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Bi- and three-dimensional fractal analysis of the brown seaweed *Gongolaria montagnei* and their relationship with gastropod molluscs assemblage

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ABSTRACT

Habitat complexity is one of the main influences on biodiversity in marine environments, particularly in coastal areas where foundation seaweeds provide substrate for highly diverse communities. We studied the 2D and 3D fractal dimensions of *Gongolaria montagnei* (Fucales) over the vegetative season and examine their relationship with the abundance, species richness and morpho-functional groups of the gastropod associated. Overall, the 3D fractal analysis method used here better describes seaweeds structural complexity compared to the traditional 2D fractal analysis, as highlighted by the higher relationship with gastropod assemblage associated to the alga in terms of abundance, number of species and morpho-functional groups. We propose this new method as a valuable tool for understanding the relationship between seaweeds and associated fauna, which is critical for gaining a better understanding of the role that algal species play in a specific habitat and the consequences of their loss.

1. Introduction

Habitat complexity is one of the main influences on biodiversity in a wide range of terrestrial, freshwater and marine environments. It can be described as the variation of several physical attributes of the living spaces and structural components (Kovalenko et al., 2012; Loke and Todd, 2016; Velasco-Charpentier et al., 2021). In general, more structurally complex habitats offer a great variety of niches, allowing to support greater species diversity than less complex habitats (Kovalenko et al., 2012; Loke and Todd, 2016; Velasco-Charpentier et al., 2021).

Among marine organisms, seaweeds are valuable foundation species enhancing the complexity and the productivity in coastal areas. They provide food and protection for rich associated biota such as fish, invertebrates and other algae (Schiel and Foster, 2006; Cheminée et al., 2013; Mineur et al., 2015), both as primary and as secondary foundation species (Thomsen et al., 2018). The ability of seaweeds in supporting rich associated communities appeared strictly related to their structural complexity (Christie et al., 2009). Moreover, seasonal variation in algal morphology can represent another crucial factor in shaping their associated fauna (Pitacco et al., 2014; Mancuso et al., 2021). In general, algae with a high structural complexity, expressed as a combination of their physical attributes (e.g. shapes, degree of branching, thallus width and height and wet weight), support a more diverse epifaunal assemblage than those with a simpler morphology (Hacker and Steneck, 1990; Chemello and Milazzo, 2002; Hauser et al., 2006; Hooper and Davenport, 2006; Bitlis, 2019).

Besides common descriptors of the macroalgal complexity, such as biomass, total volume, canopy volume, interstitial volume and algal surface, previous studies showed how fractal dimension can provide an alternative measure of structural complexity (Gee and Warwick, 1994a; Hooper and Davenport, 2006; Veiga et al., 2014, 2016). Fractal dimension provides a numerical expression of complexity relatively easy to calculate, independent of the nature of the habitat and related to the scale at which the habitat is perceived by the size hierarchies of animals which occupy it (Gee and Warwick, 1994a).

Different studies have shown the usefulness of fractal dimension in estimating the complexity of seaweeds (e.g. Gee and Warwick, 1994a; Hooper and Davenport, 2006; Veiga et al., 2014; Rubal et al., 2018). Other authors have highlighted how increasing fractal dimension has been positively related to the diversity of their associated epifauna (Veiga et al., 2014; Ape et al., 2018). Moreover, it has been shown that seaweeds can have different fractal characteristics depending either on

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the parts of the thallus analyzed (Hooper and Davenport, 2006), or on the degree of magnification used to calculate the fractal dimension (Gee and Warwick, 1994a, 1994b). For example, in comparing the fractal dimension of different seaweeds, Gee and Warwick (1994a) discovered that it not only changed between seaweeds species but also decreased with the degree of magnification used to calculate the fractal dimension. Moreover, they discovered that the increase of macroalgal complexity (high fractal dimension) was related with an increase in the diversity of two different size fractions of the epifaunal communities associated with each alga (Gee and Warwick, 1994a, 1994b). The evidence that the fractal dimension changes with the degree of magnification suggests that to better understand the relationship between fractal dimension and the abundance of epifaunal assemblage hosted by the alga, the fractal dimension at the scale equal to the body size of each organism inhabiting the alga must be analyzed.

In the Mediterranean Sea, large brown algae of the group *Cystoseira* sensu *lato* (Fucales, Phaeophyceae) - recently splitted up in the genera *Cystoseira*, *Gongolaria* and *Ericaria* - represent dominant and ecologically key seaweeds on rocky reefs (Orellana et al., 2019; Molinari Novoa and Guiry, 2020). *Cystoseira* sensu *lato* algae are among the most productive and diverse marine foundation species supporting rich associated communities (Steneck et al., 2002; Schiel and Foster, 2006; Cheminée et al., 2013; Mineur et al., 2015; Krumhansl et al., 2016; Coleman and Wernberg, 2017). They are also considered useful indicators of ecosystem quality according to the Water Framework Directive (2000/60) (European Commission, 2000).

Studies have shown that the ability of *Cystoseira s.l.* species to support rich associated communities seems to be regulated by a range of species-specific functional traits such as frond complexity, seasonal variation of the canopy and to the patch size (Chemello and Milazzo, 2002; Chiarore et al., 2019; Mancuso et al., 2021). Among the fauna inhabiting *Cystoseira s.l.* species, molluscs represent one of the main invertebrate groups, usually characterized by high species richness and a large number of trophic guilds (Milazzo et al., 2000; Chemello and Milazzo, 2002; Urra et al., 2013; Pitacco et al., 2014; Lolas et al., 2018; Piazzi et al., 2018; Bitlis, 2019; Chiarore et al., 2019; Poursanidis et al., 2019). Seaweed-associated molluscs have an important role in aquatic ecosystems as consumers as well as preys, and are considered an important food source for higher trophic levels (Martin et al., 1992; Heck et al., 2003). According to studies on the relationship between habitat complexity and meiofaunal assemblages, *Cystoseira s.l.* had greater values of fractal dimension than to surrounding seaweeds, and increasing fractal dimension was positively related to the abundance of the epifaunal assemblage (Ape et al., 2018). However, to our knowledge, no study has explicitly investigated the relationship between the fractal dimension of *Cystoseira s.l.* species and the associated gastropod assemblages.

Most studies that investigate the relationships between seaweeds complexity and associated gastropods use the well-known “taxonomic” descriptors, in which organisms are classified using an attribute (the scientific name) that includes a substantial number of “qualitative” information about the species (e.g., habit or life form). However, the identification of species attributes that are closely related to seaweed complexity features may allow the detection of simple functional descriptors of ecological systems (Russo, 1989). The morpho-functional characteristics of shells and soft parts of gastropods have been demonstrated to be alternative descriptors of functional adaptation to environmental gradients (e.g. wave action) in different habitats (Russo, 1989; Chemello et al., 1997). Shell variables such as aperture shape, spiral rate, spiral expansion, spiral translation rate, and spire distance from the envelopment axis are intercorrelated in determining the degree of shell slenderness, which, along with shell coiling, determines the capability of gastropods to move easily among algal fronds or on substratum (Russo, 1989). Furthermore, the shape of gastropod's foot combined with the degree of shell coiling determines the species' clamping ability, whereas in terms of gastropod speed of displacement, apart from the shape of the foot, the parameters of the shell balance, such as the angle of elevation and that of torsion, must be considered (Russo, 1989). Morphological characteristics of gastropods can therefore affect their distribution on the thallus of *Cystoseira s.l.*, which is composed by different parts (basal part, main axis and branches) whose spatial arrangement provide different substrates with varying degrees of complexity (Chemello and Milazzo, 2002; Mancuso et al., 2021). The gastropods' relationship with substrate is also related to their feeding habits, which are depending on the functional plasticity of their feeding apparatus (Kohn, 1983). As previously stated, a gastropod can spend the most of its time in a specific part of the seaweed or is able to migrate through it. Understanding how different morphological characteristics of gastropods respond to variations in seaweed complexity might lead to the identification of reliable morpho-functional descriptors of gastropods adaptation to variability in habitat complexity.

In this study, we calculated the fractal dimension of *Gongolaria montagnei* var. *tenuior* (Ercegovic) Molinari & Guiry (Molinari Novoa and Guiry, 2020), hereafter *G. montagnei,* coupling a standard 2D method and a novel 3D method. Using associated gastropod assemblages as a model we tested whether the 3D method can be an adequate, or better, proxy for measuring habitat complexity as well as an useful predictor of seaweed-associated invertebrates than the 2D method. We specifically estimated *G. montagnei*'s overall 2D and 3D fractal dimension over a vegetative cycle and tested for differences between the two fractal dimension methods used. Furthermore, we investigated whether there were differences in the fractal dimension of *G. montagnei* by using gastropods' body sizes corresponding to two size classes, minor and major of 2 mm. Finally, we investigated whether variation in algal complexity over a vegetative cycle are related to changes in gastropod response variables (species abundance, species richness, number of morpho-functional groups).

2. Materials and methods

2.1. Study area and algal description

Samples were taken on the shallow rocky shore in the Marine Protected Area (MPA) of “Capo Gallo-Isola delle Femmine”, in Palermo (Sicily, Italy) between May and September 2011 (Fig. 1). The area is mainly exposed to northwestern currents, with rocky carbonates gently sloping down and scattered rocks, providing rocky substrates for well-

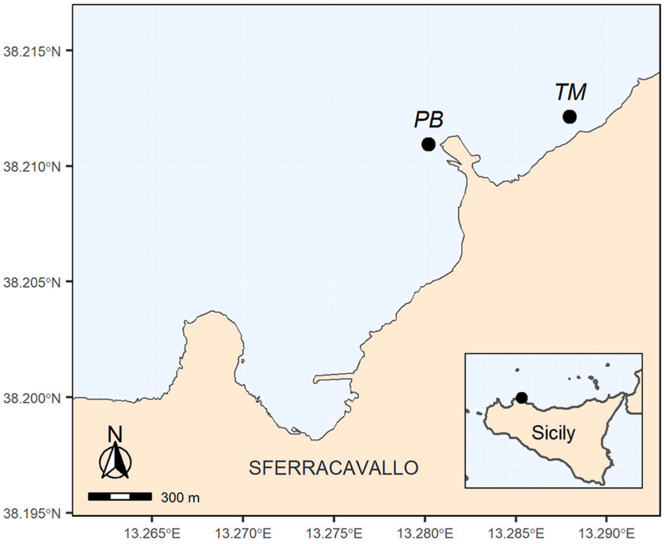


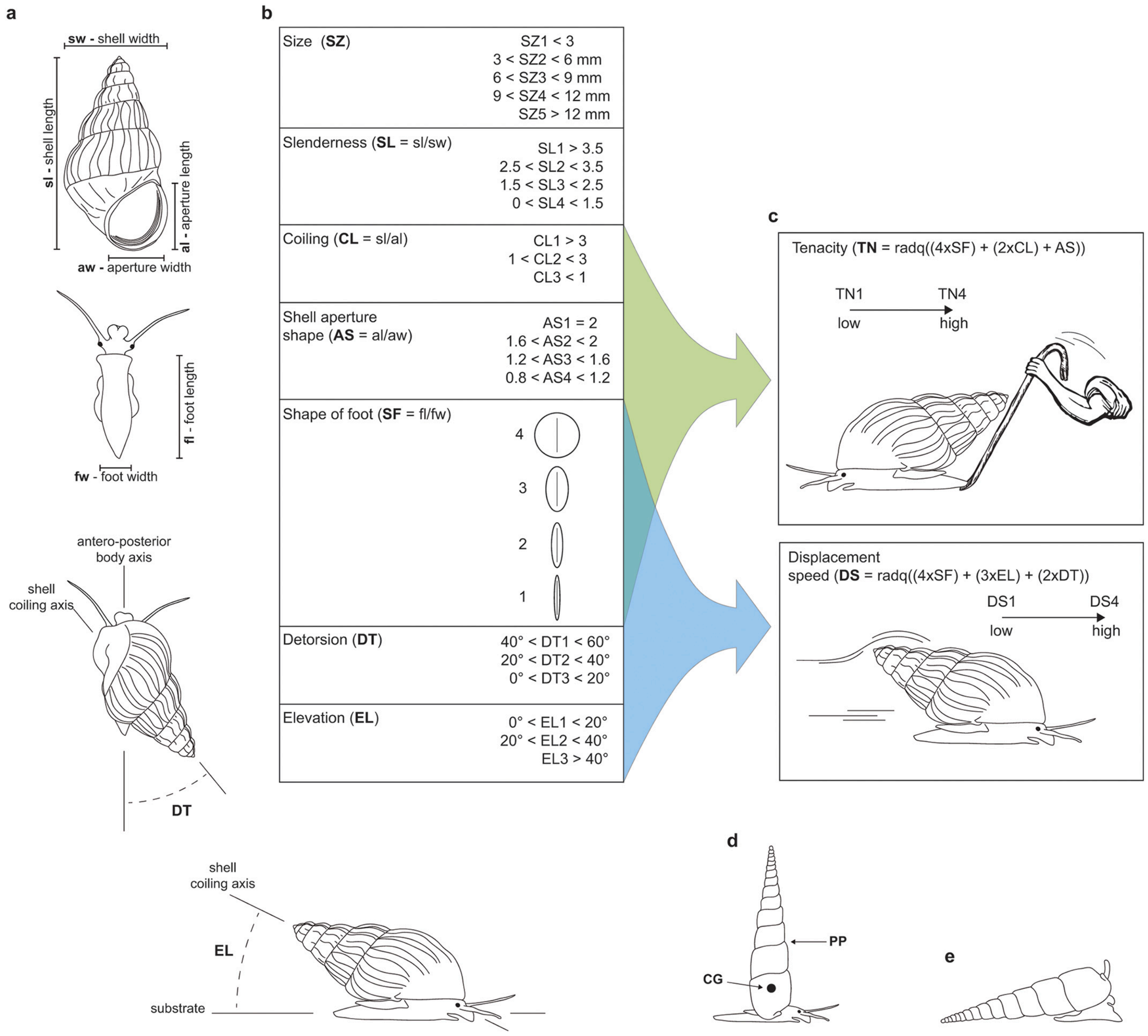
Fig. 1. Location of the two study sites (black dots) at the rocky shore of the Marine Protected Area (MPA) of Capo Gallo-Isola delle Femmine, Palermo, Sicily, Italy. ***PB*** = Punta Barcarello, ***TM*** = Tramontana.

developed seaweed vegetation (Riggio and Raimondo, 1991; Lucido, 1992). The area is characterized by large populations of perennial species of *Cystoseira s.l.* (Mannino and Mancuso, 2009) then we randomly selected two sites, Punta Barcarello and Tramontana, characterized by the presence of easily accessible dense populations of *Gongolaria montagnei*.

Gongolaria montagnei is characterized by a single perennial axis, up to 30–40 cm in height and 3–6 mm in diameter, with a basal disk attached to the substrate. For the upper two-thirds, the axis is densely covered by oblong spinose tophules at the base of the primary branches. The branches of all orders have triangular spinose appendages and are fertile in spring-summer (Gómez-Garreta et al., 2002; Mannino and Mancuso, 2009; Cormaci et al., 2012). Like other species of *Cystoseira s.l.*, *G. montagnei* exhibits marked seasonal variations in vegetative growth (Gómez-Garreta et al., 2002). At the study sites, *G. montagnei* develops new branches from the perennial axis in April reaching their maximum size in May, providing a new substratum and shelter for the associated assemblage. At the end of July and early August thalli are usually covered by epiphytes, while the fronds of *G. montagnei* start to degrade. In September–October, *G. montagnei* loses almost the totality of its upright branches, leaving a perennial axis that remains in a quiescent state throughout the cold winter season.

2.2. Sampling and gastropods analysis

Sampling was carried out at a depth of 6–7 m (Fig. 1) in three different morphological phases of the alga: maximum size (May), degrading phase (August) and quiescent state (September). For each site and algal morphological phase, 6 isolated thalli of *G. montagnei* were collected with their associated fauna by an airlift sampler supplied with 500 μm nylon mesh bag (Bianchi et al., 2004). Seaweeds were gently scraped out of the substrate using a hammer and chisel and sucked up by



Size (**SZ**)	SZ1 < 3 3 < SZ2 < 6 mm 6 < SZ3 < 9 mm 9 < SZ4 < 12 mm SZ5 > 12 mm
Slenderness (**SL** = sl/sw)	SL1 > 3.5 2.5 < SL2 < 3.5 1.5 < SL3 < 2.5 0 < SL4 < 1.5
Coiling (**CL** = sl/al)	CL1 > 3 1 < CL2 < 3 CL3 < 1
Shell aperture shape (**AS** = al/aw)	AS1 = 2 1.6 < AS2 < 2 1.2 < AS3 < 1.6 0.8 < AS4 < 1.2
Shape of foot (**SF** = fl/fw)	4 3 2 1
Detorsion (**DT**)	40° < DT1 < 60° 20° < DT2 < 40° 0° < DT3 < 20°
Elevation (**EL**)	0° < EL1 < 20° 20° < EL2 < 40° EL3 > 40°

Fig. 2. Morphological characters (**a**) and descriptors (**b**) used to assign a morpho-functional group to each gastropod. Panel (c) show how tenacity and displacement speed were calculated, while (**d**) show the height of the shell center of gravity (CG) and pressure point (PP), while (**e**) illustrate a "shell draggers". Illustration based on Fig. 1 from Russo (1989) and Fig. 4 from Chemello et al. (1997).

the airlift, then the mesh bag was immediately closed. In the laboratory, each thallus of *G. montagnei* was transferred into buckets filled with sea water and gently shaken, allowing the associated fauna to detach from the algae. The thalli were subsequently observed under a microscope to collect specimens without the dropping-off escape tactic (Watanabe, 1983). The water was then sieved through a 1 mm mesh. Molluscs were separated from the other fauna. Living gastropods were used to gather morpho-functional features (see measurement details in the following section), after which they were stored in a 70 % ethanol/seawater. Gastropods were subsequently counted and identified at species or at nearest possible taxonomic level. Juvenile gastropods were excluded from the analysis because their developmental stage precludes them from being assigned to a distinct morpho-functional group. Taxonomy and nomenclature were updated according to the World Register of Marine Species database (see http://www.marinespecies.org, accessed June 2022).

2.3. Gastropods' morpho-functional characters

Each gastropod individual was classified into a morpho-functional group using a series of morphological descriptors according to Russo (1989) and Chemello et al. (1997): size (SZ), slenderness (SL), coiling (CL), shell aperture shape (AS), foot shape (SF), detorsion (DT) and elevation degree (EL). These morphological descriptors were measured on living specimens and obtained from different measures of the gastropods' shell and the foot and then categorized into rank classes (Fig. 2 a, b). Three individuals from each species were placed in a petri dish filled with sea water and observed under a microscope with a micrometric eyepiece and camera. Each gastropod's morphometric characteristics were quantified using photographs taken with a reference scale. For species with less than three specimens, only available individuals were measured.

Size (SZ) distinguishes gastropods based on shell length (mm). Slenderness (SL) is calculated as the ratio between shell length (sl) and shell width (sw), and it is classified into four rank classes, with SL1 representing more slenderness and SL4 representing lesser slenderness (Fig. 2 a, b). The degree of shell coiling (CL) is calculated as the ratio of the shell's length (sl) over its aperture length (al) (Fig. 2 a, b). It is classified into three rank classes, with CL1 indicating higher shell coiling and CL3 indicating lesser shell coiling. Both SL and CL have an effect on a gastropod's ability to move among the fronds of an alga and to resist to water flow. Gastropods with low SL and CL may move more easily through the algal fronds than those with high SL and high CL. Shell aperture shape (AS) is determined by ratio between the length (al) and width (aw) of the shell aperture, and it is classified into four rank classes, with AS1 and AS4 signifying smaller and larger shell apertures respectively (Fig. 2 a, b). The shape of the foot (SF) is valued by the ratio of foot length (fl) over foot width (fw) and is classified into four classes, with SF1 representing taxa with long and narrow (oblong) feet and SF4 representing species with circular feet (Fig. 2 b). The shape of a gastropod's foot influences its adhesive strength, speed, and displacement along the thallus or on the substratum (Ponder et al., 2019). Gastropods with oblong feet could move easily among tiny branches of algae, but they have low adhesivity strength and velocity (Russo, 1989). In contrast, gastropods with circular feet require a bigger surface to move on (e.g., the basal portion or the main axis of the alga) but they have great adhesive strength and higher speed (Miller, 1974). From the previously given characteristics, two morpho-functional descriptors are obtained, namely tenacity (TN) and displacement speed (DS). Tenacity (TN) is estimated from SL, AS and SF and determines the property to remain adherent to an algae substrate when disturbed by an external force such as wave motion. It is divided into four rank classes, with TN1 indicating low tenacity and TN4 indicating greatest tenacity (Fig. 2 b, c). Displacement speed (DS) determines a gastropod's velocity on a substratum and is calculated from SF and two other characteristics: detorsion and elevation (Fig. 2 c). Detorsion (DT) is the angle formed by the shell coiling axis and the gastropods' antero-posterior body axis, whereas elevation (EL) is the angle formed by the shell coiling axis and the substrate (Fig. 2 a, c). DT and EL help gastropods maintain their gravitational stability (or shell balance).

Aside from the area of the frontal shell section, other important factors that may contribute to the gastropod's velocity include the height of the shell center of gravity (CG) and the height of the pressure point (PP) (Fig. 2 d, e). Gastropods with a small frontal shell section, a low CG and a low PP can move quickly. Moreover, the shape of foot and coiling determine the degree of fixation to the substrate of gastropods (their clamping capacity). In particular, in the low-spiralled shells the position of the retractor muscle allows gastropods to easily keep the shell against the substrate (even when the gastropod is on vertical surfaces or is upside down) since the muscle can pull easily the shell in a straight line. In high-spiralled shells, however, the retractor muscle must bend quite sharply between the insertion on the columella and the foot; this means that, especially when the animal is on vertical surfaces, or even turned upside down, gravity pushes the coil down and the muscle is not well positioned to counterbalance it (Russo, 1989). With the increase of coil's length, the elevation decreases and the shell is balanced through the detorsion. As a result, the area of the frontal shell section, as well as the height of the shell center of gravity (CG) and pressure point (PP), gradually decrease, resulting in an increase in the hydrodynamics of the shell and, consequently, increase in the speed of displacement. If the coil is too long, the CG moves too far away from the shell aperture, the elevation becomes zero, and the shell aperture and the pedal muscle take on an elongated shape. As a result, gastropods have some difficulty keeping the shell on the pedal mass, which is then dragged on the substrate, slowing the organisms. These gastropods are referred to as “shell draggers” (Fig. 2 e) (Russo, 1989).

Species living in the algal canopy should be small in sized, with a slender shell and a long and narrow foot. Shell size and slenderness, as well as foot shape and dimensions, may be irrelevant for gastropods dwelling on the thallus. The presence of oblong spinose tophules in *G. montagnei*, on the other hand, can increase substratum complexity, favoring small gastropods with long, thin feet. Finally, gastropods that live on the basal section of the algae should have a large round foot (similar to *Patella* sp.) that allows the gastropod to remain tight to the algae. In this case, shell size is irrelevant.

2.4. Estimation of bi- and three- dimensional fractal dimension

In order to calculate the fractal dimension, each thallus of *G. montagnei* was placed on a plastic graph paper (28 × 38 cm) and photographed using a digital camera mounted on a copy-stand, so that the plane of the camera was parallel with the plastic graph paper (Fig. S1). A focal length of 50 mm was used to reduce the lens distortion. The pictures were elaborated by the open source GNU Image Manipulation Program (GIMP) (The GIMP Development Team, 2020) as follow. Firstly, the images were scaled into a 1:1 ratio and the background was removed. Then, the images were converted into black and white by the function threshold and saved in Joint Photographic Experts Group (*.jpg) format (Fig. S1). Then, the bi-dimensional fractal dimension (D_{2D}) of each thallus of *G. montagnei* was calculated using the “fract2D” function in the “fractD” R-package (https://CRAN.R-project.org/package=fractD).

To estimate the fractal dimension of the three-dimensional surface of *G. montagnei*, layers of the thallus were made as follow. Each thallus of *G. montagnei* was placed in a white plastic box with a graduated (±5 mm) wall. The box was filled up with a white liquid every 5 mm and a picture of the thallus was made as described before until it was completely covered by the liquid. Then, the liquid was removed from the box, the thallus flipped and the procedure was repeated for the other half of the thallus in order to get image slices of the entire thallus of *G. montagnei*. The images were elaborated in GIMP as described before. Finally, the three-dimensional fractal dimension (D_{3D}) of *G. montagnei* was estimated using the "fract3D" function in the "fractD" R-package (https://CRAN.R-project.org/package=fractD).

The package fractD estimates the fractal dimension (D) through the box-counting method (Klinkenberg, 1994). Box-counting method is useful to calculate the fractal dimension of various sets of any dimension and patterns with or without self-similarity (Klinkenberg, 1994). The method overlay a series of squares (for fract2D) or cubes (for fract3) of different sizes. Then, for each size-step the functions keep track of the number of squares or cubes occupied by the black area into the image. Finally, the fractal dimension (D) is estimated by linear regression of log (n°boxes) on log(box.size) (https://CRAN.R-project.org/package=fractD).

2.5. Data analyses

The gastropods assemblage was characterized according to the total abundance of individuals (N) and the total number of species (S). A two-way analysis of variance (ANOVA) was used to test differences in the values of N and S between algal morphological phases (fixed and orthogonal with 3 levels: maximum size, degrading phase, and quiescent state) and sites (random and orthogonal with 2 levels: Punta Barcarello and Tramontana). Cochran's test was used to check for the homogeneity of variances (Underwood, 1996). Student-Newman-Keuls (SNK) procedure was used to separate means (at $\alpha = 0.05$) following significant effects in the ANOVAs (Underwood, 1996).

Cluster analysis was used to classify each gastropod into the different morpho-groups. The analysis was based on a Euclidean distance matrix of normalized morphological descriptors (SZ, SL, TN and DS). Then, a dendrogram was made to display the results using a hierarchical agglomerative clustering with group averaging.

Bi- (D_{2D}) and three- (D_{3D}) dimensional fractal dimension were estimated with the following step size: 1, 2, 4, 6, 8, 16, 32, 64, 128, 256 and 512 pixels. These steps corresponded to 0.25 to 128 mm of the real length. Moreover, D_{2D} and D_{3D} were calculated for the step size corresponding to the organisms' $Sz < 2$ mm (step size = 4, 5, 6, 7 and 8 pixels) and $Sz > 2$ mm (step size = 8, 16, 32, 64 and 128 pixels).

A two-way analysis of variance (ANOVA) was used to test differences in both D_{2D} and D_{3D} following the model described before. Moreover, a three-way analysis of variance (ANOVA) was used to test differences in both D_{2D} and D_{3D} between organisms' size range (fixed and orthogonal with 2 levels: $Sz < 2$ mm and $Sz > 2$ mm), algal morphological phases (fixed and orthogonal with 3 levels: maximum size, degrading phase, and quiescent state) and sites (random and orthogonal with 2 levels: Punta Barcarello and Tramontana).

Linear regression (LM) analysis was used to test which fractal dimension (D_{2D} and D_{3D}) explained better the variation of the abundance (N), species richness (S) of the gastropod assemblage.

Statistical analyses were performed in R software 3.5.1 (R Core Team, 2018). See the "*Data availability and reproducible research*" section for further details.

3. Results

3.1. Gastropods assemblage

A total of 425 individuals belonging to 33 taxa made up the gastropods assemblage associated to *G. montagnei*. All these taxa belonged to 17 families mostly represented by Rissoidae (15 %), Costellariidae (9 %) and Cystiscidae (9 %) (Tables S1–S2). At the species levels, *Barleeia unifasciata* (Montagu, 1803) was the dominant taxon (24 % of the total individuals) followed by *Alvania lineata* (Risso, 1826) with 12 % (Tables S1–S2).

Total abundance (**N**) and species richness (**S**) showed not significant variations between different algal morphological conditions, while their values differed significantly between sites (Fig. S2, Table S3). On average total abundance tended to increase from the maximum size to the degrading phase of the alga, while the number of species remained constant (Fig. 3).

3.2. Gastropods' morpho-functional characters

The gastropods assemblage of *G. montagnei* was clustered into 4 morpho-functional groups (**a–d**) (Fig. 4 a). The morpho-group ***a*** included 8 species belonged to the genera *Columbella, Cyrillia, Conus, Episcomitra, Mitrella, Muricopsis,* and *Rissoa* (Fig. 4 a). These genera are characterized by species with low tenacity, and low displacement speed (Fig. 4 b). The morpho-group ***b*** is composed by 13 species of the genera *Monophorus, Bittium, Marshallora, Alvania, Rissoina, Pusia, Mangelia, Barleeia* and *Tricolia* are distinct to the other taxa for a low slenderness and relatively high tenacity (Fig. 4 a, b). The morpho-group ***c*** made by 6 species belonged to *Tritia, Calliostoma, Jujubinus, Aplus* and *Trivia,* which are distinct to the other taxa for a relatively large size and low slenderness and high displacement speed (Fig. 4 a, b). Finally, the morpho-group ***d*** composed by 6 taxa belonged to *Tectura, Gibbula, Gibberula* and *Granulina* all are characterized by small sizes and very low slenderness (Fig. 4 a, b).

The morpho-functional group ***b*** was the most abundant across different algal morphological conditions (~56 %) with values that were higher in autumn (Fig. 4 c). The morpho-functional group ***a*** was the second in terms of relative abundance (~30 %) and showed higher values during the degrading phase of the alga, while the morpho-functional groups ***c*** and ***d*** were always the less abundant (<15 %) (Fig. 4 c).

3.3. Fractal dimension of G. montagnei and relationship with associated gastropods and their morpho-functional groups

Bi- and three-dimensional fractal dimension (D) of *G. montagnei* changed significantly across the different algal morphological conditions, with values that tended to be higher at the maximum size/degrading phase of the alga and lower in the quiescent state (Fig. 5, Table S4). D_{2D} ranged on average from 1.76 in the maximum size to 1.64 in the quiescent state, while D_{3D} varied from 2.52 in maximum size and 2.46 in quiescent state (Fig. 5, Table S4).

Overall, D_{3D} explained better the variation of the abundance and species richness of the molluscan assemblage inhabiting *G. montagnei*

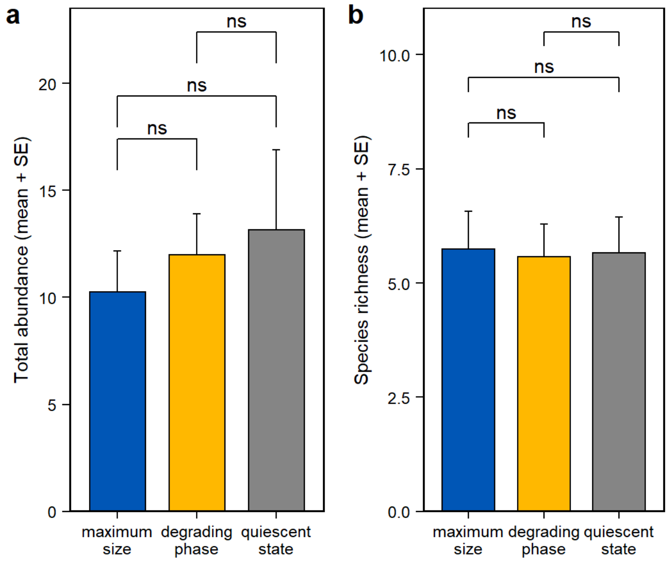


Fig. 3. Variation of the abundance (a) and species richness (b) of the gastropods assemblage associated with *G. montagnei* across different morphological conditions. Bar plots show mean + standard error ($n = 6$), $p \geq 0.05$ ns. See Table S3 for more details.

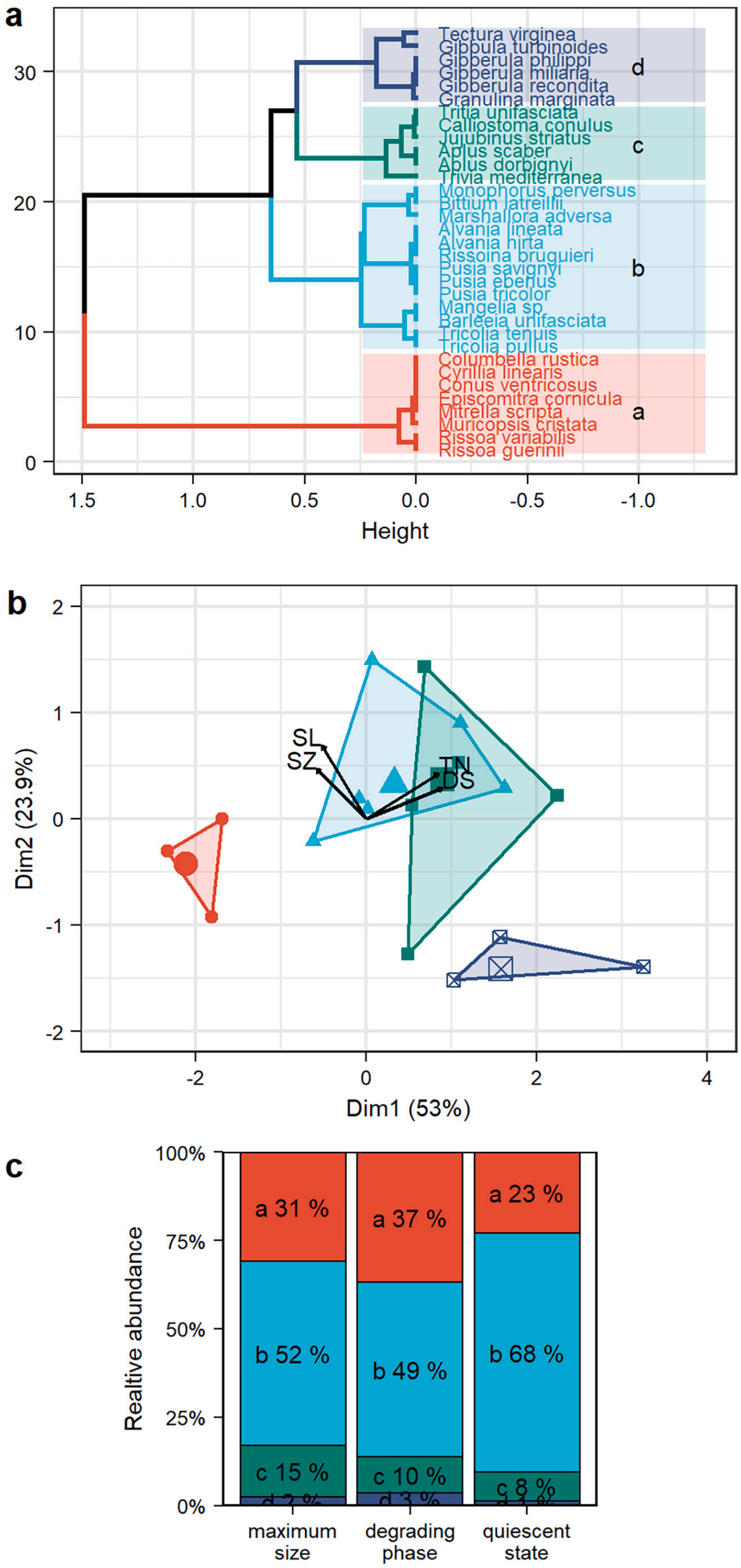


Fig. 4. The four gastropods' morpho-functional groups (a–d) identified in this study. Results of cluster analysis (a), the relationship between the four morpho-groups and the morphological descriptors (b), and variation in the abundance of the four morpho-functional groups across different algal morphological conditions (c). Red = morpho-functional group a; blue = morpho-functional group b, green = morpho-functional group c and violet = morpho-functional group d. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

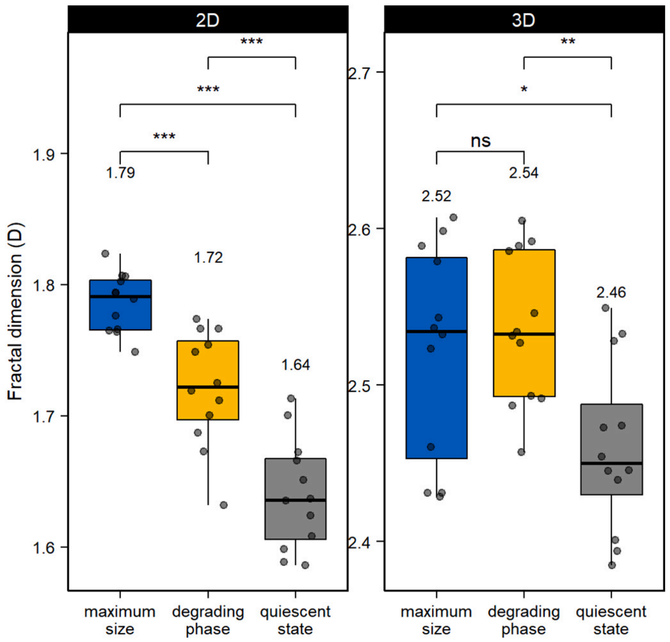


Fig. 5. Variation of bi- (D_{2D}) and three- (D_{3D}) dimensional fractal dimension of *G. montagnei* over different algal morphological conditions. Average fractal dimension is shown above boxplots. Significant differences (*t*-test) between seasons are shown above the plots (see Table S4 material for more details). $p < 0.001$ ***, $p < 0.05$ *, $p \geq 0.05$ ns.

compared to D_{2D} (Figs. 6, S3). When the alga is on its maximum size, D_{3D} explained 72 % and 79 % of the variation of both gastropods' abundance and species richness respectively. These relationships tend to decrease during the degrading phase ($D_{3D\text{-}N}$ = 37 %, $D_{3D\text{-}S}$ = 48 %) and the quiescent state ($D_{3D\text{-}N}$ = 22 %, $D_{3D\text{-}S}$ = 30 %) (Figs. 6, S3). Conversely, when the alga is in its maximum size D_{2D} explained the 29 % of the variation of gastropods' abundance and the 21 % of the variation of species richness (Figs. 6, S3). During the degrading phase no relationship was discovered between D_{2D} and gastropods variables, while in the quiescent state D_{2D} explained the 16 % of abundance and 10 % of species richness (Figs. 6, S3).

The fractal dimensions (D) of *G. montagnei* were examined for the step length corresponding to animal body sizes <2 mm and >2 mm (Fig. 7). Overall, for Sz < 2 mm, *G. montagnei* was more complex (D_{2D} = 1.86; D_{3D} = 2.75) compared to the step sizes corresponding to the organism's size >2 mm (D_{2D} = 1.66; D_{3D} = 2.41) (Fig. 7). In addition, at a smaller scale (from 1 to 2 mm) values of fractal dimension were comparable across the different algal morphological conditions. Conversely, for organisms >2 mm the fractal dimension changed significantly across the algal morphological phases, with values that tended to decrease from the degrading phase to the quiescent state of the alga (Fig. 7, Table S5).

The relationship between fractal dimension (both D_{2D} and D_{3D}) by individual size was weaker for gastropods between Sz < 2 mm and Sz > 2 mm (Figs. 8, S4). Overall, the D_{3D} explain a larger part of variation compared to D_{2D}, unless in some morphological conditions. During the maximum size of the alga, for gastropods of S < 2 mm, D_{3D} explained 40 % and 39 % of the molluscan abundance and species richness respectively, while no relationship with D_{2D} was found (Figs. 8, S4). During the degrading phase of the alga, no relationship with gastropods was found for both 2D and 3D fractal dimension, while in autumn the D_{2D} explained a larger variation of the abundance (39 %) and species richness (40 %) compared to D_{3D} (R^2_N = 29 %, R^2_S = 31 %). On the other hand, for gastropods >2 mm, during the degrading phase and quiescent state of *G. montagnei*, D_{3D} explained a larger part of variation compared to D_{2D}, either for the abundance ($R^2 = 0.22$, $R^2 = 0.31$) that for species richness ($R^2 = 0.19$, $R^2 = 0.34$) of the gastropods associated with *G. montagnei* (Figs. 8, S4). Conversely, when *G. montagnei* was on its maximum size the variation of gastropods >2 mm were more related with D_{2D} than D_{3D} (Figs. 8, S4).

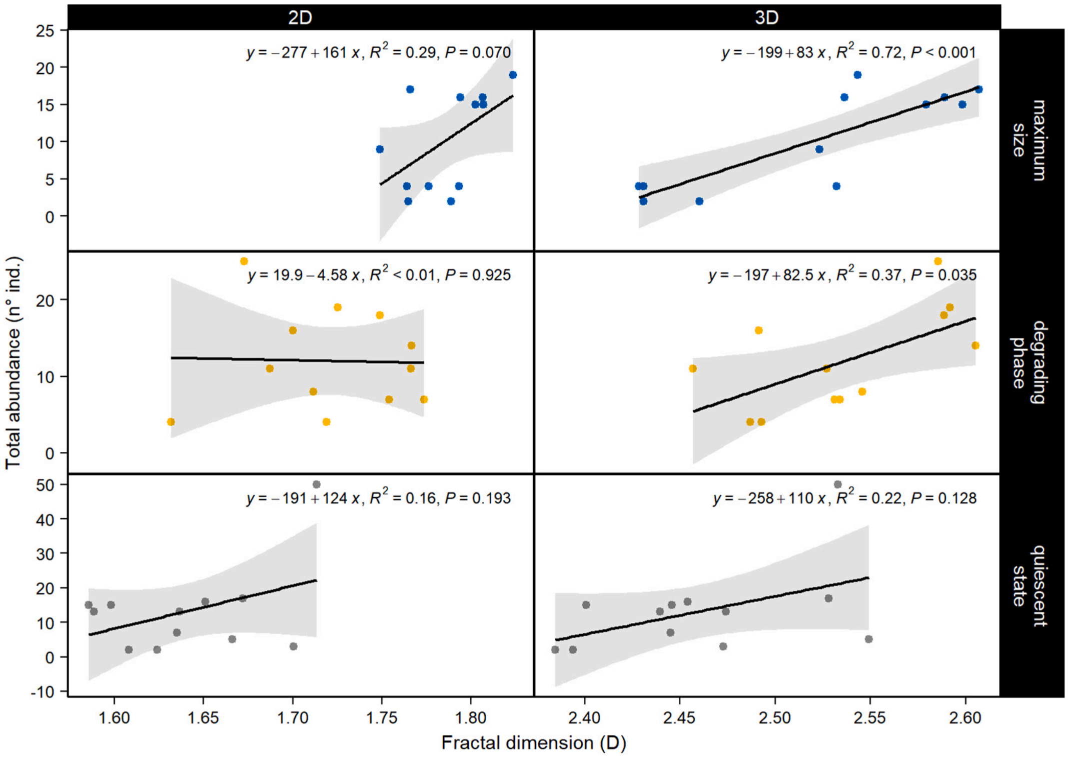


Fig. 6. Relationship between the abundance (N) of the gastropods' assemblage and the bi- (D_{2D}) and three- (D_{3D}) dimensional fractal dimension of *G. montagnei* across the different algal morphological conditions. Grey area shows 95 % confidence interval.

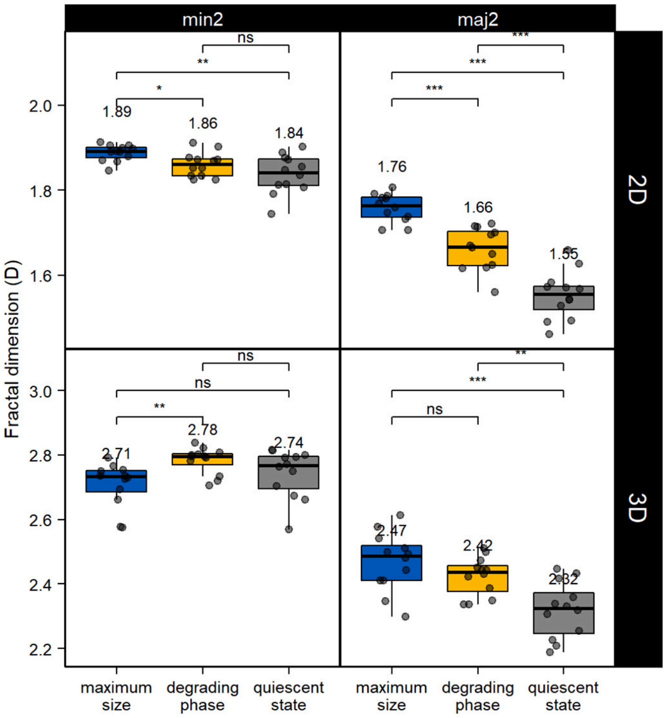


Fig. 7. Variation of bi- (D_{2D}) and three- (D_{3D}) dimensional fractal dimension of *G. montagnei* over the different algal morphological conditions and between animal body-size. Average fractal dimension is shown above boxplots. Significant differences (*t*-test) between seasons are shown above the plots (see Table S5 material for more details).

Fractal dimension (both D_{2D} and D_{3D}) was also related to the abundance of morpho-functional groups (Fig. 9). Overall, more complex thalli were associated to higher number of morpho-groups, however, the D_{3D} explained a larger part of variation compared to D_{2D} (Fig. 9).

4. Discussion

The structural complexity of seaweeds has been proven to play an important role in shaping marine assemblages. Most of the studies done so far, however, used biomass, total volume, canopy volume, interstitial volume, and algal surface as main descriptors of macroalgal complexity (Hacker and Steneck, 1990; Chemello and Milazzo, 2002; Jormalainen and Honkanen, 2008; Pitacco et al., 2014; Veiga et al., 2014; Bitlis, 2019; Chiarore et al., 2019; Mancuso et al., 2021), while few studies investigated the role of fractal dimension as a proxy for seaweed complexity (Gee and Warwick, 1994a, 1994b; Davenport et al., 1996; Hooper and Davenport, 2006). Moreover, these studies used fractal dimension on macroalgae in a bi-dimensional way, while, to our knowledge, the role of 3D fractal dimension in seaweeds have not been explored yet. Our findings indicate that *G. montagnei* has high structural complexity, as shown by high fractal dimensional values, which evolves over time, indicating the importance of this alga as foundation species. Moreover, we found not only that fractal dimension is a good descriptor of *G. montagnei* complexity across the different morphological phases of the alga, but also that 3D fractal dimension represents better the seaweed complexity compared to the 2D method, as shown by the higher variance explained by D_{3D} on the abundance and species diversity of associated fauna compared to D_{2D}. Our results show that the gastropods associated with *G. montagnei* clustered in four different morpho-functional groups based on their morphological characteristics.

4.1. Gastropods

G. montagnei hosted a diversified gastropods' assemblage over its vegetative cycle, being mostly represented at family level by Rissoidae followed by Costellariidae and Cystiscidae, supporting results from other studies where *Cystoseira s.l.* species seems to be able to support rich and diverse gastropods assemblages (Milazzo et al., 2000; Chemello and Milazzo, 2002; Pitacco et al., 2014; Chiarore et al., 2017, 2019; Lolas et al., 2018; Piazzi et al., 2018; Bitlis, 2019; Mancuso et al., 2021). At the species level, most of the taxa were the same found on other species of

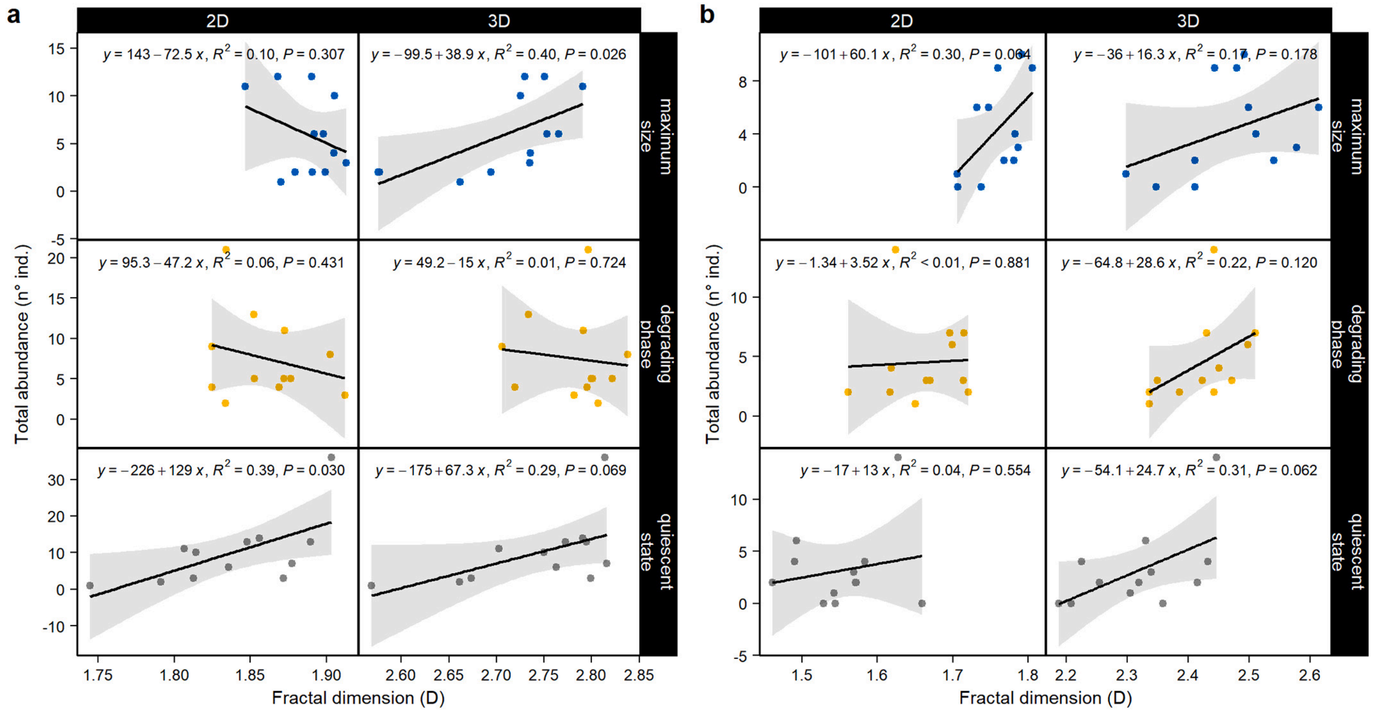


Fig. 8. Relationship between the abundance (N) of the gastropods' assemblage smaller (a) or larger (b) than 2 mm and the bi- (2D) and three- (3D) dimensional fractal dimension of *G. montagnei* across different algal morphological conditions. Grey area shows 95 % confidence interval.

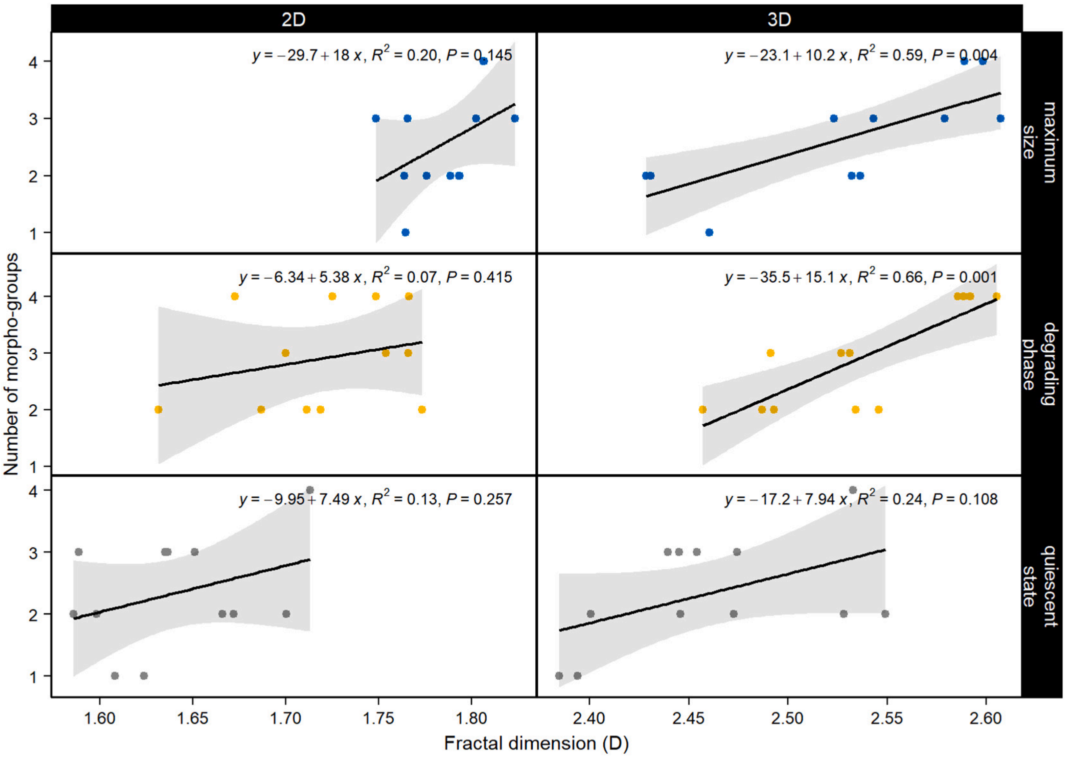


Fig. 9. Relationship between the number of morpho-functional groups of the gastropods' assemblage and the bi- (D_{2D}) and three- (D_{3D}) dimensional fractal dimension of *G. montagnei* across the different algal morphological conditions.

Cystoseira s.l. (Chemello and Milazzo, 2002; Pitacco et al., 2014; Chiarore et al., 2017, 2019; Lolas et al., 2018; Piazzi et al., 2018; Bitlis, 2019; Mancuso et al., 2021), with *Barleeia unifasciata* and *Alvania lineata* being the dominant species.

4.2. Gastropods morpho-functional characters

Our results indicate that gastropods are more likely to prefer a certain portion of *G. montagnei* due to their ability to adapt to seaweeds' substrate features (e.g. shape or complexity degree). This ability is achieved through a combination of morphological traits of their shell and foot, resulting in a particular morpho-functional group capable of adapting to specific environmental variables. Moreover, we assume that the selection of morpho-functional groups by different parts of the alga is related not only to the algal substrate properties, but also to the possible exposure to external environmental variables. When *G. montagnei* is on its quiescent state, for example, we noticed an increase in gastropods with high tenacity and low slenderness. High tenacity allows gastropods to easily stick to the substrate provided by the main axis of *G. montagnei* (the predominant algal substrate left during this season) and resist external perturbations such as water movement (Russo, 1989; Chemello et al., 1997). Then, even if much of the seaweed's substrate is reduced, exposing its inhabitants to more stressful physical conditions, the gastropods that persist in autumn have functional characteristics (e.g. small gastropods with high tenacity) that allow them to live on what is left of the alga as substrate. To the best of our knowledge, our findings provide the first evidence of a relationship between different morphological features in algal substrate and the morpho-functional characteristics of associated molluscs, and we recognized the ability of these descriptors in clarifying the relationships between seaweeds and their associated malacofauna (Russo, 1989; Chemello et al., 1997).

4.3. Fractal dimension of G. montagnei

Overall, the fractal dimension of *G. montagnei* (both D_{2D} and D_{3D}) changed across the different algal morphological conditions with higher values during the maximum size and degrading phase of the alga compared to the quiescent state. The low values found during the quiescent state can be explained by the fact that *G. montagnei* during this algal morphological phase lacks almost all of its upright branches, leaving a perennial axis that persists in a quiescent state during the cold winter season. The branches of *G. montagnei* have triangular spinose appendages that give the algal fronds a complex geometrical pattern. The axis of *G. montagnei*, on the other hand, is less complex, despite being covered for the upper two-thirds by oblong tophules. Then, we suggest that the loss of *G. montagnei* branches reduces macroalgal complexity, which is reflected by low values of fractal dimension.

Although the use of fractal dimension as descriptors of habitat complexity in natural environment was introduced decades ago (Sugihara and May, 1990), studies aimed to explore the fractal dimension of marine seaweeds are still scarce (e.g. Gee and Warwick, 1994a; Hooper and Davenport, 2006; Veiga et al., 2014, 2016) while no studies, to our knowledge, have been done on *Cystoseira s.l.* species. For these reasons, we were unable to directly compare the fractal values found in this study with other studies on *Cystoseira s.l.* species. However, when compared to other seaweeds, *G. montagnei* exhibited fractal values similar to *Bifurcaria bifurcata* R. Ross, *Sargassum muticum* Yendo (Fensholt), *Chondrus crispus* Stackhouse and *Cladophora rupestris* (Linnaeus) Kutzing (Hooper and Davenport, 2006; Veiga et al., 2014, 2016).

The analysis of fractal dimension per organisms' body-size revealed that *G. montagnei* was more complex (high values of D_{2D} and D_{3D}) at the magnification levels of gastropods with Sz < 2 mm compared to those >2 mm. These differences were evident during each morphological algal condition. These results are consistent with previous research showing that the same seaweed species may exhibited different fractal values according to the degree of magnification (length of organism body-size) used to estimate fractal dimension (Gee and Warwick, 1994a, 1994b). Gee and Warwick (1994a, 1994b), for example, demonstrated that the fractal dimension of four distinct seaweeds decreased as the degree of magnification used to calculate the fractal dimension increased.

Therefore, their findings suggest that the complexity of seaweeds decreases for smaller organisms. In contrast, our results showed that the fractal dimension increased with the degree of magnification. This suggests that the thallus of *G. montagnei* provides a more complex habitat for organisms with Sz $<$ 2 mm than those $>$2 mm. Once again, we believe that this aspect can be explained by considering the morphology of the alga. In particular, the triangular spinose appendages on the branches of *G. montagnei* are placed so close to each other that organisms $>$2 mm cannot perceive them, while smaller organisms are likely to use majority of the branches' surface to move (Fig. 10). Interestingly, we observed a variation of both bi- and three-dimensional fractal dimension during the different algal morphological phases for values of D corresponding to gastropods $>$2 mm, while for species between 1 mm and 2 mm D remained nearly constant throughout algal stages. This aspect led to hypothesize that algal morphological variation in fractal dimension could primarily affect the fraction of molluscs $>$2 mm.

Although the current study focuses on the differences in morphological stages of *G. montagnei* that occur during the vegetative cycle, we recognize that the lack of comparison between different algal species may limit the generalization of our findings, making this aspect an intriguing extension of the current study. However, we believe that, as compared to the traditional 2D fractal method, the 3D fractal analysis proposed here can better describe differences in structural complexity across different *G. montagnei* morphological conditions, as well as explain a larger variation of gastropods associated. This bodes well for the effectiveness of applying the new proposed method in comparing the structural complexity of different algal species.

4.4. Relationship between fractal dimension of G. montagnei and its associated gastropods

Fractal dimension was related to the variation of both abundance and species richness of the gastropods inhabiting the frond of *G. montagnei*. The relationships changed across the different algal morphological conditions, as well as between D_{2D} and D_{3D}. Overall, D_{3D} explained a larger part of the variation of the gastropods' abundance and species richness than D_{2D}. The relationship between D_{3D} and the gastropods assemblage was higher during the maximum size of the alga and decreased during the degrading phase and the quiescent state. Other studies have shown that macroalgal complexity is related to the variation of associated epifauna (Hacker and Steneck, 1990; Chemello and Milazzo, 2002; Hauser et al., 2006; Hooper and Davenport, 2006; Bitlis, 2019). In terms of fractal dimension, different authors have demonstrated that seaweeds with high fractal values hosted a more abundant and diverse associated epifauna (Gee and Warwick, 1994a; Hooper and Davenport, 2006; Veiga et al., 2014). Our results support these finding and highlight how the relationship between the fractal dimension of *G. montagnei* and the associated gastropods changed over the algal vegetative cycle. However, as opposed to D_{2D}, D_{3D} seems to better explain the variation of gastropods across the algal vegetative cycle. We hypothesize that the greater variation explained by D_{3D} indicates that a three-dimensional approach will provide a more accurate indication of algal complexity.

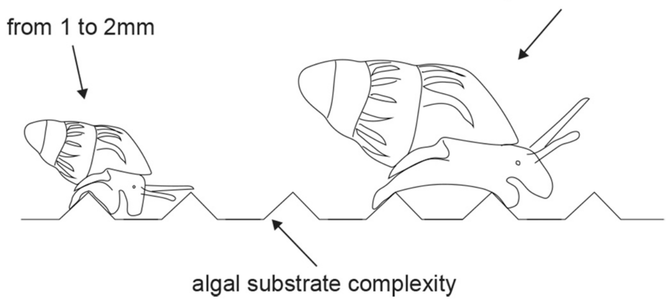


Fig. 10. Gastropods' substrate perception change with the body-size of the organism.

Interesting, fractal dimension was also related to the number of morpho-functional groups present on *G. montagnei*. Complex thalli of *G. montagnei* hosted a higher number of morpho-functional groups, indicating that complexity play an important role also in supporting well-structured gastropods assemblage.

In conclusion, we confirm the role of *G. montagnei* in supporting a diverse gastropods assemblage and the role of macroalgal complexity in shaping its associated gastropods assemblage. In this regard, fractal dimension has been shown to be a strong descriptor of the seaweeds structural complexity. In addition, although the bi-dimensional fractal dimension analysis was the most widely used method in previous studies, we believe that the three-dimensional approach used in this study would provide a more accurate indication of the algal complexity. However, due to the impossibilities of comparing our data with other studies, further application of D_{3D} to other seaweeds would help to validate the methodology used in this study. Our findings also demonstrate that macroalgal complexity can modulate its associated gastropod assemblage based on functional morphological characteristics, emphasizing the importance of including gastropod morpho-functional groups in understanding the relationships between gastropods and algal substrate. Finally, we suggest that a more holistic approach that considers not just morpho-functional features but also the species' life cycle and relationship with the algal substrate is required to better understand the relationships between algal substrate and associated gastropods.

A thorough understanding of all the characteristics and mechanisms provided by a specific habitat is a must for its conservation (De La Fuente et al., 2019). Knowledge of the ecosystem services provided by a given foundation species, for example, can help not only to raise social awareness about the habitat, but also to understand its economic value and to estimate how much its loss can affect local biodiversity at different spatial and temporal scales (Beaumont et al., 2008; Lee and Lautenbach, 2016). In this context, the new method for estimating the 3D fractal dimension of seaweeds introduced here can better represent the species' structural complexity than the traditional 2D method (as highlighted by the higher relationship with gastropod assemblage associated to the alga), and can be viewed as a valuable tool for understanding the relationship between seaweed and associated fauna, which is critical for gaining a better understanding of the role that those species play in a specific ecosystem and the consequences of their loss.

CRediT authorship contribution statement

Conceptualization, R.C. and F.P.M.; Methodology, R.C. and F.P.M.; Investigation, F.P.M.; Formal Analysis, F.P.M.; Data curation, F.P.M., M. M. and R.C.; Writing – Original Draft Preparation, F.P.M., R.C.; Writing – Review & Editing, M.F.P., M.M., G.S., R.C.; Visualization, F.P.M.; Validation, F.P.M.; Supervision, R.C.; Project Administration, R.C.; Funding Acquisition, R.C.; Resources, R.C; identification and analysis of the architectural features of *G. montagnei*, F.P.M.; identification and analysis of Gastropods, R.C.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability and reproducible research

The data that support the findings of this study are available on Mendeley Data DOI: 10.17632/43j4nyxyjx.1.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2022.114396.

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