RESEARCH ARTICLE

Unleashing The Potential Of Artificial Reefs Design: A Purpose-Driven Evaluation Of Structural Complexity

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ABSTRACT

Artificial reefs (AR) must be built according to their objective and show high complexity to mimic the characteristic of natural habitats. To enhance the integration of artificial structures into ecosystems, a new quantitative method has been developed to evaluate their complexity, using 3D computer-aided design (CAD) models of ARs. The method utilizes six metrics: three related to geometric complexity (C-Convexity, P-Packing, and D-Fractal dimension) and three related to informational complexity (R-Orientation Richness, H-Orientation Diversity, J-Orientation Evenness). This method categorizes artificial reefs based on their complexity and has the potential to aid in designing more effective artificial reefs in the future while providing a quantitative way to analyze the correlation between complexity and diversity on the scale of artificial reefs. Additionally, the method may identify specific complexity thresholds for attracting certain species or achieving particular goals. This approach fills a gap in the current lack of quantitative methods for assessing artificial reef complexity, potentially leading to more effective and ecologically integrated artificial reef designs.

KEYWORDS Artificial reef, habitat complexity, 3D CAD model

1 | INTRODUCTION

Among the artificial structures spread across the ocean, artificial reefs (AR) can be defined as "submerged structures placed on the seabed deliberately to mimic some characteristics of natural habitats" (Jensen et al., 2000). The use of artificial reefs made of rocks, wood or bamboo by fishermen dates back at least 3000 years in the Mediterranean (Riggio et al., 2000) but also in Japan since the seventeenth century (Thierry, 1988). Over time, These handcrafted practices have been developed on a larger scale using objects from their immediate environment. Recycled materials, such as shipwrecks, offshore platforms, construction waste, and used tires, were favoured, with no regard for the environmental impacts (Pickering et al., 1998; Tessier et al., 2015). During the 1970s and 1980s, specific programs for fisheries management were developed on the impulse of the first International Conference on Artificial Reefs and Related Aquatic Habitats (CARAH) (Jensen et al., 2000).

Finally, in the late 2000s, the United Nations Environment Programme published the first guidelines, establishing a precise framework for artificial reef deployment and enlarging their objectives to fish production, habitat protection, habitat restoration and/or regeneration, and recreational opportunities. Nowadays, artificial reefs have to be made from non-polluting inert materials and designed with a structural complexity that mimics the natural habitats of the location (UNEP, 2009; UNEP MAP, 2005).

Despite establishing these guidelines, there is still a lack of scientific basis to monitor and compare the effectiveness of such structures (Ramm et al., 2021). To evaluate the quality and theoretical adequacy of the structure before immersion, precise information is needed regarding the material and design of the reefs. Some studies have investigated the effect of different materials on the primary communities and macrofouling communities that settle on the artificial reef to select the most suitable substrates according to objectives (Liu et al., 2017; Riera et al., 2018; Salamone et al., 2016). As far as three-dimensional structure is concerned, artificial reefs are mainly designed empirically on the basis of expert recommendations by quantifying the number of spaces, voids and crevices to assess fish preference for different types of shelter (Bohnsack, 1991). Since the early 90s, most of the structures used have been simple in shape and have been aggregated without offering much heterogeneity. Assuming that habitat complexity strongly influences the diversity and abundance of species colonizing artificial reefs (Bohnsack, 1989; Charbonnel et al., 2002; Hackradt et al., 2011; Pickering and Whitmarsh, 1997; Rouanet et al., 2015; Sherman et al., 2002; Svane and Petersen, 2001; Tessier et al., 2015), some studies have practiced post-complexification of artificial reefs to improve their effectiveness (Bodilis et al., 2011; Charbonnel et al., 2002; Tessier et al., 2015). More recently, giant 3D printing has given rise to a new generation of artificial reefs that more closely mimic the structural complexity of natural habitats (Levy et al., 2022). A few studies have attempted to use surface roughness (Ferreira et al., 2001; Wilding et al., 2007) or fractal dimension (Caddy and Stamatopoulos, 1990; Lan et al., 2008) as indicators of the structural complexity of artificial reefs. However, no standardized method is available for assessing the structure of artificial reefs prior to immersion.

The link between the complexity of the habitat and species diversity is a pillar of functional ecology. In natural ecosystems, a myriad of studies has been published since the studies of MacArthur & MacArthur (MacArthur et al., 1962; MacArthur and MacArthur, 1961), who proposed that the structural complexity or heterogeneity of the habitat influences the diversity of bird species in an area. The idea that habitat structure can affect species diversity is based on the notion that different species have different ecological requirements and may prefer or require different types of habitats for survival, reproduction, and resource use. Habitats with greater structural complexity can provide a wider range of ecological niches or opportunities for species with different ecological needs, leading to higher species richness and diversity (Beck, 2000; McCoy and Bell, 1991; Tagliapietra and Sigovini, 2010; Tews et al., 2004; Tokeshi and Arakaki, 2012), but also functional diversity (Mocq et al., 2021), and higher prey-predator dynamics (Kovalenko et al., 2012; Smith et al., 2019).

Although there is a consensus on the existence of this link, the definition and methods for evaluating it are, on the other hand, debated. McCoy and Bell (1991) defined the habitat structure by three different aspects, namely scale, complexity, and heterogeneity, which are closely related to the shape of the structures and the abundance, diversity and arrangement of the structural elements that compose the habitat. The metrics used to assess complexity and heterogeneity can vary according to the scale of the study; this scale dependency can bring high variability between studies and must be precisely defined. This definition has been followed for decades in the literature (Kovalenko et al., 2012; Lazarus and Belmaker, 2021; Tokeshi and Arakaki, 2012). Therefore, the metrics that evaluate habitat structure are classified into two categories. To name the most famous: fractal dimension, rugosity, or vertical relief fall into the complexity category that evaluates the global shape; whereas diversity, richness, or standard deviation fall into the heterogeneity that evaluates the variation of elements in the shape. More recently, Loke and Chisholm

(2022) proposed to define complexity and heterogeneity by geometric and informational complexity respectively, and gave recommendations for choosing the most suitable metrics and ensuring comparability between studies. This framework provides a valuable tool to help advance research in these areas, and we will use their categorization hereafter to describe complexity. They also expressed stringent criticisms and limitations on the use of some geometric complexity metrics, in favor of informational complexity metrics. However, as Madin et al. (2023), we agree that well-defined geometric complexity metrics are relevant to highlight important ecological responses. Moreover, we believe that no metrics prevail over others if they assess different parameters of the habitat structure.

Facing these heated debates, we have been cautious in evaluating both geometric and informational complexity of the structure of artificial reefs designed by 3D computer-aided design (CAD). We chose six different measures: fractal dimension (D), Packing (P) and Convexity (C) (as proxies of geometric complexity); and richness (R), diversity (H) and evenness (J) (as proxies of informational complexity). We then used these metrics to categorize a variety of artificial reefs that were built for different purposes (protection, production and bio-mimicry) produced by moulding or 3D printing. This approach helped us to identify four distinct categories of artificial reefs, each characterized by different complexity factors.

This method can potentially enhance the effectiveness of artificial reef design by providing a clear understanding of their structural properties that designers can adjust. Moreover, it can provide a quantitative approach to examine the relationship between habitat complexity and diversity of biotic assemblages at the scale of artificial reefs, potentially identifying specific complexity metric thresholds for particular species attraction or objectives. This information could be crucial for developing more efficient and targeted artificial reef projects in the future.

2 | MATERIALS AND METHODS

2.1 | Complexity Assessment of 3D CAD Models

2.1.1 | 3D CAD models

Our methodology was developed using 3D computer-aided design (CAD) models to generate functional virtual prototypes of three-dimensional artificial reefs. Using STL files, which describe the geometry of the artificial reefs, we extracted various parameters such as surface area, volume, and point clouds with associated normals (refer to Figure 1 for details). We extracted all parameters with a 1 cm resolution, striking a balance between computation time and structural definition. We assumed this resolution was sufficient for most study objectives, ranging from benthic macrofouling to mobile species. Using the extracted parameters and elements, we selected relevant metrics from the literature to evaluate both geometric and informational complexity (Figure 1).

2.1.2 | Geometric complexity

An organism needs a specific volume when mobile or a surface when sessile. Moreover, its resource intake is predominantly a surface-dependent activity. To welcome a rich trophic network, an artificial reef needs to display microhabitats at different scales. Therefore, to assess quantitatively these parameters, we got inspired by the metrics "Packing" (P) and "Convexity" (C) from Zunic and Rosin (2004) to assess parameters associated with volume and surface of the 3D CAD model and its convex hull (the smallest possible convex shape that completely contains the 3D model, with no concave areas). However we adapted the formulas to our aims. P is based on the surface ratio of the convex hull to 3D CAD model. For C, instead of using the volume of the structure that is inaccessible to mobile organisms, we used the volume available within the convex hull that is accessible to them. Therefore C is the ratio of volume available within the convex hull to the volume of its convex hull. C and P have been computed on Python (Figure 1). To encompass the multiscale structure of the artificial reef models, we used the fractal dimension (D), which is a widely recognised metric in natural environment complexity analysis that defines how an object occupies space at all scales. It was computed on the point clouds of the 3D CAD models with the Minkowski-Bouligand method (or "box-counting") using the R statistical framework (version 4.0.3) and “est.boxcount” function of the package “Rdimtools” (You and Shung, 2022). The method involves counting the number of boxes needed to cover an object, with each successive box having a smaller length than the previous one.

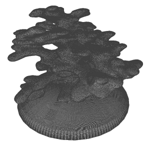
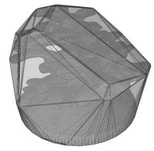
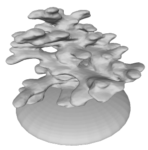
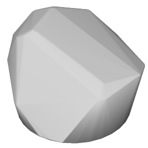
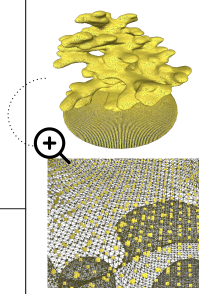
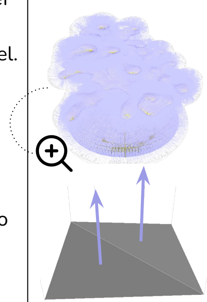
	Metrics & formulas	Parameters	Artificial reef (ar)	Convex Hull (ch)
Geometrical complexity/Complexity	**Packing - P:** measure of the degree of space between different parts of an object. $$P = \frac{A_{ar}}{A_{ch}} \Rightarrow P_t = 1 - \frac{A_{ch}}{A_{ar}}$$	**Based on the surface area of the artificial reef (A_{ar}) and of its convex hull (A_{ch})** Resolution: **1 cm^2**		
	Convexity - C: measure of the degree of space available between different parts of an object. $$C = \frac{V_{av}}{A_{ch}}$$	**Based on the volume available (V_{av})** within the **volume of convex hull** of the artificial reef **(V_{ch})** Resolution: **1 cm^3**		
	Fractal dimension - D: measure the way an object fills the space, at all scales. $$D = \lim_{\varepsilon \to 0} \frac{\log N(\varepsilon)}{\log \frac{1}{\varepsilon}} \Rightarrow D_t = 1 - (3 - D)$$	**Based on the 3D coordinates of the points in the points cloud** that forms the surface of the artificial reef. where N(ε) is a number of boxes of diameter at most ε required to cover the object. Resolution: **1/cm^2**		
Informational complexity/heterogeneity	**Orientation richness - R:** measure the proportion of the different orientation of the normals. $$R = \frac{S}{N}$$	**Based on the normals** to the artificial reef surface. The normals are defined at each points of the surface of the 3D CAD model. with: i : a normal of the 3D CAD model S : total of different normal N: total number of normal p_i: Proportion of one normal i compared to the total number of normal		
	Orientation diversity - H: measure the diversity of the orientation of the normals. $$H = -\sum_{i=1}^{S} p_i.log\,(p_i) \Rightarrow H_t = log\,(1 + H)$$			
	Orientation evenness - J: measure the evenness of the orientation of the normals. $$J = \frac{H}{\log\,(S)}$$			

FIGURE 1 Summary figure providing an overview of the complexity metrics used in the study, which are classified as geometric (3 first rows) and informational (3 last rows). The first column describes the definition and formula for each metric, while the second column lists the parameters used to compute these metrics, including surface, volume, point clouds, and normals. The last columns of the figure include an example of a 3D CAD artificial reef and its convex hull, which illustrate the application of these parameters.

2.1.3 | Informational complexity

To welcome a rich and diverse community, artificial reefs need to display different types of microhabitats. We thus considered each normal of the 3D CAD model as an anchor point or a surface that promotes the settlement of certain species and used it to define the orientation of the surface in 3D space. The greater the difference between anchor points, the greater the potential for the artificial reef to host a diverse range of species. Moreover, greater variability in surface orientations increases the likelihood of creating cavities or shelters for mobile species.

We assess the Informational complexity of the normals using specific richness (Webb et al., 1967), Shannon, (1948), and Pielou indexes (Pielou, 1966) to determine respectively "Orientation Richness" (R), "Orientation diversity" (H) and "Orientation Evenness" (J). All metrics were computed on Python, and we used the function "entropy" from "scipy.stat" to compute H.

To have an equivalent weight of the variables, P and D, H has been transformed (named here after Pt, Dt and H_t, Figure 1).

2.1.3 | Artificial reef modules

Our analysis included a range of artificial reef models, comprising both nine conventional models for moulding and biomimetic models designed by three 3D printing. We also created four classical moulded reefs and four biomimetic 3D-printed reefs that we included in the analysis. To ensure comparability between the reef types, we excluded cases where different modules were aggregated together (which is a common practice aimed at increasing habitat complexity). Constructors directly provided the 3D-printed reef models, while the classical ones were created on Tinkercad® using dimensions and shapes collected from the literature (Tessier et al., 2015). Detailed information about the artificial reefs, including their objectives, names, references, production process and parameters extracted (area, volume, normals) is available in the supplementary materials (S1).

2.2 | Data analyses

2.2.1 | Categorisation of artificial reefs

Statistical analyses were conducted using the open-source software R (version 4.0.3). To classify the artificial reefs based on their structure and verify if it was consistent with their intended usage, we performed a Multiple Factor Analysis (MFA) on the indices using the "FactoMineR" package. We grouped the two types of indices (geometric and informational) into separate categorical groups. To identify different groups based on the MFA results, we conducted hierarchical clustering on principal components using the "HCPC" function of "FactoMineR". The optimal number of groups was determined using the K-means cascading method with the "cascadeKM" function of the "vegan" package, which creates several partitions from 2 to 5 groups. The Calinski-Harabasz (CH) criterion was used to select the best partition, with the maximum value of CH indicating the correct number of groups. Finally, the "Catdes" function of "FactoMineR" was used on the Euclidean distance matrix of the scaled complexity variables to describe the clusters. More details about the statistical analyses are provided in Supplementary Materials (S2).

Data and scripts are available respectively on zenodo and github:
https://github.com/ELI-RIERA/ArtificialReef_Complexity
(DOI:10.5281/zenodo.8091788)

3 | RESULTS

3.1 | Evaluation of the structure of the AR modules

The computed complexity indices for the 3D CAD models of the artificial reefs did not show consistent rankings across all structures. Regarding geometric complexity, the

Convexity (C) values ranged from 0.145 (PROD1) to 0.924 (PROT1), Packing (P_t) values ranged from -0.031 (PROT5) to 0.765 (BIOM6), and Fractal dimension (D_t) values ranged from 0.026 (PROT2) to 0.529 (BIOM6). In terms of indices related to informational complexity, the Orientation Richness (R) values ranged from $1.16.10^{-6}$ (PROT1) to 0.905 (BIOM6), Orientation diversity (H_t) values ranged from 0.527 (PROT1) to 2.603 (BIOM6), and Orientation Evenness (J) values ranged from 0.414 (PROD7) to 1 (for PROT1, PROT3, PROD5) (Table 1).

TABLE 1 | indexes computed on the artificial reef's models

	C - Convexity	Pt - Packing	Dt - Fractal dimension	R -Orientation Richness	Ht - Orientation Diversity	J -Orientation Eveness
BIOM1	6.33E-01	3.62E-01	2.10E-01	6.72E-01	2.44E+00	8.89E-01
BIOM2	3.10E-01	3.69E-01	2.46E-01	6.94E-01	2.47E+00	9.04E-01
BIOM3	3.82E-01	2.70E-01	2.03E-01	6.58E-01	2.43E+00	8.81E-01
BIOM4	3.11E-01	3.88E-01	2.46E-01	7.00E-01	2.48E+00	9.07E-01
BIOM5	6.46E-01	5.78E-01	3.90E-01	8.39E-01	2.59E+00	9.95E-01
BIOM6	8.28E-01	7.65E-01	4.82E-01	9.05E-01	2.60E+00	9.97E-01
BIOM7	6.24E-01	4.51E-01	3.04E-01	5.39E-01	2.50E+00	9.88E-01
PROD1	1.45E-01	3.69E-01	2.49E-01	1.10E-02	1.56E+00	4.50E-01
PROD2	1.93E-01	3.94E-01	2.60E-01	1.20E-02	1.62E+00	4.78E-01
PROD3	4.30E-01	7.21E-01	5.29E-01	6.40E-02	2.20E+00	7.36E-01
PROD4	2.21E-01	5.20E-01	3.57E-01	6.60E-02	1.97E+00	5.93E-01
PROD5	5.64E-01	6.11E-01	4.97E-01	0.00E+00	5.27E-01	1.00E+00
PROD6	6.76E-01	6.08E-01	3.59E-01	0.00E+00	1.76E+00	9.94E-01
PROD7	8.15E-01	6.48E-01	3.52E-01	0.00E+00	1.22E+00	4.12E-01
PROT1	9.24E-01	9.00E-03	8.10E-02	0.00E+00	5.27E-01	1.00E+00
PROT2	9.22E-01	-2.60E-02	2.60E-02	2.00E-03	1.78E+00	8.15E-01
PROT3	6.49E-01	1.08E-01	1.29E-01	0.00E+00	5.27E-01	1.00E+00
PROT4	7.61E-01	3.98E-01	2.13E-01	1.00E-03	1.55E+00	6.65E-01
PROT5	6.33E-01	-3.10E-02	1.24E-01	0.00E+00	1.20E+00	5.23E-01
PROT6	2.62E-01	1.03E-01	1.16E-01	1.00E-03	1.48E+00	6.75E-01

The two first dimensions represented 68.97% of total inertia and mainly structured the factor map (Dim.1: 43.34% & Dim.2: 25.63%). These dimensions displayed a good projection of the data, as evidenced by the proximity of all variables to the correlation circle. According to the Karlis-Saporta-Spinakis (KSP) rule (Karlis et al., 2003) for selecting the number of principal components to retain for the analysis, the third dimension displayed a cumulative (of the two groups of variables) eigenvalue of 0.18 which was below the KSP threshold (2.03). Thus only the first two dimensions were retained for the analysis.

H_t, R, P_t and D_t contributed equally to building the first dimension (respectively, 22.41 %, 21.80 %, 26.38 %, and 23.64 %), while J and C mainly contributed to building the second one (respectively, 38.04 % and 25.32 %) (Figure 2.A). Our method utilizing the cascade K-means algorithm to cut the dendrogram resulted in four distinct clusters (Figure 2.B & Table S2). The first cluster includes all artificial reefs models designed for protection purposes (except PROT4), which is characterized negatively by dimension 1 and metrics H_t, D_t, and P_t; and positively by the dimension 2 and metric C (Table S2). The second cluster comprises three artificial reefs designed for production purposes (PROD1, PROD2, PROD4) and one artificial reef designed for protection (PROT6), which are described negatively by dimension 2 and metrics C and J (Table S2). The third cluster consists of all other artificial reefs designed for production purposes and one for protection (PROT4), characterized positively by P_t and D_t metrics (Table 2). The fourth cluster comprises biomimetic structures described positively by both dimension and the metrics R, H_t and J (Table S2). The score of clusters increases gradually along the first dimension that summarizes the Multiscale Complexity Index (MCI) of artificial reef structure (Figure 1.C)

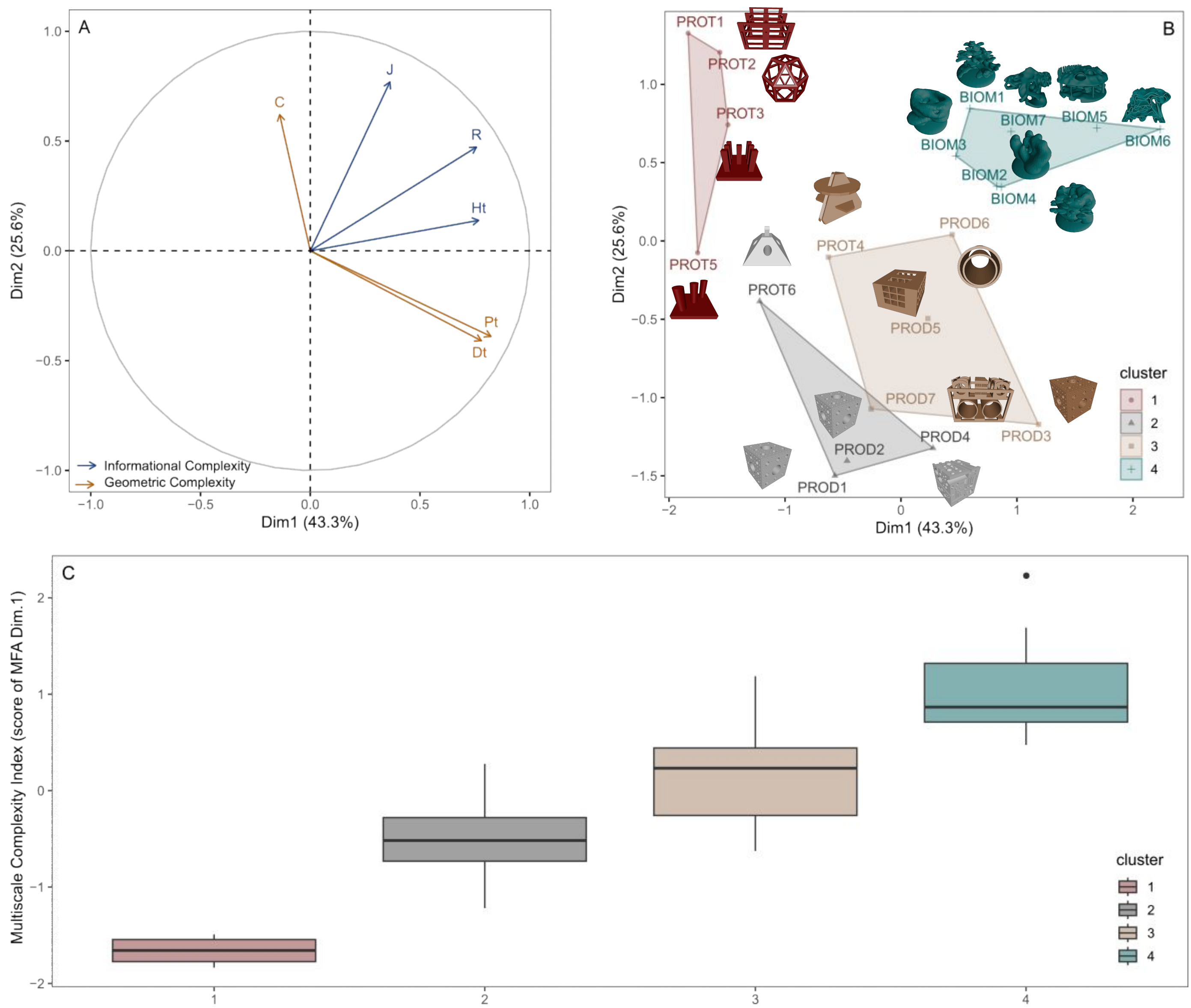


FIGURE 2 | Multiple factor analysis. A: correlation circle of the variable of complexity coloured according to the type of complexity measurement (i.e. geometric vs informational) B: the score map of the artificial reef models, coloured according to their construction objectives and ordinated according to the optimal clustering computed by K-means cascades with Calinski criterion). C: boxplot representing the average score of each cluster along the axes of dimension 1, determined as Multiscale Complexity Index.

4 | DISCUSSION

The selection of appropriate metrics is paramount for evaluating the 3D characteristics of artificial reef structures in the context of ecological processes. To assess all aspects of the structure of the artificial reef models, we based our method on 3 metrics related to geometric complexity (D_t, P_t and C) and 3 metrics related to informational complexity (R, H_t and J). Our methodology aimed to quantitatively assess the geometric and informational complexity of artificial reefs using 3D computer-aided design (CAD) models. Because the habitat structure cannot be summarised by one metric or parameter (Loke and Chisholm, 2022; Tokeshi and Arakaki, 2012), we extracted parameters such as surface area, volume, and point clouds with associated normals to evaluate both geometric and informational complexity and proposed a framework that evaluated the global complexity of the structure based on a wide range of artificial reef models, comprising both conventional models for moulding and biomimetic models designed for 3D printing.

4.1 | Surface and Volume Metrics as Basic Indicators for Assessing Ecological Suitability of Artificial Reefs

The surface is crucial for marine organisms as it provides a physical substrate to attach, grow, move and spread. It also plays a vital role in facilitating the exchange of nutrients, or other vital substances between the organism and its surrounding environment. Additionally, the surface area available determines the number of resources that the organisms can obtain, making it a significant factor in their survival and growth. In habitat complexity literature, surface-derived metrics are frequently employed, the most famous being rugosity. The concept of rugosity refers to the refolding aspect of the surface in relation to an orthogonal plan. This parameter is often evaluated through the chain and tape method (Luckhurst and Luckhurst, 1978), which provides a linear measurement of rugosity. However, with the advancements in 3D modelling and reconstruction techniques, it has progressed to encompass 3D surface rugosity (Friedman et al., 2012) and, more recently, the concept of Packing (Zunic and Rosin, 2004) has been introduced and successfully used to compare the refolding surface of the coral structure in relation to its convex hull (Zawada et al., 2019).

The available volume within the habitat structure provides the necessary physical space for organisms to move and carry out their life processes. It provides shelter to survive, reproduce, or maintain their ecological roles. Volume metrics are less commonly used in habitat complexity studies, likely due to the challenges in evaluating it in a natural environment. More recently, thanks to tomography or scanner technology, volume driven metrics can be computed on fragments of habitat, such as coral, that can be reproduced (Hennige et al., 2020; Reichert et al., 2017; Zawada et al., 2019). with 3D CAD models, volume parameters become easily accessible. We got inspired by the metrics Convexity introduced with Packing by Zunic and Rosin (2004).

4.2 | Incorporating Surface Orientation and Fractal Metrics in Habitat Evaluation: Addressing Multiscale Complexity

Habitats are inherently multiscale in nature and provide a diverse range of microhabitats that meet the needs of different life stages and ecological roles of organisms. From primary producers to predators, it supports a wider range of species and ecological interactions, providing a rich food web for biodiversity and resilience to environmental stressors. To support a diverse and abundant ecosystem, an artificial reef must provide various microhabitats at different scales. Therefore, we used the fractal dimension to measure how an object fills space at different scales. It has been widely used in marine ecology to describe the relationship between species diversity and the structure of different marine habitats, such as coral reefs, seagrass beds, and rocky intertidal zones (Tokeshi and Arakaki, 2012). Nowadays, it is even easier to compute it on habitat reconstruction with 3D CAD modelling by photogrammetry or 3D scanning (Reichert et al., 2017; Young et al., 2017). We have been cautious in choosing a resolution to compute the fractal dimension relevant for our study case (1 point/cm^2). We have attempted to achieve a balance between computation time and structural clarity, thereby excluding finer details. We assumed this resolution will satisfy our objectives, including benthic macrofouling and mobile species.

We also based our evaluation of the informational complexity of the artificial reef models on the distribution of normals which was the only parameter whose variability could be quantified without relying on subjective observation. Although cavities or access to structures could have been potential candidates, counting them on biomimetic 3D-printed reefs is challenging due to complex interconnected shapes. Determining thresholds for shape differences related to microhabitats can be subjective. Moreover, normal distribution gives information on the surface orientation of the structure, which is critical for both fixed and mobile marine species as it determines the availability and accessibility of resources and the suitability of the habitat. For fixed species, such as corals, sponges, and algae, surface orientation affects their ability to capture light, nutrients, and planktonic prey (for coral and sponge), essential for their survival and growth (Connell, 1999; Irving and Connell, 2002; Relini et al., 1994; Ushiama et al., 2016). The orientation can also influence their ability to resist physical disturbances such as strong water currents or waves (Sokołowski et al., 2016). For mobile species, surface orientation provides shelter and plays a crucial role in the ability of species to navigate, detect prey, and avoid predators (Langhamer et al., 2009). Overall, surface orientation is an important factor that affects the distribution, abundance, and diversity of marine species and their interactions with each other and their environment. Therefore, we support using normal as a parameter in our study. Existing metrics use the normal parameters (Beck, 2000, 1998; Carleton and Sammarco, 1987; Grohmann et al., 2009; Kovalenko et al., 2012; Young et al., 2017), offering diverse values to identify surface topography: strength vector, vector dispersion, several standard deviations to the plane. We preferred using commonly used metrics to determine habitat informational complexity that we named orientation Richness (R), Orientation diversity (H_t), and Orientation evenness (J), derived respectively from Webb et al. (1967), Shannon (1948) Pielou (1966) indexes. These metrics provide information on the proportion of the different types of surface orientations, their diversity in relation to their relative abundance and their distribution.

4.3 | Scaling up: Proposing a Multiscale Framework to Assess the Ecological Potential of Artificial Reefs

It is important to consider that no clear-cut values exist for these metrics, which might change according to environmental factors, such as the depth, the type of habitat and its connectivity to surrounding adjacent habitats. However, irrespective of these external factors, these metrics have to be considered altogether to better understand the nature of the habitat structure and be able to give relevant interpretations regarding ecological responses. In the case of artificial reef structure, we can assume that if the Multiscale Complexity Index (MCI) of a model is high, it might imply a structure with refolded surfaces with various surface orientations, providing shaded or exposed shelters and crevices at all scales for all organism sizes. Such a structure might welcome a healthy and diverse community, supporting the growth and survival of a range of species from primary producers to predators, and promoting resilience to environmental stressors.

Our method proved valuable in evaluating and classifying 20 artificial reef structures into four categories based on their complexity metrics. According to the results of the multiple factor analysis (MFA), the P_t, D_t, R, and H_t metrics mainly explain the complexity of the structures, while C and J do not follow the same increasing order of complexity as the other metrics. For J, indeed, it does not necessarily assess complexity, as it measures the equitability of the distribution of normals, so a simple structure such as a cube may have a value of J = 1, which does not reflect its simplicity. Concerning C, it should be noted that it is the only volume-based metric, while all others are surface-derivative. As for J, values of C are not so easy to interpret. Indeed, C = 1 reflects an empty structure, while C = 0 reflects a structure without space, values in between would be preferable. The surface-derived metrics that describe the first axis are easier to interpret and may be sufficient to determine the overall complexity of the structure. Indeed, the four categories are perfectly distributed along the first dimension of the MFA that was mainly constructed by these four metrics. The score of the structures on this first dimension can be considered as the Multiscale Complexity Index for artificial reefs. However, we consider that the evaluation of the C and J metrics can be retained because they provide additional information about the structure that can be useful for artificial reef design. For example, the two first clusters, which gathered the simplest structures and displayed the lowest Multiscale Complexity Index scores, were defined by opposite values of C. High and low C values opposing “voided simple designs” (cluster 1) to “solid simple designs” (cluster 2). The first cluster consisted of protection structures, while the second included structures designed for production. While it is expected that structures designed solely to protect habitats may exhibit low complexity, those designed to produce biomass should aim to achieve high geometric complexity (as measured by P_t and D_t) with a refolded surface at multiple scales. This will ensure that such structures fall into the third cluster, which is better suited for attracting a diverse range of species. Thus, the third cluster could be defined as "complex geometric designs". The fourth cluster consisted of biomimetic structures defined by high values of informational complexity (R, H_t, and J), that we defined as "complex informational designs".

Using this method and the framework provided in this study, designers can evaluate new artificial reef structures prior to their deployment and categorize them accordingly. This process can help designers identify areas for improvement and optimize design characteristics to enhance ecological performances of the reef. For instance, new structures falling in the second cluster could be improved by increasing the available volume, expanding the surface, and introducing greater variability in surface orientation to promote the coexistence of a diverse and abundant community, resulting in improved ecological performance and increased species diversity. Interestingly, the biomimetic designs, that emulate the natural reef structures, displayed the highest Multiscale Complexity Index (MCI). Comparing these MCI values with those obtained from natural reefs reconstructed using photogrammetry would be interesting. However, if our method could be applied on any reconstruction of natural habitat by 3D CAD model, there is some limitation in comparing a created ex-nihilo object with an *in situ* reconstruction of a marine landscape. Indeed, the limitations of *in situ* reconstruction method, such as the inability to access all the cavities hidden by biocenosis or within the structure itself (Loke and Chisholm, 2022), make them less accurate in comparison with 3D CAD models of artificial reefs. The latter are constructed before their immersion and therefore provide a complete understanding of their geometric and informational metrics. However, despite the limitations of *in situ* reconstruction, laboratory reconstruction using tomography or surface scanner on fragments of the habitat studied, such as corals or coralligenous algae (Reichert et al., 2017; Zawada et al., 2019) can provide a more complete understanding of the 3D structure of natural reefs and could be implemented in our framework.

5 | CONCLUSION

We argue that our approach, which focuses on the structural aspects of artificial reefs, has the potential to contribute to the development of global artificial reef design and support ecological reconciliation and restoration efforts by enhancing landscape complexity in face of growing marine artificialization and habitat degradation (Morris et al., 2019; Perricone et al., 2023; Solé and Levin, 2022). In conjunction with the methodology developed by (Carral et al., 2022), which considers other extrinsic parameters such as stakeholder engagement and immersion site selection, the effectiveness of artificial reef deployment projects may be, nowadays, enhanced by a more rigorous scientific framework.

AUTHORS CONTRIBUTIONS

ER, PF, CH: Design and conceptualization; ER: Data Curation; ER: Formal Analysis; PF, CH: Funding Acquisition; ER: data acquisition; ER, BM: Methodology; PF, CH: Project Administration, supervision and validation; ER, BM: Software; ER: Visualization; ER, PF, CH, BM: Writing – Original Draft Preparation

CONFLICT OF INTEREST STATEMENT

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.

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REFERENCES

Beck, M.W., 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. J. Exp. Mar. Biol. Ecol. 249, 29–49.

Beck, M.W., 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Mar. Ecol. Prog. Ser. 169, 165–178. https://doi.org/10.3354/meps169165

Bodilis, P., Seytre, C., Charbonnel, E., Patrice, F., 2011. Monitoring of the artificial reef fish assemblages of golfe juan marine protected area (France, North-Western Mediterranean). Braz. J. Oceanogr. 59, 167–176.

Bohnsack, J.A., 1991. Habitat structure and the design of artificial reefs, in: Habitat Structure. pp. 412–426.

Bohnsack, J.A., 1989. Are high densities of fishes at artificial reefs the results of habitat limitation or behavioural preference? Bull. Mar. Sci. 44, 631–645.

Caddy, J.F., Stamatopoulos, C., 1990. Mapping Growth and Mortality Rates of Organisms onto a Perforated Surface: The Relevance of "Cover" to the Carrying Capacity of Natural and Artificial Habitats. Estuar. Coast. Shelf Sci. 31, 87–106.

Carleton, J.H., Sammarco, P.W., 1987. Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques. Bull. Mar. Sci. 40, 85–98.

Carral, L., Lamas, M.I., Barros, J.J.C., Lopez, I., Carballo, R., 2022. Proposed Conceptual Framework to design Artifcial reefs Based on Particular Ecosystem Ecology Traits. MDPI Biol. 11.

Charbonnel, E., Serre, C., Ruitton, S., Harmelin, J., Jensen, A., 2002. Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). ICES J. Mar. Sci. 59, 208–213. https://doi.org/10.1006/jmsc.2002.1263

Connell, S.D., 1999. Effects of surface orientation on the cover of epibiota. Biofouling 14, 219–226. https://doi.org/10.1080/08927019909378413

Ferreira, C.E.L., Gonçalves, J.E.A., Coutinho, R., 2001. Community structure of fishes and habitat complexity on a tropical rocky shore. Environ. Biol. Fishes 61, 353–369.

Friedman, A., Pizarro, O., Williams, S.B., Johnson-Roberson, M., 2012. Multi-Scale Measures of Rugosity, Slope and Aspect from Benthic Stereo Image Reconstructions. PLoS ONE 7. https://doi.org/10.1371/journal.pone.0050440

Grohmann, C.H., Smith, M.J., Riccomini, C., 2009. Surface Roughness of Topography : A Multi-Scale Analysis of Landform Elements in Midland Valley, Scotland. Proc. Geomorphometry 2009 140–148.

Hackradt, C.W., Félix-Hackradt, F.C., Garcia-Charton, J.A., 2011. Influence of habitat structure on fish assemblage of an artificial reef in southern Brazil. Mar. Environ. Res. 72, 235–247. https://doi.org/10.1016/j.marenvres.2011.09.006

Hennige, S.J., Wolfram, U., Wickes, L., Murray, F., Roberts, J.M., Kamenos, N.A., Schofield, S., Groetsch, A., Spiesz, E.M., Aubin-Tam, M.-E., Etnoyer, P.J., 2020. Crumbling Reefs and Cold-Water Coral Habitat Loss in a Future Ocean: Evidence of "Coralporosis" as an Indicator of Habitat Integrity. Front. Mar. Sci. 7, 668. https://doi.org/10.3389/fmars.2020.00668

Irving, A., Connell, S., 2002. Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. Mar. Ecol. Prog. Ser. 245, 83–91. https://doi.org/10.3354/meps245083

Jensen, A., Collins, K., Lockwood, P., 2000. Introduction and Background to artificial Reefs in European Seas, in: Al., A.C.J. et (Ed.), Artificial Reefs in European Seas. Kluwer Academic Publishers, pp. ix–xi. https://doi.org/10.1017/CBO9781107415324.004

Karlis, D., Saporta, G., Spinakis, A., 2003. A Simple Rule for the Selection of Principal Components. Commun. Stat. - Theory Methods 32, 643–666. https://doi.org/10.1081/STA-120018556

Kovalenko, K.E., Thomaz, S.M., Warfe, D.M., 2012. Habitat complexity: approaches and future directions. Hydrobiologia 685, 1–17.

https://doi.org/10.1007/s10750-011-0974-z

Lan, C.H., Lan, K.T., Hsui, C.Y., 2008. Application of fractals: create an artificial habitat with several small (SS) strategy in marine environment. Ecol. Eng. 32, 44–51. https://doi.org/10.1016/j.ecoleng.2007.08.007

Langhamer, O., Wilhelmsson, D., Engström, J., 2009. Artificial reef effect and fouling impacts on offshore wave power foundations and buoys - a pilot study. Estuar. Coast. Shelf Sci. 82, 426–432.

Lazarus, M., Belmaker, J., 2021. A review of seascape complexity indices and their performance in coral and rocky reefs. Methods Ecol. Evol. 12, 681–695. https://doi.org/10.1111/2041-210X.13557

Levy, N., Berman, O., Yuval, M., Loya, Y., Treibitz, T., Tarazi, E., Levy, O., 2022. Emerging 3D technologies for future reformation of coral reefs: Enhancing biodiversity using biomimetic structures based on designs by nature. Sci. Total Environ. 830, 154749–154749. https://doi.org/10.1016/j.scitotenv.2022.154749

Liu, L., Du, R., Zhang, X., Dong, S., Sun, S., 2017. Succession and seasonal variation in epilithic biofilms on artificial reefs in culture waters of the sea cucumber Apostichopus japonicus. J. Oceanol. Limnol. 35, 132–152.

Loke, L.H.L., Chisholm, R.A., 2022. Measuring habitat complexity and spatial heterogeneity in ecology. Ecol. Lett. 25, 2269–2288. https://doi.org/10.1111/ele.14084

Luckhurst, E., Luckhurst, K., 1978. Analysis of the Influence of Substrate Variables on Coral Reef Fish Communities. Mar. Biol. 49, 317–323.

MacArthur, R.H., MacArthur, J.W., 1961. On Bird Species Diversity. Ecology 42, 594–598.

MacArthur, R.H., MacArthur, J.W., Preer, J., 1962. On Bird Species Diversity II. Prediction of Bird Census from Habitat Measurements. Am. Soc. Nat. XCVI, 167–174.

Madin, J.S., Asbury, M., Schiettekatte, N., Dornelas, M., Pizarro, O., Reichert, J., Torres-Pulliza, D., 2023. A word on habitat complexity. Ecol. Lett. 26, 1021–1024. https://doi.org/10.1111/ele.14208

McCoy, E.D., Bell, S.S., 1991. Habitat structure : The evolution and diversification of a complex topic, in: Habitat Structure.

Mocq, J., Soukup, P.R., Näslund, J., Boukal, D.S., 2021. Disentangling the nonlinear effects of habitat complexity on functional responses. J. Anim. Ecol. 90, 1525–1537. https://doi.org/10.1111/1365-2656.13473

Morris, R.L., Heery, E.C., Loke, L.H.L., Lau, E., Strain, E.M.A., Airoldi, L., Alexander, K.A., Bishop, M.J., Coleman, R.A., Cordell, J.R., Dong, Y.W., Firth, L.B., Hawkins, S.J., Heath, T., Kokora, M., Lee, S.Y., Miller, J.K., Perkol-Finkel, S., Rella, A., Steinberg, P.D., Takeuchi, I., Thompson, R.C., Todd, P.A., Toft, J.D., Leung, K.M.Y., 2019. Design options, implementation issues and evaluating success of ecologically engineered shorelines, Oceanography and Marine Biology. https://doi.org/10.1201/9780429026379-4

Perricone, V., Mutalipassi, M., Mele, A., Buono, M., Vicinanza, D., Contestabile, P., 2023. Nature-based and bioinspired solutions for coastal protection: an overview among key ecosystems and a promising pathway for new functional and sustainable designs. ICES J. Mar. Sci. 80, 1218–1239. https://doi.org/10.1093/icesjms/fsad080

Pickering, H., Whitmarsh, D., 1997. Artificial reefs and fisheries exploitation: A review of the “attraction versus production” debate, the influence of design and its significance for policy. Fish. Res. 31, 39–59. https://doi.org/10.1016/S0165-7836(97)00019-2

Pickering, H., Whitmarsh, D., Jensen, A., 1998. Artificial Reefs as a Tool to aid Rehabilitation of Coastal Ecosystemes: Investigating the Potential. Mar. Pollut. Bull. 37, 505–514. https://doi.org/10.1016/S0025-326X(98)00121-0

Pielou, E.C., 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theor. Biol. 10, 370–383. https://doi.org/10.1016/0022-5193(66)90133-0

Ramm, L.A., Florisson, J.H., Watts, S.L., Becker, A., Tweedley, J.R., 2021. Artificial reefs in the Anthropocene: a review of geographical and historical trends in their design, purpose, and monitoring. Bull. Mar. Sci. 97, 699–728. https://doi.org/10.5343/bms.2020.0046

Reichert, J., Backes, A.R., Schubert, P., Wilke, T., 2017. The power of 3D fractal dimensions for comparative shape and structural complexity analyses of irregularly shaped organisms. Methods Ecol. Evol. 8, 1650–1658. https://doi.org/10.1111/2041-210X.12829

Relini, G., Zamboni, N., Tixi, F., Torchia, G., 1994.

Patterns of Sessile Macrobenthos Community Development on an Artificial Reef in the Gulf of Genoa (Northwestern Mediterranean). Bull. Mar. Sci. 55, 745–771.

Riera, E., Lamy, D., Goulard, C., Francour, P., Hubas, C., 2018. Biofilm monitoring as a tool to assess the efficiency of artificial reefs as substrates: Toward 3D printed reefs. Ecol. Eng. 120, 230–237. https://doi.org/10.1016/j.ecoleng.2018.06.005

Riggio, S., Badalamenti, F., D'Anna, G., 2000. Artificial Reefs in Sicily: An Overview, in: Jensen, A.C., Collins, K.J., Lockwood, A.P.M. (Eds.), Artificial Reefs in European Seas. Springer Netherlands, Dordrecht, pp. 65–73. https://doi.org/10.1007/978-94-011-4215-1_4

Rouanet, E., Astruch, P., Antonioli, A., 2015. How Artificial Reef Design and Architectural Complexity Affect the Benthic Colonization. RECIF Conf.- Fr. 53–60.

Salamone, A.L., Robicheau, B.M., Walker, A.K., 2016. Fungal diversity of marine biofilms on artificial reefs in the north-central Gulf of Mexico. Bot. Mar. 59, 291–305. https://doi.org/10.1515/bot-2016-0032

Shannon, C.E., 1948. A Mathematical Theory of Communication. Bell Syst. Tech. J. 27, 379–423.

Sherman, R.L., Gilliam, D.S., Spieler, R.E., 2002. Artificial reef design : void space , complexity , and attractants. ICES J. Mar. Sci. 59, 196–200. https://doi.org/10.1006/jmsc.2001.1163

Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J., Bidder, O.R., Middleton, A.D., 2019. Habitat complexity mediates the predator–prey space race. Ecology 100. https://doi.org/10.1002/ecy.2724

Sokołowski, A., Ziołkowska, M., Balazy, P., Kuklinski, P., Plichta, I., 2016. Seasonal and multi-annual patterns of colonisation and growth of sessile benthic fauna on artificial substrates in the brackish low-diversity system of the Baltic Sea. Hydrobiologia 790, 183–200. https://doi.org/DOI 10.1007/s10750-016-3043-9

Solé, R., Levin, S., 2022. Ecological complexity and the biosphere: the next 30 years. Philos. Trans. R. Soc. B Biol. Sci. 377. https://doi.org/10.1098/rstb.2021.0376

Svane, I., Petersen, J.K., 2001. On the Problems of Epibioses, Fouling and Artificial Reefs, a Review. Mar. Ecol. 22, 169–188.

Tagliapietra, D., Sigovini, M., 2010. Biological diversity and habitat diversity: a matter of Science and perception. Curric. Nat. Environ. Sci. 88, 147–155.

Tessier, A., Francour, P., Charbonnel, E., Dalias, N., Bodilis, P., Seaman, W., Lenfant, P., 2015. Assessment of French artificial reefs: due to limitations of research, trends may be misleading. Hydrobiologia 753, 1–29. https://doi.org/10.1007/s10750-015-2213-5

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.

Thierry, J.M., 1988. Artificial reefs in Japan - A general outline. Aquac. Eng. 7, 321–348. https://doi.org/10.1016/0144-8609(88)90014-3

Tokeshi, M., Arakaki, S., 2012. Habitat complexity in aquatic systems : fractals and beyond. Hydrobiologia 685, 27–47. https://doi.org/10.1007/s10750-011-0832-z

UNEP, 2009. An introduction to Artificial Reefs, in: London Convention and Protocol/UNEP: Guidelines for the Placement of Artificial Reefs. International Maritime Organization, London, pp. 1–8.

UNEP MAP, 2005. Guidelines for the placement at sea of matter for purpose other than the mere disposal (Construction of artificial reefs). Athens.

Ushiama, S., Smith, J.A., Suthers, I.M., Lowry, M., Johnston, E.L., 2016. The effects of substratum material and surface orientation on the developing epibenthic community on a designed artificial reef. Biofouling 32, 1049–1060. https://doi.org/10.1080/08927014.2016.1224860

Webb, L.J., Tracey, J.G., Williams, W.T., Lance, G.N., 1967. Studies in the Numerical Analysis of Complex Rain-Forest Communities: I. A Comparison of Methods Applicable to Site/Species Data. J. Ecol. 55, 171. https://doi.org/10.2307/2257724

Wilding, T.A., Rose, C.A., Downie, M.J., 2007. A novel approach to measuring subtidal habitat complexity. J. Exp. Mar. Biol. Ecol. 353, 279–286. https://doi.org/10.1016/j.jembe.2007.10.001

You, K., Shung, D., 2022. Rdimtools: An R package for

dimension reduction and intrinsic dimension estimation. Softw. Impacts 14, 100414. https://doi.org/10.1016/j.simpa.2022.100414
Young, G.C., Dey, S., Rogers, A.D., Exton, D., 2017. Cost and time-effective method for multiscale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D models. PLoS ONE 12, 1–18. https://doi.org/10.1371/journal.pone.0175341
Zawada, K.J.A., Dornelas, M., Madin, J.S., 2019. Quantifying coral morphology. Coral Reefs 38, 1281–1292. https://doi.org/10.1007/s00338-019-01842-4
Zunic, J., Rosin, P.L., 2004. A new convexity measure for polygons. IEEE Trans. Pattern Anal. Mach. Intell. 26, 923–934. https://doi.org/10.1109/TPAMI.2004.19

SUPPLEMENTS

TABLE S1 | Names, references and parameters (number of normals, number of different normals, mesh area, convex hull area, mesh volume, convex hull volume) of the 3D CAD artificial reef's modules.

	Names	References	Nb of normals	Nb of different normals	Mesh area (cm2)	Convex hull area (cm2)	Mesh volume (cm3)	Convex hull volume (cm3)	Available volume (cm3)
Biomimetism (3D-print production)	BIOM1	Designed by the authors for project EBSM	1.07E+07	2.27E+05	2.10E+05	1.44E+05	1.48E+06	3.96E+06	2.49E+06
	BIOM2	Designed by the authors for project EBSM	1.11E+07	2.37E+05	2.23E+05	1.64E+05	3.11E+06	5.03E+06	1.92E+06
	BIOM3	Designed by the authors for project EBSM	9.55E+06	2.06E+05	1.91E+05	1.59E+05	2.48E+06	4.73E+06	2.25E+06
	BIOM4	Designed by the authors for project EBSM	1.14E+07	2.49E+05	2.29E+05	1.65E+05	3.11E+06	5.13E+06	2.02E+06
	BIOM5	Designed by Boskalis©	5.43E+06	2.60E+05	2.69E+05	1.14E+05	1.04E+06	2.93E+06	1.90E+06
	BIOM6	Designed by Seaboost©	6.18E+06	3.08E+05	3.09E+05	7.25E+04	2.38E+05	1.38E+06	1.14E+06
	BIOM7	Designed by D-shape©	3.18E+06	9.69E+04	1.59E+05	8.72E+04	6.37E+05	1.69E+06	1.06E+06
Production (moulded production)	PROD1	Designed by the authors for project EBSM	1.90E+07	9.40E+01	3.80E+05	2.40E+05	6.84E+06	8.00E+06	1.16E+06
	PROD2	Designed by the authors for project EBSM	1.98E+07	9.50E+01	3.96E+05	2.40E+05	6.45E+06	8.00E+06	1.55E+06
	PROD3	Designed by the authors for project EBSM	4.30E+07	2.43E+02	8.59E+05	2.40E+05	4.56E+06	8.00E+06	3.44E+06
	PROD4	Designed by the authors for project EBSM	2.50E+07	2.72E+04	5.00E+05	2.40E+05	6.23E+06	8.00E+06	1.77E+06
	PROD5	From Tessier et al. 2015	2.10E+06	2.00E+00	1.05E+05	4.08E+04	2.35E+05	5.39E+05	3.04E+05
	PROD6	From Tessier et al. 2015	1.05E+07	1.80E+01	5.24E+05	2.05E+05	2.28E+06	7.05E+06	4.77E+06
	PROD7	From Tessier et al. 2015	4.99E+07	4.60E+01	2.50E+06	8.79E+05	1.04E+07	5.66E+07	4.61E+07
Protection (moulded production)	PROT1	From Tessier et al. 2015	3.45E+07	2.00E+00	1.72E+06	1.71E+06	1.19E+07	1.55E+08	1.44E+08
	PROT2	From Tessier et al. 2015	3.80E+06	4.20E+01	1.90E+05	1.95E+05	5.90E+05	7.54E+06	6.95E+06
	PROT3	From Tessier et al. 2015	5.29E+06	2.00E+00	2.64E+05	2.36E+05	2.70E+06	7.69E+06	4.99E+06
	PROT4	From Tessier et al. 2015	5.04E+06	5.20E+01	2.52E+05	1.52E+05	1.17E+06	4.88E+06	3.72E+06
	PROT5	From Tessier et al. 2015	4.32E+06	1.80E+01	2.16E+05	2.23E+05	2.63E+06	7.17E+06	4.54E+06
	PROT6	From Tessier et al. 2015	2.41E+06	2.30E+01	1.20E+05	1.08E+05	1.36E+06	1.84E+06	4.81E+05

T A B L E S 2 | description of the clusters of the Hierarchical Clustering on Principal Components (HCPC) by variables and dimensions

	dimension and variables	v.test	Mean in category	Overall mean	sd in category	Overall sd	p.value
Cluster 1: PROT1, PROT3, PROT2, PROT5	Dim.2	1.983	0.799	0.000	0.550	0.878	0.047
	Dim.1	-3.168	-1.660	0.000	0.139	1.142	0.002
	C	2.128	0.782	0.546	0.141	0.241	0.033
	Ht	-2.420	1.008	1.771	0.522	0.687	0.016
	Dt	-2.845	0.090	0.269	0.041	0.137	0.004
	Pt	-3.338	0.015	0.381	0.056	0.239	0.001
Cluster 2: PROD2, PROD1, PROD4, PROT6	Dim.2	-2.860	-1.153	0.000	0.448	0.878	0.004
	J	-2.616	0.549	0.795	0.090	0.205	0.009
	C	-3.082	0.205	0.546	0.043	0.241	0.002
Cluster 3: PROD6, PROT4, PROD3, PROD7, PROD5	Dim.3	3.088	0.956	0.000	0.428	0.779	0.002
	Pt	2.281	0.597	0.381	0.108	0.239	0.023
	Dt	2.232	0.390	0.269	0.114	0.137	0.026
Cluster 4: BIOM4, BIOM2, BIOM3, BIOM1, BIOM7, BIOM5, BIOM6	Dim.1	3.056	1.091	0.000	0.590	1.142	0.002
	Dim.2	2.193	0.602	0.000	0.181	0.878	0.028
	R	4.270	0.715	0.258	0.112	0.342	0.000
	Ht	3.395	2.501	1.771	0.063	0.687	0.001
	J	2.218	0.937	0.795	0.049	0.205	0.027