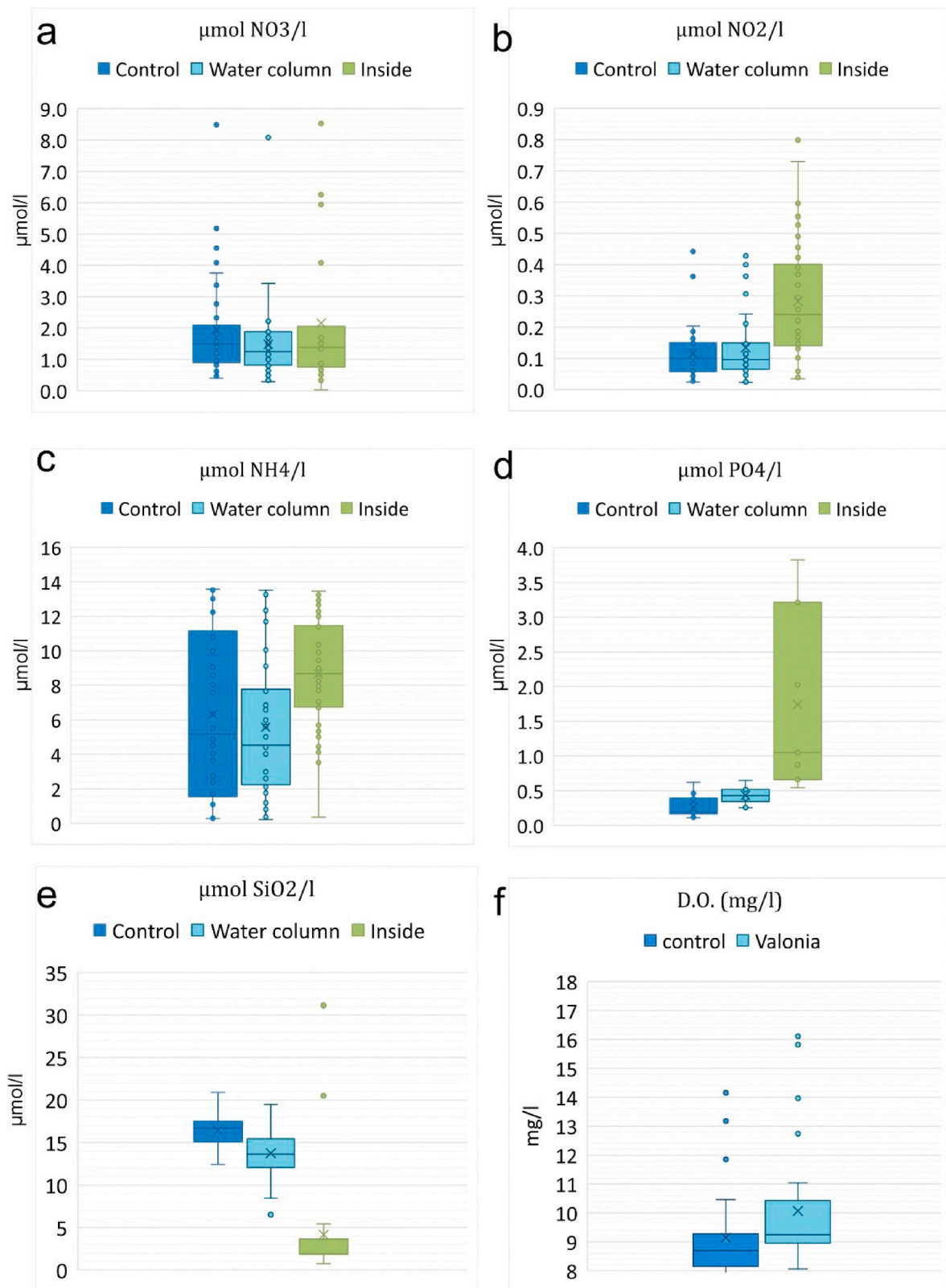


Fig. 2. Comparison of nutrients [a) NO_3 , b) NO_2 , c) NH_4 , d) PO_4 , e) SiO_2] in $\mu\text{mol/l}$ and dissolved oxygen [f) D.O.] in mg/l in the water column [Light blue] and inside the balls [green] compare with the controls [dark blue]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

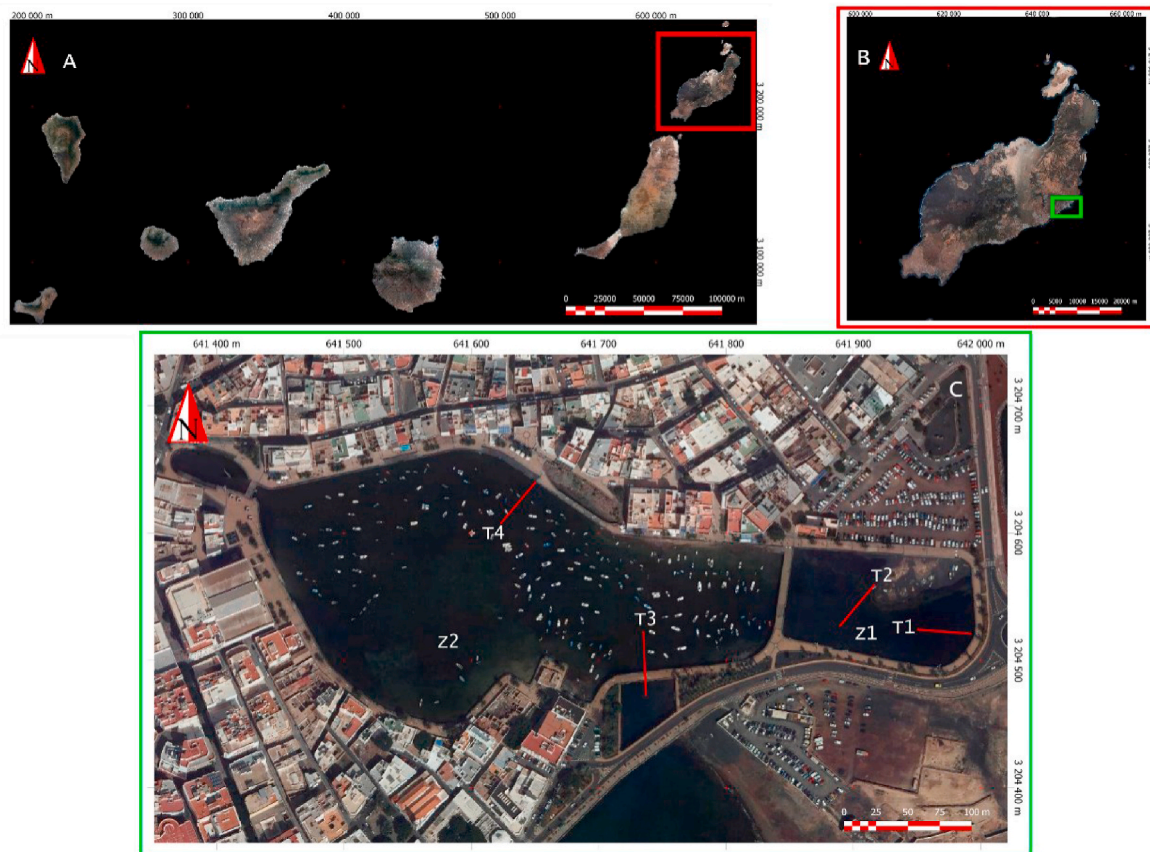


Fig. 3. Geographical location of Charco de San Ginés ©, Lanzarote (B), Canary Islands (A). The sampling zones [Z1, Z2] and transects [T1, T2, T3, T4] are shown marked in white and red. *Vallonia* balls in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(GLMs) to assess the level of correlation between pellet characteristics, including Total volume (cm^3), Total species richness, and Relative faunal abundance (number of individuals) (refer to Table II).

We categorized the identified organisms into trophic groups based on their dietary preferences and feeding strategies. In total, we grouped the organisms into 5 classes: Primary producer (Algae), Primary consumer (Herbivorous), Secondary consumer (Carnivorous), Decomposer (Detritivorous), and Filter feeders (Suspensivorous). We conducted a biomass description for each group (see Table III) and examined the contribution of each group to the total biomass of the system (see Fig. 5). Following the observation of specific biomass contributions, we performed an analysis of the percentage of similarity (SIMPER) to determine the contribution of species to the differences between the samples collected in 2012 and 2014 (Clarke and Warwick, 2001). Using the results from this analysis (see Table VI), we estimated the productivity of the various groups and compared the differences between the two sampled years using ANOVA contrasts (see Table IV).

3. Results

3.1. Incubation experiments

The results of the incubation experiments showed a high stability in the maintenance of environmental conditions and nutrient balance over up to 12 days of incubation. Oxygen concentration values showed significant differences between the Control cylinders and those containing the *Valonia aegagropila* balls with their associated community, the latter being slightly higher indicating a positive net balance of oxygen production during daylight hours. The daily cycle is consistent with a photosynthetic production cycle, by the phytoplankton in the controls

and by the phytoplankton and algal assemblage that constituted the balls in their corresponding cylinders. Oxygen and net production peaks occurred in the central hours of the day, between 11 a.m. and 17 p.m., decreasing significantly at dawn and dusk, reflecting the production/respiration net balance. The pH also showed significant differences (Table V), being slightly higher in the cylinders containing *Valonia* balls compared to the controls. The daily cycle of pH was significantly associated with that of oxygen (Pearson correlation coefficient = 0.44, $p = 0.000$), with the most intense drop in pH around 6 p.m., in the hours of the day when oxygen production decreased sharply and the relative importance of respiration increases. On the other hand, the nutrients showed great stability throughout the duration of the experiments, suggesting a stable, self-regulating system. Neither NO_3 , NH_4 , PO_4 nor SiO_2 showed significant differences between the controls and the tanks with *Valonia* balls (Table VI). Only nitrite was significant ($p = 0.05$). Some nutrients, except SiO_2 and NO_2 showed significant differences in the Treatment \times Time interaction. However, the pair-wise tests showed that, in all cases, such significance occurs between the water column and the internal environment of the balls, but not between the water columns of the controls and incubation cylinders. The significance of the differences between cylinders and their small temporal oscillations can be considered as the variability associated with differences between balls (e.g. their size and variations in their associated fauna that may induce small differences in their rhythms and self-regulatory capacities) (Fig. 1) (see Table VI).

3.2. *Valonia* balls assemblage

The basic description of the balls showed differences within their characteristics between the two sampled years in almost all the studied

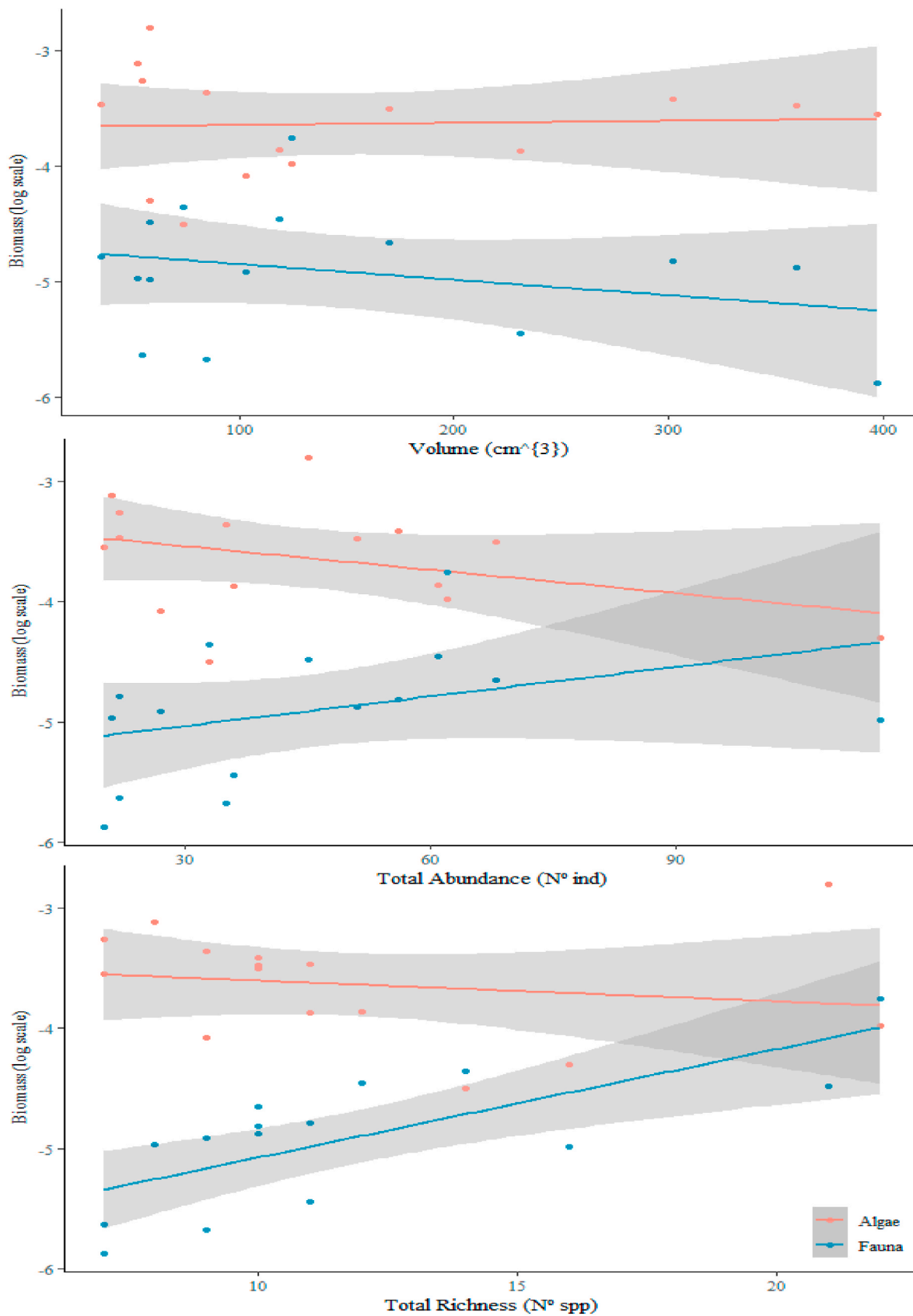


Fig. 4. Relationships of the biomass calculated on a logarithmic scale for the algae (Red) and the associated fauna (Blue) with respect to; the total volume of *Valonia* balls (cm³); the total abundance of fauna (number of individuals); and the total n° of species (for algae and for faunal species). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

The parameters measured for each transect in the two years sampled (Average per transect) and for the whole sample amount (Total average). The shown variables are: Date [October 2012, May 2014]; Transect [T1, T2, T3, T4]; Lagoon zones [1, 2]; sampled depth (m); ellipsoid diameters (cm) [minor (d), mayor (D)]; total volume of the structure (cm^3), species richness (n° of species) [for Algae (S_{Algae}), for fauna (S_{Fauna})]; faunal abundances (n° of individuals) [N_{Fauna}]; Biomass estimated (mg/cm^3) [for Algae (B_{Algae}), for fauna (B_{Fauna})]; and Productivity (mg/cm^3).

	Average per transect					Total average
	Oct-12	T2	T3	T4	May-14	Oct-12/May-14
Date	Oct-12				May-14	Oct-12/May-14
Transect	T1	T2	T3	T4	T1	T1-T4
Zones	1	1	2	2	1	Z1-Z2
Depth	1	1	1	1	1	1
d	5.00	6.88	7.00	5.00	4.17	5.61
D	7.75	9.50	8.50	6.00	5.23	7.40
Total Volume	112.15	248.20	239.09	80.63	47.81	145.58
S_{Algae}	5.75	7.50	8.50	9.50	4.67	7.18
S_{Fauna}	12.50	12.25	11.00	15.00	8.67	11.88
N_{Fauna}	54.75	51.50	56.00	36.00	21.67	43.98
B_{Algae}	2.003E-02	2.748E-02	2.597E-02	3.867E-02	3.787E-02	3.000E-02
B_{Fauna}	6.862E-03	1.093E-02	9.598E-03	9.335E-03	6.290E-03	8.604E-03
P_{Algae}	7.627E-01	9.947E-01	9.510E-01	1.275 E+00	1.288 E+00	1.054 E+00
P_{Fauna}	3.219E-01	4.596E-01	4.287E-01	4.192E-01	3.040E-01	3.867E-01

Table 2

Relationship between the algae biomass and fauna associated with *Valonia* balls through estimates by Generalized Linear Models. The dependencies are defined for the total volume occupied by the samples (cm^3), individual abundance (n° ind.) and total richness (n° spp.). Significant differences ($p < 0.05$) are highlighted in bold.

Org	Variable	Estimate	Std. Error	t-value	p-Value	R-squared	p-Value
Algae	Intercept	-3.665 E+00	1.998E-01	-1.835 E+01	1.130E-10	-7.470E-02	8.722E-01
	Volume	1.749E-04	1.066E-03	1.640E-01	8.720E-01		
	Intercept	-3.346 E+00	2.377E-01	-1.408 E+01	3.010E-09	6.441E-02	1.845E-01
	N	-6.506E-03	4.643E-03	-1.401 E+00	1.850E-01		
	Intercept	-3.435 E+00	3.405E-01	-1.009 E+01	1.620E-07	-4.419E-02	5.343E-01
Fauna	S	-1.723E-02	2.699E-02	-6.380E-01	5.340E-01		
	Intercept	-4.713 E+00	2.369E-01	-1.990 E+01	4.050E-11	9.337E-03	3.067E-01
	Volume	-1.345E-03	1.264E-03	-1.064 E+00	3.070E-01		
	Intercept	-5.280 E+00	2.928E-01	-1.804 E+01	1.390E-10	6.959E-02	1.761E-01
	N	8.181E-03	5.718E-03	1.431 E+00	1.760E-01		
	Intercept	-5.974 E+00	2.888E-01	-2.069 E+01	2.480E-11	5.076E-01	1.730E-03
	S	8.994E-02	2.289E-02	3.929 E+00	1.730E-03		

Table 3

Biomass contributions of the trophic groups reported in the *Valonia* pellets: Algae, Herbivores, Carnivorous, Detritivores, Suspensivores. The statistics are Average, Variance (Var), Sum, Maximum (Max), Minimum (Min), and contribution to the total biomass (%).

Trophic Group	Average	Var	Sum	Max	Min	Biomass contribution (%)
Algae	7.793E-03	2.533E-04	1.714E-01	6.059E-02	6.733E-06	34.97%
Carnivorous	7.115E-03	1.527E-05	1.281E-01	1.073E-02	1.233E-03	26.13%
Detritivores	6.365E-03	2.127E-05	6.365E-02	1.073E-02	1.728E-03	12.98%
Herbivorous	5.829E-03	1.642E-05	9.327E-02	1.073E-02	1.544E-03	19.03%
Suspensivores	8.445E-03	6.952E-06	3.378E-02	1.073E-02	6.162E-03	6.89%
Total	3.555E-02	3.132E-04	4.902E-01	1.035E-01	1.067E-02	100%

variables (Table I). Regarding the minor (d) and major (D) diameters of the structure, in 2012 the balls were on average 5.97 ± 1.6 cm (minor) and 7.94 ± 1.5 cm (major) in diameter, respectively. On the other hand, for the 2014 samples, their values were on average 4.17 ± 0.6 cm (d) and 5.23 ± 0.3 cm (D), respectively. The mean total volumes (V) were 170.02 ± 120.2 cm^3 in 2012 and 47.81 ± 10.9 cm^3 in 2014. The richness of flora and fauna estimated in the 2012 balls showed values of up to 12 and 22 species, respectively. In 2014, the richness of flora and associated fauna abruptly diminished relative to 2012 samples, with 6 and 11 species, respectively.

The overall fauna abundance of the 2012 *Valonia* balls showed an average of 49.65 ± 25.2 individuals but reaching up to 115 in some samples. In 2014, the average abundance was 21.67 ± 0.6 ind. on average, reaching a maximum of 22 ind. in some samples. Among all the balls measured, the four most abundant species were: the crustacean *Chondrochelia dubia* (Krøyer, 1842) with a total of 105 individuals; the polychaete *Eurythoe complanata* (Pallas, 1766) (96 ind.), the mollusk *Tricolia pullus canarica* (Nordsieck, 1973) (86 ind.) and the echinoderm

Amphipholis squamata (Delle Chiaje, 1828) (79 ind.). Regarding the estimated average biomass (B) for flora and fauna, they were respectively $2.804 \text{ E}^{-2} \pm 1.285 \text{ E}^{-2}$ mg cm^{-3} and $9.182 \text{ E}^{-2} \pm 0.511 \text{ E}^{-2}$ mg cm^{-3} in 2012 and $3.787 \text{ E}^{-2} \pm 0.664 \text{ E}^{-2}$ mg cm^{-3} and $6,290 \text{ E}^{-2} \pm 0.245 \text{ E}^{-2}$ mg cm^{-3} in 2014. In addition, the average production for flora and fauna was 1228 ± 0.373 mg cm^{-3} and 0.304 ± 0.193 mg cm^{-3} in 2012, respectively; and 0.407 ± 0.181 mg cm^{-3} and 0.304 ± 0.097 mg cm^{-3} in 2014, respectively.

Algal and invertebrate biomass trends depending on the size of the *Valonia* balls, total abundance of fauna and the species richness in each ball showed different patterns (Fig. 2, Table II). While the algal biomass did not show a clear trend (Estimate = 0.0001749 ± 0.0010659) or slightly tend to increase the total volume of balls; the faunal biomass, on the contrary, showed a negative correlation with the balls size (Estimate = -0.001345 ± 0.001264) (Table III). Regarding the abundance of associated fauna, the algae biomass showed a clear tendency to decrease (Estimate = -0.006506 ± 0.004643) while the animal biomass increased (Estimate = 0.008181 ± 0.005718). For the observed biomass

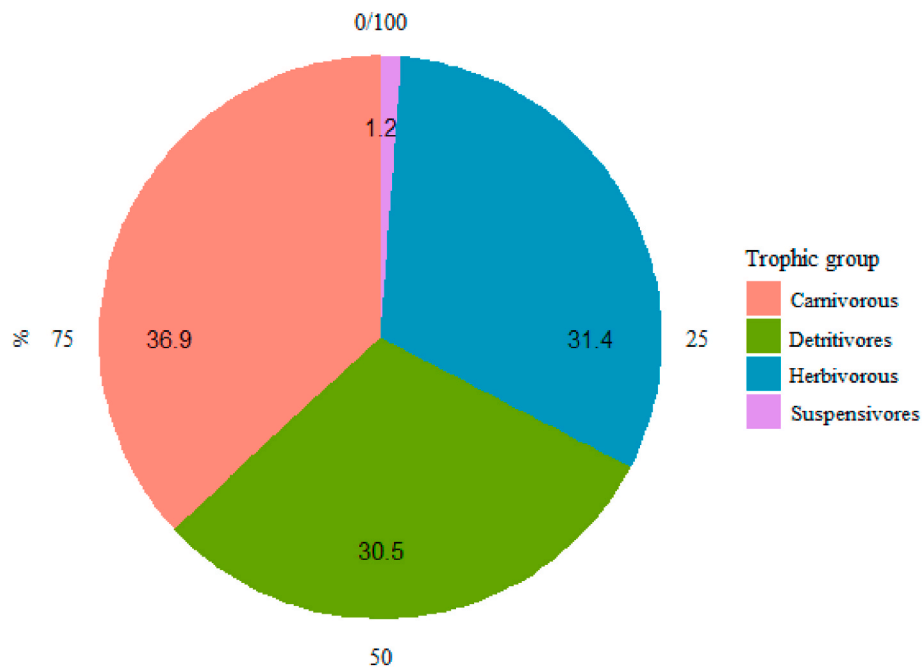


Fig. 5. Trophic groups (carnivores, detritivores, herbivores, and filter feeders) to which the representative associated fauna species of the *Valonia* balls belong and their mean respective percentages (%) with respect to the total. The percentages were obtained from the results of the similarity analysis (SIMPER).

Table 4

One-way ANOVAs of biomass estimation for the factor trophic group [with five levels: Algae, Herbivores, Carnivorous, Suspensivores and Detritivores]. Significant differences ($p < 0.05$) are highlighted in bold.

Trophic Group	Variable	Df	Sum sq	Mean Sq	F	p
Filter feeders	P	1	2.55E-06	2.55E-06	5.35E+30	<2e-16
	Residuals	2	0.00E+00	0.00E+00		
Algae	P	1	1.50E-01	1.50E-01	4.81E+02	1.84E-15
	Residuals	20	6.23E-03	3.10E-04		
Detritivores	P	1	2.02E-05	2.02E-05	1.39E+01	5.84E-03
	Residuals	8	1.16E-05	1.45E-06		
Herbivorous	P	1	1.03E-04	1.03E-04	6.23E+00	2.57E-02
	Residuals	14	2.31E-04	1.65E-05		
Carnivorous	P	1	7.53E-05	7.53E-05	3.49 E+00	8.01E-02
	Residuals	16	3.45E-04	2.16E-05		

Table 5

PERMANOVA table of results for dissolved oxygen concentration (DO), temperature and pH in the water column in incubation experiments of balls from *Valonia aegagropila*. The treatment factor (tr) has two levels, control, consisting of the incubation tank with seawater only, and *Valonia*, in which the tank contains a ball of *Valonia* and its internal fauna. Bold characters indicate significant ($p < 0.05$) differences.

DO	df	SS	MS	Pseudo-F	P(MC)
Tr	1	0.33776	0.33776	4.6978	0.0371
Res	62	4.4577	0.071898		
Total	63	4.7954			
Temperature	df	SS	MS	Pseudo-F	P(MC)
Tr	1	0.044796	0.044796	1.6597	0.197
Res	62	1.6734	0.026991		
Total	63	1.7182			
pH	df	SS	MS	Pseudo-F	P(MC)
Tr	1	0.0048942	0.0048942	27.659	0.0001
Res	62	0.010971	0.00017695		
Total	63	0.015865			

as a function of species richness S , the algal biomass did not show a clear trend to vary significantly (Estimate = -0.01723 ± 0.02699), however, the faunal biomass increases considerably (Estimate = 0.08994 ± 0.02289).

A total of 10 taxa of the 48 animal species represented up to 70.7% of the faunal diversity in the *Valonia* balls (Table VII). These species can be classified into 4 trophic groups or feeding strategies (Table III), which would allow establishing a pattern in the structure of the ecosystem (Fig. 3). Most of the biomass is contributed by algae (34.97%), followed by carnivores (26.13%), herbivores (19.03%), detritivores (12.98%) and suspension feeders (6.89%) (Table III). The production of 4 out of 5 trophic groups was significantly lower ($p < 0.05$) in 2014 compared to 2012, changing the contribution of the different trophic groups (Fig. 6). The comparisons between both years were made using an ANOVA test (Table IV).

4. Discussion

Despite the usual assumptions regarding coastal lagoons as bottom-up controlled systems and conditioned by environmental and anthropogenic pressures, in recent years evidence has been presented that both the r-vs. K- strategies (Pérez-Ruzafa et al., 2013), such as the ability to exert top-down control of the food web (Pérez-Ruzafa et al., 2002, 2011,

Table 6

PERMANOVA table of results for nutrient concentration in the water column in incubation experiments of balls from *Valonia aegagropila*. The treatment factor (Tr) has three levels, control, consisting of the water column in incubation tank with seawater only, Water column in the tanks containing a ball of *Valonia* and Inside balls. Time corresponds to the 12 consecutive days of the experiment and Cy is the Cylinder. Bold characters indicate significant ($p < 0.05$) differences. For pair-wise tests, only significant differences are shown.

Source	df	SS	MS	Pseudo-F	P(MC)	PAIR-WISE TESTS	t	P(MC)
NO3								
Tr	2	0.49	0.25	0.60	0.556	Within level 'T4' of factor 'Tiempo'		
Time	11	3.68	0.33	1.21	0.297	Control vs. Inside	4.17	0.034
Cy(Tr)	10	5.01	0.50	1.55	0.143	Water column vs. Inside	5.19	0.023
TrxTime	18	9.52	0.53	1.92	0.033	Within level 'T5' of factor 'Tiempo'		
Cy(Tr)xTime	48	13.04	0.27	0.84	0.724	Control vs. Water column	2.22	0.048
Res	54	17.44	0.32					
Total	143	57.73						
NO2								
Tr	2	0.30	0.15	6.71	0.005	Term 'Tip'	t	P(MC)
Time	11	0.43	0.04	1.88	0.057	Control vs. Inside	3.55	0.003
Cy(Tr)	10	0.32	0.03	2.21	0.031			
TrxTime	21	0.43	0.02	0.99	0.494			
Cy(Tr)xTime	64	1.36	0.02	1.47	0.070			
Res	58	0.84	0.01					
Total	166	4.88						
NH4								
Tr	2	3.86	1.93	1.60	0.229	Within level 'T2' of factor 'Tiempo'	t	P(MC)
Time	11	44.70	4.06	10.25	0.000	Control vs. Inside	3.25	0.022
Cy(Tr)	10	20.06	2.01	4.29	0.000	Water column vs. Inside	4.10	0.009
TrxTime	21	15.93	0.76	1.91	0.020	Within level 'T3' of factor 'Tiempo'		
Cy(Tr)xTime	66	25.83	0.39	0.84	0.765	Water column vs. Inside	4.02	0.005
Res	64	29.93	0.47			Within level 'T7' of factor 'Tiempo'		
Total	174	186.47				Control vs. Water column	3.17	0.035
						Water column vs. Inside	2.65	0.056
SiO2								
Tr	2	25.49	12.74	2.19	0.187			
Time	11	120.16	10.92	1.82	0.074			
Cy(Tr)	6	34.89	5.82	0.97	0.453			
TrxTime	20	185.77	9.29	1.55	0.096			
Res	60	360.13	6.00					
Total	99	733.86						
PO4								
Tr	2	0.47	0.24	2.81	0.097	Within level 'T1' of factor 'Tiempo'		
Time	11	1.42	0.13	10.32	0.000	Control vs. Inside	6.32	0.006
Cy(Tr)	8	1.35	0.17	5.82	0.000	Water column vs. Inside	4.98	0.037
TrxTime	7	1.17	0.17	13.72	0.000			
Cy(Tr)xTime	28	0.29	0.01	0.36	0.998			
Res	45	1.31	0.03					
Total	101	10.48						

2020a; Fernández-Alfás et al., 2022), must be reconsidered.

The results observed in the *Valonia* balls in the Charca de San Ginés in the coastal lagoon of Lanzarote indicate key characteristics of an ecological system that tends to maintain its self-sustainability despite the differences between the sampling years. Variations in the size and volume of *Valonia* balls may be related to the system's ability to adapt to changing conditions. A smaller amount of material may require fewer resources to maintain, which can be interpreted as an adaptation strategy to seasonal changes in the lagoon (Chapin et al., 1996). Although species richness (S) declined in 2014, the system still supported a variety of considered organisms (Fig. 6). This suggests that, in an apparently adverse environment, the system can maintain a species diversity for each food group specific for self-sustainability (Jørgensen et al., 1998). The negative trade-off between algal biomass and faunal abundance indicates possible regulation within the system. As the herbivorous fauna becomes more abundant, it can consume the biomass (mg/mm^2) produced by the algae that structure the ball and that limit the habitable space available in the *Valonia* balls. This could contribute to maintaining the balance of the ecosystem due to the need for organisms to regulate and manage their habitat (Hollick, 1993; Weaver and Dyke, 2012).

Despite variations in the productivity of different feeding groups, overall productivity remained relatively stable. This suggests that the system can adjust production according to the conditions and needs of the different trophic groups, which is an indication of its self-

sustainability (Connell and Orias, 1964). The presence of key species in trophic groups (such as algae) indicates the importance of certain organisms in the functioning of the system. Their waste products are those that would feed the groups of filter feeders and detritivores. The flow of matter in this ecological system shows a closed cycle by allowing filter-feeding and detritivorous organisms to transform the organic matter they capture from the waste of other species. In this way, the inorganic nutrients are once again captured by the algae so that the growth process is repeated, and the system remains self-managed (Perry, 1995).

The trophic web's autocatalytic capacity enhances the persistence of coexisting organisms within the algal environment. Autocatalysis, a form of positive feedback, strengthens each successive connection in the network over time (Kauffman, 1995; Castillo et al., 2015). Seasonal productivity variations, possibly linked to reproductive cycles, replenish resources needed for self-regulation without external nutrient inputs. The absence of production in suspension feeders in 2014 may result from morphological constraints within the ball structure, limiting water circulation and filtering function. It could also reflect the system rejecting certain species that lack direct connections to other trophic groups. Considering the concept of centripetality, where a network manages resources to sustain itself (Kauffman, 1995), it is not unreasonable to speculate that the ecosystem may eventually expel suspension-feeding organisms. This feeding group has minimal direct impact on the

Table 7

Similarity analysis (SIMPER) between the species recorded in 2012 and 2014. The variables were the name of the species (Simper); the belonging trophic group (Trophic group); the average contribution between the contrasted groups (average); the standard deviation of the contribution; the ratio between the average and the standard deviation (ratio); the average abundances per group (2012 and 2014); ordered cumulative contribution (cumsum); the permuted p-value or the probability of getting a larger or equal average contribution in random permutation of the group factor (p-value), and the individual contribution of each species to the entire System (% Contribution).

Species	Trophic Group	Average	SD	Ratio	2012	2014	Cumsum	p-Value	Descap %
<i>Amphipholis squamata</i> (Delle Chiaje, 1828)	Detritívoro	0.092	0.107	0.863	6.583	0.000	0.124	0.331	0.124
<i>Tricolia pullus canarica</i> (Nordsieck, 1973)	Herbívoro	0.083	0.085	0.976	6.917	1.000	0.236	0.372	0.112
<i>Chondrochelia dubia</i> (Krøyer, 1842)	Carnívoro	0.078	0.121	0.644	7.917	3.333	0.341	0.317	0.105
<i>Eurythoe complanata</i> (Pallas, 1766)	Carnívoro	0.075	0.070	1.081	7.083	3.667	0.443	0.265	0.102
<i>Ophiocomina nigra</i> (Abildgaard in O.F. Müller, 1789)	Detritívoro	0.065	0.063	1.034	2.917	4.000	0.531	0.149	0.088
<i>Cirriformia tentaculata</i> (Montagu, 1808)	Detritívoro	0.031	0.046	0.670	1.917	1.333	0.573	0.213	0.042
<i>Elasmopus rapax</i> (Costa, 1853)	Herbívoro	0.029	0.026	1.104	2.333	1.667	0.612	0.354	0.039
<i>Lumbrineris cingulata</i> (Ehlers, 1897)	Carnívoro	0.027	0.035	0.765	0.333	1.667	0.648	0.188	0.036
<i>Protoarcia oerstedii</i> (Claparède, 1864)	Detritívoro	0.023	0.027	0.855	1.583	0.667	0.679	0.402	0.031
<i>Hyale perieri</i> (Lucas, 1849)	Herbívoro	0.021	0.036	0.580	1.583	0.000	0.707	0.391	0.028
<i>Tanais dulongii</i> (Audouin, 1826)	Carnívoro	0.021	0.029	0.724	1.333	0.000	0.735	0.385	0.028
Nemertea sp1	Carnívoro	0.020	0.021	0.964	0.000	1.333	0.763	0.025	0.028
<i>Sunamphitoe pelagica</i> (H. Milne Edwards, 1830)	Herbívoro	0.017	0.020	0.851	0.917	0.667	0.785	0.276	0.022
<i>Cymodoce truncata</i> (Leach, 1814)	Herbívoro	0.016	0.025	0.660	1.250	0.000	0.807	0.438	0.022
<i>Tritia cuvierii</i> (Payraudeau, 1826)	Herbívoro	0.013	0.023	0.555	1.000	0.000	0.825	0.432	0.018
<i>Lumbrineris latreilli</i> (Audouin and Milne Edwards, 1834)	Carnívoro	0.011	0.017	0.640	0.667	0.000	0.839	0.326	0.014
<i>Turritella brocchii</i> (Bronn, 1831 †)	Herbívoro	0.010	0.015	0.686	0.833	0.000	0.853	0.377	0.014
<i>Nototropis swammerdamii</i> (H. Milne Edwards, 1830)	Herbívoro	0.010	0.008	1.245	0.000	0.667	0.867	0.025	0.014
<i>Sipunculus nudus</i> (Linnaeus, 1766)	Detritívoro	0.010	0.016	0.618	0.667	0.000	0.880	0.348	0.013
<i>Maera grossimana</i> (Montagu, 1808)	Herbívoro	0.007	0.008	0.913	0.500	0.333	0.890	0.186	0.010
<i>Corophium</i> sp. (Latreille, 1806)	Herbívoro	0.007	0.023	0.297	0.583	0.000	0.899	0.205	0.009
<i>Dorvillea</i> sp. (Parfitt, 1866)	Carnívoro	0.007	0.010	0.649	0.417	0.000	0.908	0.388	0.009
<i>Syllis</i> sp1	Carnívoro	0.006	0.015	0.439	0.417	0.000	0.917	0.361	0.009
<i>Lysidice unicornis</i> (Grube, 1840)	Carnívoro	0.006	0.009	0.731	0.167	0.333	0.925	0.367	0.008
<i>Chiton canariensis</i> (d'Orbigny, 1840)	Herbívoro	0.006	0.009	0.676	0.500	0.000	0.933	0.625	0.008
Nemertea sp2	Carnívoro	0.005	0.008	0.656	0.000	0.333	0.940	0.194	0.007
<i>Nicidion longula</i> (Ehlers, 1887)	Carnívoro	0.005	0.008	0.657	0.000	0.333	0.947	0.188	0.007
<i>Ampithoe rubricata</i> (Montagu, 1818)	Herbívoro	0.005	0.008	0.657	0.000	0.333	0.954	0.188	0.007
<i>Eunice</i> sp. (Cuvier, 1817)	Carnívoro	0.003	0.012	0.297	0.250	0.000	0.958	0.192	0.004
Porifera sp1	Suspensívoro	0.003	0.008	0.428	0.167	0.000	0.963	0.370	0.005
<i>Bittium latreillii</i> (Payraudeau, 1826)	Herbívoro	0.003	0.010	0.297	0.167	0.000	0.967	0.204	0.004
<i>Elasmopus canarius</i> (Krapp-Schickel and Ruffo, 1990)	Herbívoro	0.003	0.010	0.297	0.167	0.000	0.971	0.204	0.004
<i>Syllis</i> sp2	Carnívoro	0.003	0.010	0.297	0.250	0.000	0.975	0.205	0.004
<i>Branchioma bombyx</i> (Dalyell, 1853)	Suspensívoro	0.002	0.005	0.440	0.167	0.000	0.978	0.384	0.003
Nematoda sp1	Carnívoro	0.002	0.006	0.297	0.083	0.000	0.980	0.209	0.002
Paraonidae (Cerruti, 1909)	Detritívoro	0.002	0.006	0.297	0.083	0.000	0.982	0.209	0.002
<i>Parapseudes latifrons</i> (Grube, 1864)	Carnívoro	0.002	0.005	0.297	0.083	0.000	0.985	0.204	0.003
<i>Coscinasterias tenuispina</i> (Lamarck, 1816)	Detritívoro	0.001	0.004	0.297	0.083	0.000	0.986	0.214	0.001
<i>Botrylloides cf leachii</i> (Savigny, 1816)	Suspensívoro	0.001	0.004	0.297	0.083	0.000	0.988	0.214	0.002
<i>Phascolosoma stephensoni</i> (Stephen, 1942)	Detritívoro	0.001	0.004	0.297	0.083	0.000	0.989	0.214	0.001
<i>Dexamine spinosa</i> (Montagu, 1813)	Herbívoro	0.001	0.003	0.297	0.083	0.000	0.991	0.209	0.002
Anthuridae (Leach, 1814)	Carnívoro	0.001	0.003	0.297	0.083	0.000	0.992	0.209	0.001
<i>Asterina gibbosa</i> (Pennant, 1777)	Detritívoro	0.001	0.003	0.297	0.083	0.000	0.993	0.209	0.001
<i>Clathrina</i> sp. (Gray, 1867)	Suspensívoro	0.001	0.003	0.297	0.083	0.000	0.995	0.205	0.002
Nereididae (Blainville, 1818)	Carnívoro	0.001	0.003	0.297	0.083	0.000	0.996	0.205	0.001
<i>Syllis</i> sp3	Carnívoro	0.001	0.003	0.297	0.083	0.000	0.997	0.205	0.001
Oligochaeta sp1	Detritívoro	0.001	0.003	0.297	0.083	0.000	0.999	0.205	0.002
<i>Gammaropsis</i> sp. (Lilljeborg, 1855)	Herbívoro	0.001	0.003	0.297	0.083	0.000	1.000	0.211	0.001

closed energy flow exhibited by other organisms. Furthermore, if various organism groups acquire useful materials for subsequent algal biomass production, the ecosystem may favor those offering more efficient energy utilization (Castillo et al., 2015). A thorough understanding of the ecosystem properties and characteristics is pivotal to undertake conservation actions (Chaplin-Kramer et al., 2022). Key Biodiversity Areas (KBAs) offer a global standard for identifying sites that contribute substantially to the global persistence of biodiversity (IUCN, 2016). However, most of KBAs are Important Bird Areas (BirdLife International., 2019), being scarce the number of marine KBAs (Maxwell et al., 2020). However, recent approaches have been focused on the conservation of coastal biodiversity through the implementation of KBAs in the marine realm (Edgar et al., 2008). For example, Riera et al. (2020) identified the coastal biodiversity hotspots in the Canary archipelago, and within them, the study area (Charco de San Ginés-Marina from Arrecife) was included as KBA because of the presence of the most abundant populations of the common goby (*Pomatoschistus microps*) in

the Canary Islands. This species is scarce at the regional level, being catalogued as “Of interest for Canarian Ecosystems” in 2010, and of “Least Concern” in the IUCN Red List. It seems paradoxical that the study area harbours highly diverse coastal communities, including the populations of this goby since this coastal site is highly anthropogenic, with a modified coastal fringe and located in the capital of the island (Arrecife). This coastal lagoon has a series of characteristics that made it unique in the study region, with interspersed patches of unconsolidated (sand and silt and clay) and consolidated (rocks and rocky platform) in the intertidal and shallow subtidal (Pérez-Ruzafa et al., 2017), stochastic freshwater inputs and drastic daily tide variations. This lagoon has been also subjected to continuous fishing and harvesting pressure by professional and recreational fishermen (e.g., Noguera and Riera, 2011). The *Valonia* balls behave as ecosystem engineering, with the development of rich-associated flora and infauna communities. Thus, the presence of these structures constitutes an added value to the biodiversity of this singular place, however, it needs to be taken into consideration that

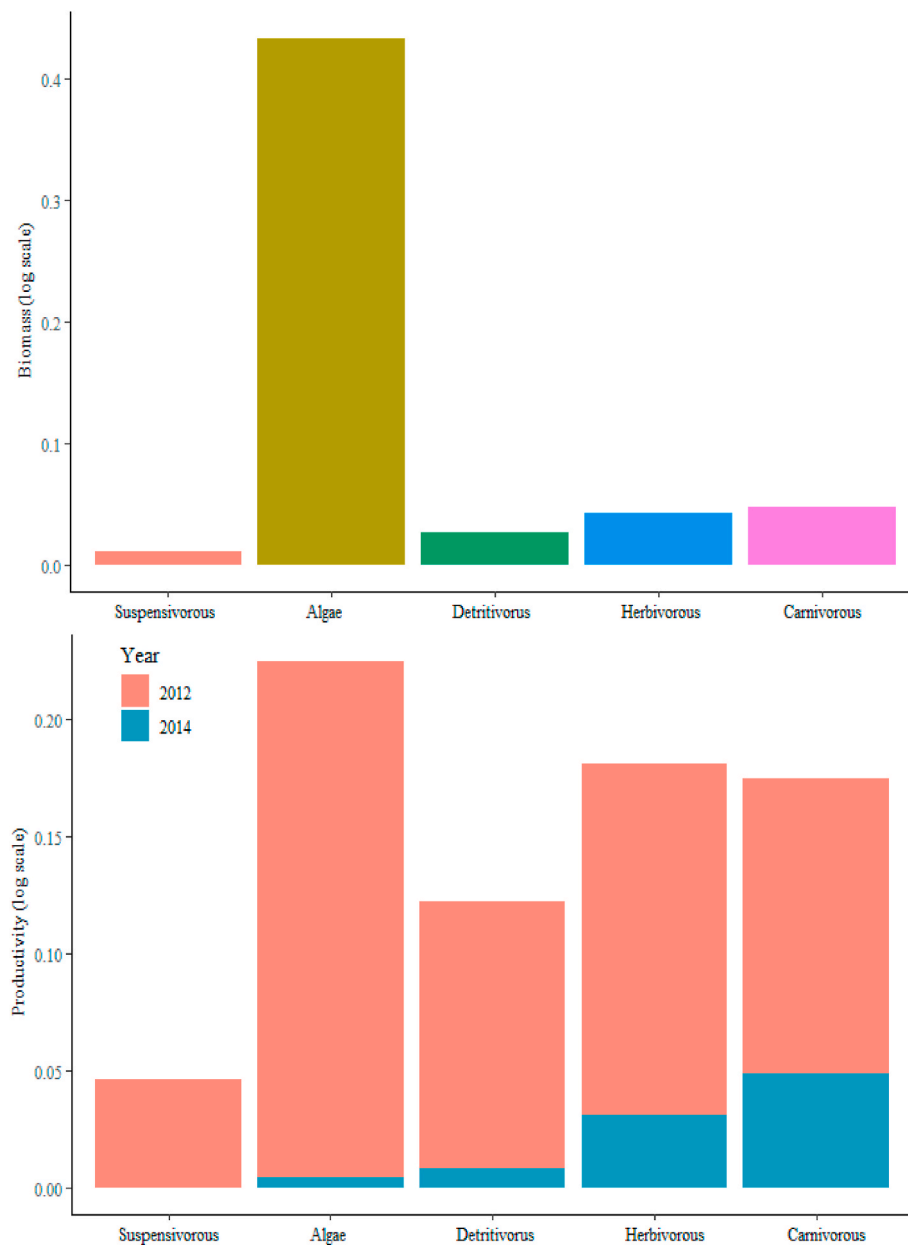


Fig. 6. Estimated biomass productivity on a log scale at each trophic group (algae, herbivores, carnivores, suspension feeders, detritus feeders) for: a) all samples analysed; b) and for each year of sampling (2012 (red), 2014 (blue)). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

these “balls” are stochastically subjected to environmental variations, mostly related to runoff input from the terrestrial realm and to eutrophication from urban waters.

An important aspect that needs to be taken into consideration is the isolation (an oceanic island) and the limited dimensions (<1 km² surface area) of this coastal lagoon relative to other coastal lagoons from adjacent regions such as the Mediterranean Sea where large lagoons harbour a wide range of coastal communities, even including fish assemblages (e.g., Riera et al., 2018). The importance of preserving biodiversity from small habitats and limited-sized ecosystems have been shown to be of utmost importance (Chase et al., 2020). However, the biodiversity decline is more pronounced in smaller habitats than in larger ones due to ecological processes such as the ecosystem decay (Lovejoy et al., 1984). Hence, the probabilities of local and regional extinction risks of species are higher in small sites relative to large areas, since biological processes in small and large sites are different in terms of fragmentation and edge

effect, dispersal and demographic noise and stochasticity (Adler and Drake, 2008; Vergara and Hahn, 2009; Jones et al., 2015).

Together, this suggests that the Charca de San Ginés coastal lagoon and its *Valonia* balls possess an ecological system that shows adaptability and resilience despite fluctuations in environmental conditions. Although the sample size is different in each year, the homogeneity of the balls collected in 2014 could allow us to accept their representativeness to the system studied. On the contrary, the 2012 samples, which were more abundant, require a larger sample size to improve their representativeness due to their greater morphological diversity. This would allow us to assume that the trends observed in the results give rise to representative preliminary hypotheses for this case study. This may be important to define a pattern of self-sustainability based on relationships between organisms. In this way it would be able to maintain its structure and functioning over time, even when located in an anthropized environment.

These findings emphasize the significance of comprehending and conserving ecosystems like this, which can host valuable biodiversity and fulfill critical ecological roles. Moreover, this system serves as a valuable research model for defining self-management patterns in controlled environments. By extending this model to larger systems, it becomes possible to investigate how the size and configuration of communities linked by their feeding habits may affect system stability and self-regulation through the interplay of biomass and species richness. This approach also opens avenues for studying species diversity and the interactions among different trophic groups that impact sustainability, along with the design of artificial systems that foster ecological resilience. Additionally, the exploration of modular designs in artificial self-sustaining systems, where individual units interact to maintain stability and self-sufficiency within a larger framework, becomes an intriguing avenue for further research.

However, it is essential not to dismiss the requirement for statistical confirmation in subsequent studies. Designing continuous monitoring methods to investigate these ecological structures in areas impacted by human activity is crucial to preserve the affected resources and ecosystems. In future studies, it is important to standardize the groups of samples collected to confirm the observed trends and changes. Prioritizing environmental monitoring whenever samples are collected is also essential. This practice would enable researchers to investigate the environmental impacts and interactions of self-sustaining systems in the environment, facilitating the establishment of patterns in the behavioral changes of organisms contributing to their own self-sustainability.

5. Conclusions

This study provides evidence that coastal lagoons have the capacity to develop intricate ecosystems with robust self-regulation and the ability to exert top-down control over environmental conditions. Ecological systems demonstrating self-regulation and self-preservation capabilities serve as important reference models for designing management and regulatory frameworks in human-impacted environments with limited resources. The preservation of these coastal ecosystems is imperative to sustain the high levels of biodiversity and trophic interactions exhibited by the organisms within them, such as the *Valonia* balls. While the Charco de San Ginés coastal lagoon in the Canary

archipelago has previously been designated as a Key Biodiversity Area (KBA) (Riera et al., 2020) due to the presence of threatened or locally restricted species, this study reveals additional considerations for its conservation. It highlights the complexity and applicability of intricate systems that are scarcely represented or defined in the archipelago. As a result, the uniqueness and potential significance of this area present an opportunity for comprehensive protection. The atypical systems of interest for study underscore the need for an integrated approach to manage and conserve this coastal location. Such an approach should take into account not only socioeconomic and industrial factors but also aspects that may prove valuable for future research and applications in the realms of conservation and adaptability.

CRedit authorship contribution statement

Eros Geppi: Writing – original draft, Software, Methodology, Formal analysis, Conceptualization. **Rodrigo Riera:** Writing – review & editing, Supervision, Project administration, Investigation, Conceptualization. **Itziar Colodro:** carrying out the incubation experiments in the laboratory and 2014 sampling. **Ángel Pérez-Ruzafa:** Writing – review & editing, Supervision, Resources, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no competing interest of any kind.

Data availability

Data will be made available on request.

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ANNEX: Complementary information

Table V

Taxonomic and trophic classification of the species found in the *Valonia* balls collected in the San Ginés lagoon in 2012 and 2014.

Trophic Group	Phylum	Specie
Filter feeders	Annelida	<i>Branchioma bombyx</i> (Dalyell, 1853)
	Chordata	<i>Botrylloides cf. leachii</i> (Savigny, 1816)
	Porifera	<i>Clathrina</i> sp.
Algae	Chlorophyta	Porifera sp1
		<i>Bryopsis plumosa</i> (Hudson & C. Agardh)
		<i>Caulerpa racemosa</i> (Forsskål & J. Agardh)
		<i>Chaetomorpha aerea</i> (Dillwyn & Kützing)
		<i>Cladophora pellucida</i> (Hudson & Kützing)
		<i>Cladophora prolifera</i> (Roth & Kützing)
		<i>Valonia aegagropila</i> (C. Agardh)
		<i>Amphiroa beauvoisii</i> (J.V. Lamouroux)
		<i>Amphiroa rigida</i> (J.V. Lamouroux)
		<i>Asparagopsis armata</i> (Harvey)
	<i>Caulacanthus ustulatus</i> (Mertens ex Turner & Kützing)	
	<i>Womersleyella setacea</i> (G. J. Hollenberg & R.E. Norris)	
	<i>Ellisolandia elongata</i> (J. Ellis & D. Solander, K. Hind et G.W. Saunders)	
	<i>Halitilon virgatum</i> (Zanardini, D. J. Garbary & H. W. Johansen)	
	<i>Herposiphonia secunda</i> (C. Agardh & Ambronn)	
	<i>Hydrolythion farinosum</i> (J.V. Lamouroux, D. Penrose & Y.M. Chamberlain)	
	<i>Hypnea spinella</i> (C. Agardh & Kützing)	
	<i>Jania rubens</i> (Linnaeus & J.V. Lamouroux)	
	<i>Lithophyllum incrustans</i> (Philippi)	

(continued on next page)

Table V (continued)

Trophic Group	Phylum	Specie	
Detritivores	Annelida	<i>Lithothamnion</i> sp.	
		<i>Palisada perforata</i> (Bory de Saint-Vicent & K. W. Nam)	
		<i>Spyridia filamentosa</i> (Wulfen & Harvey)	
		<i>Wundermania miniata</i> (Sprengel & J. Feldmann & G. Hamel)	
		<i>Cirriiformia tentaculata</i> (Montagu, 1808)	
		Oligochaeta sp1	
		Paraonidae sp1	
		<i>Phascolosoma stephensoni</i> (Stephen, 1942)	
		<i>Protoarcia oerstedii</i> (Claparède, 1864)	
		<i>Sipunculus nudus</i> (Linnaeus, 1766)	
		Echinodermata	<i>Amphipholis squamata</i> (Delle Chiaje, 1828)
			<i>Asterina gibbosa</i> (Pennant, 1777)
<i>Coscinasterias tenuispina</i> (Lamarck, 1816)			
<i>Ophiocomina nigra</i> (Abildgaard in O.F. Müller, 1789)			
<i>Ampithoe rubricata</i> (Montagu, 1818)			
Herbivorous	Arthropoda	<i>Corophium</i> sp.	
		<i>Cymodoce truncata</i> (Leach, 1814)	
		<i>Dexamine spinosa</i> (Montagu, 1813)	
		<i>Elasmopus canarius</i> (Krapp-Schickel and Ruffo, 1990)	
		<i>Elasmopus rapax</i> (Costa, 1853)	
		<i>Gammaropsis</i> sp.	
		<i>Hyalae perieri</i> (Lucas, 1849)	
		<i>Maera grossimana</i> (Montagu, 1808)	
		<i>Nototropis swammerdamei</i> (H. Milne Edwards, 1830)	
		<i>Sunamphitoe pelagica</i> (H. Milne Edwards, 1830)	
		Mollusca	<i>Bittium latreillii</i> (Payraudeau, 1826)
			<i>Chiton canariensis</i> (d'Orbigny, 1840)
<i>Tricolia pullus canarica</i> (Nordsieck, 1973)			
<i>Tritia cuvierii</i> (Payraudeau, 1826)			
<i>Turritella brocchii</i> (Bronn, 1831 †)			
Carnivorous	Annelida	<i>Dorvillea</i> sp.	
		<i>Eunice</i> sp.	
		<i>Eurythoe complanata</i> (Pallas, 1766)	
		<i>Lumbrineris cingulata</i> (Ehlers, 1897)	
		<i>Lumbrineris latreilli</i> (Audouin and Milne Edwards, 1834)	
		<i>Lysidice unicornis</i> (Grube, 1840)	
		Nereididae sp1	
		<i>Nicidion longula</i> (Ehlers, 1887)	
		Syllis sp1	
		Syllis sp2	
		Syllis sp3	
		Arthropoda	Anthuridae sp1
			<i>Chondrochelia dubia</i> (Krøyer, 1842)
			<i>Parapseudes latifrons</i> (Grube, 1864)
			<i>Tanais dulongii</i> (Audouin, 1826)
		Nematoda	Nematoda sp1
			Nemertea sp1
		Nemertea	Nemertea sp1
Nemertea sp2			

Table VI

Similarity analysis (SIMPER) between the species recorded in 2012 and 2014. The variables were the name of the species (Simper); the belonging trophic group (Trophic group); the average contribution between the contrasted groups (average); the standard deviation of the contribution; the ratio between the average and the standard deviation (ratio); the average abundances per group (2012 and 2014); ordered cumulative contribution (cumsum); the permuted p-value or the probability of getting a larger or equal average contribution in random permutation of the group factor (p-value), and the individual contribution of each species to the entire System (% Contribution).

Species	Trophic Group	Average	SD	Ratio	2012	2014	Cumsum	p-Value	% Contribution
<i>Amphipholis squamata</i> (Delle Chiaje, 1828)	Detritivores	0.092	0.107	0.863	6.583	0.000	0.124	0.331	0.124
<i>Tricolia pullus canarica</i> (Nordsieck, 1973)	Herbivorous	0.083	0.085	0.976	6.917	1.000	0.236	0.372	0.112
<i>Chondrochelia dubia</i> (Krøyer, 1842)	Carnivorous	0.078	0.121	0.644	7.917	3.333	0.341	0.317	0.105
<i>Eurythoe complanata</i> (Pallas, 1766)	Carnivorous	0.075	0.070	1.081	7.083	3.667	0.443	0.265	0.102
<i>Ophiocomina nigra</i> (Abildgaard in O.F. Müller, 1789)	Detritivores	0.065	0.063	1.034	2.917	4.000	0.531	0.149	0.088
<i>Cirriiformia tentaculata</i> (Montagu, 1808)	Detritivores	0.031	0.046	0.670	1.917	1.333	0.573	0.213	0.042
<i>Elasmopus rapax</i> (Costa, 1853)	Herbivorous	0.029	0.026	1.104	2.333	1.667	0.612	0.354	0.039
<i>Lumbrineris cingulata</i> (Ehlers, 1897)	Carnivorous	0.027	0.035	0.765	0.333	1.667	0.648	0.188	0.036
<i>Protoarcia oerstedii</i> (Claparède, 1864)	Detritivores	0.023	0.027	0.855	1.583	0.667	0.679	0.402	0.031
<i>Hyalae perieri</i> (Lucas, 1849)	Herbivorous	0.021	0.036	0.580	1.583	0.000	0.707	0.391	0.028
<i>Tanais dulongii</i> (Audouin, 1826)	Carnivorous	0.021	0.029	0.724	1.333	0.000	0.735	0.385	0.028
Nemertea sp1	Carnivorous	0.020	0.021	0.964	0.000	1.333	0.763	0.025	0.028
<i>Sunamphitoe pelagica</i> (H. Milne Edwards, 1830)	Herbivorous	0.017	0.020	0.851	0.917	0.667	0.785	0.276	0.022
<i>Cymodoce truncata</i> (Leach, 1814)	Herbivorous	0.016	0.025	0.660	1.250	0.000	0.807	0.438	0.022
<i>Tritia cuvierii</i> (Payraudeau, 1826)	Herbivorous	0.013	0.023	0.555	1.000	0.000	0.825	0.432	0.018

(continued on next page)

Table VI (continued)

Species	Trophic Group	Average	SD	Ratio	2012	2014	Cumsum	p-Value	% Contribution
<i>Lumbrineris latreilli</i> (Audouin and Milne Edwards, 1834)	Carnivorous	0.011	0.017	0.640	0.667	0.000	0.839	0.326	0.014
<i>Turritella brocchii</i> (Bronn, 1831)	Herbivorous	0.010	0.015	0.686	0.833	0.000	0.853	0.377	0.014
<i>Nototropis swammerdamei</i> (H. Milne Edwards, 1830)	Herbivorous	0.010	0.008	1.245	0.000	0.667	0.867	0.025	0.014
<i>Sipunculus nudus</i> (Linnaeus, 1766)	Detritivores	0.010	0.016	0.618	0.667	0.000	0.880	0.348	0.013
<i>Maera grossimana</i> (Montagu, 1808)	Herbivorous	0.007	0.008	0.913	0.500	0.333	0.890	0.186	0.010
<i>Corophium</i> sp.	Herbivorous	0.007	0.023	0.297	0.583	0.000	0.899	0.205	0.009
<i>Dorvillea</i> sp.	Carnivorous	0.007	0.010	0.649	0.417	0.000	0.908	0.388	0.009
<i>Syllis</i> sp1	Carnivorous	0.006	0.015	0.439	0.417	0.000	0.917	0.361	0.009
<i>Lysidice unicornis</i> (Grube, 1840)	Carnivorous	0.006	0.009	0.731	0.167	0.333	0.925	0.367	0.008
<i>Chiton canariensis</i> (d'Orbigny, 1840)	Herbivorous	0.006	0.009	0.676	0.500	0.000	0.933	0.625	0.008
Nemertea sp2	Carnivorous	0.005	0.008	0.656	0.000	0.333	0.940	0.194	0.007
<i>Nicidion iongula</i> (Ehlers, 1887)	Carnivorous	0.005	0.008	0.657	0.000	0.333	0.947	0.188	0.007
<i>Ampithoe rubricata</i> (Montagu, 1818)	Herbivorous	0.005	0.008	0.657	0.000	0.333	0.954	0.188	0.007
<i>Eunice</i> sp.	Carnivorous	0.003	0.012	0.297	0.250	0.000	0.958	0.192	0.004
Porifera sp1	Suspensivores	0.003	0.008	0.428	0.167	0.000	0.963	0.370	0.005
<i>Bittium latreillii</i> (Payraudeau, 1826)	Herbivorous	0.003	0.010	0.297	0.167	0.000	0.967	0.204	0.004
<i>Elasmopus canarius</i> (Krapp-Schickel and Ruffo, 1990)	Herbivorous	0.003	0.010	0.297	0.167	0.000	0.971	0.204	0.004
<i>Syllis</i> sp2	Carnivorous	0.003	0.010	0.297	0.250	0.000	0.975	0.205	0.004
<i>Branchiomma bombyx</i> (Dalyell, 1853)	Suspensivores	0.002	0.005	0.440	0.167	0.000	0.978	0.384	0.003
Nematoda sp1	Carnivorous	0.002	0.006	0.297	0.083	0.000	0.980	0.209	0.002
Paraonidae sp1 (Cerruti, 1909)	Detritivores	0.002	0.006	0.297	0.083	0.000	0.982	0.209	0.002
<i>Parapseudes latifrons</i> (Grube, 1864)	Carnivorous	0.002	0.005	0.297	0.083	0.000	0.985	0.204	0.003
<i>Coscinasterias tenuispina</i> (Lamarck, 1816)	Detritivores	0.001	0.004	0.297	0.083	0.000	0.986	0.214	0.001
<i>Botrylloides</i> cf. <i>leachii</i> (Savigny, 1816)	Suspensivores	0.001	0.004	0.297	0.083	0.000	0.988	0.214	0.002
<i>Phascolosoma stephensoni</i> (Stephen, 1942)	Detritivores	0.001	0.004	0.297	0.083	0.000	0.989	0.214	0.001
<i>Dexamine spinosa</i> (Montagu, 1813)	Herbivorous	0.001	0.003	0.297	0.083	0.000	0.991	0.209	0.002
Anthuridae sp1	Carnivorous	0.001	0.003	0.297	0.083	0.000	0.992	0.209	0.001
<i>Asterina gibbosa</i> (Pennant, 1777)	Detritivores	0.001	0.003	0.297	0.083	0.000	0.993	0.209	0.001
<i>Clathrina</i> sp. (Gray, 1867)	Suspensivores	0.001	0.003	0.297	0.083	0.000	0.995	0.205	0.002
Nereididae sp1 (Blainville, 1818)	Carnivorous	0.001	0.003	0.297	0.083	0.000	0.996	0.205	0.001
<i>Syllis</i> sp3	Carnivorous	0.001	0.003	0.297	0.083	0.000	0.997	0.205	0.001
Oligochaeta sp1	Detritivores	0.001	0.003	0.297	0.083	0.000	0.999	0.205	0.002
<i>Gammaropsis</i> sp.	Herbivorous	0.001	0.003	0.297	0.083	0.000	1.000	0.211	0.001

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