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REVIEW PAPER

# Physical habitat structure in marine ecosystems: the meaning of complexity and heterogeneity

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**Abstract** Habitat structure (HS) corresponds to the presence of physical structures in a system and is one of the most important ecological features that influences patterns and processes of biological communities. In this study, the use of *complexity* and *heterogeneity* in marine empirical studies in the context of HS was investigated. Empirical publications that discussed the role of physical structure on marine communities were surveyed and the use of different HS-related terms were analyzed and classified as: (i) complexity; (ii) heterogeneity; (iii) both as synonymous; and (iv) both as non-synonymous. A cluster analysis showed different patterns of use on different habitats. A conceptual clarification, through studies that presented definitions, was performed and a conceptual scheme was built considering two applications: (i) multidimensional or unidimensional measures; and (ii) quantitative, qualitative, or quali-quantitative measures. There was no agreement in the use and application of HS related terms in different marine habitats, and the analyses performed here indicated that (i) *complexity* corresponds to a multidimensional measurement with parts that interact and (ii) *heterogeneity* is one dimension of the habitat complexity. The present study provided the starting point for closer communication within different areas of ecology and contributes to future robust generalizations regarding HS.

**Keywords** Structural elements · Conceptual clarification · Standardization · Biodiversity

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## Introduction

Habitat structure (HS) corresponds to the presence of physical structures in a system and is characterized by different dimensions, considering qualitative (type of structural elements, such as different kinds of rocks, vegetation and sediment fractions) and quantitative measures (number of distinct structural elements and relative or absolute abundance of them) (McCoy & Bell, 1991; Wiens, 2000; Tews et al., 2004; Tokeshi & Arakaki, 2012). A highly structured ecosystem provides a greater number of microhabitats and niches, increasing the potential persistence of populations, coexistence of competitors, as well as prey and predators, and can positively influence biodiversity (MacArthur & Levins, 1964; Wiens, 1976, 2000;

Buhl-Mortensen et al., 2010). On the other hand, some studies such as Bourget et al. (1994), Feller & Mathis (1997), Kelaher (2003), and Sueiro et al. (2011) showed that biological aspects may not respond positively to the increase of HS. Reviews by McCoy & Bell (1991) and Tews et al. (2004) pointed out that one important explanation for these distinctive patterns might be the conceptual miscellany in the literature.

McCoy & Bell (1991) showed that characteristics of the HS have received different nominations (e.g., diversity, heterogeneity, complexity, topography), and most of them had a vague ecological application. Some terms are used with different definitions and applications, which is typically a consequence of the independent development of different specialties of knowledge in ecology (Pickett et al., 2007). Thus, there is a clear need to clarify the conceptual framework and facilitating communication between different specialties of knowledge.

McCoy & Bell (1991) proposed a description for HS based on three axes. The two main axes are *heterogeneity* and *complexity*, which are dependent on the third axis, the *scale*. Heterogeneity was defined as the relative abundance of different structural components of the environment and complexity as the absolute abundance of these components. Tokeshi & Arakaki (2012) diverged with McCoy & Bell (1991) and proposed that habitat complexity must be interpreted as encompassing different characteristics of structure, rather than referring solely to the abundance of structural components. Then, they recognized at least five traits that need to be taken into account when assessing habitat complexity (i.e., scale, diversity of elements, spatial arrangement, size, and abundance of elements). The disagreement between these two previously mentioned studies represents a problem observed in ecological literature, and the terms *complexity* and *heterogeneity* continue to be used in different ways (e.g., Bourget et al., 1994; Kelaher, 2003; Meager et al., 2011; Nunes et al., 2015).

Potential lack of clarity in the definition and implementation of concepts can mask ecological trends of the relationship between biological communities and HS (Wiens, 2000). HS has a crucial role for conservation, serving as a guideline for selection of protected areas, as well as the recovery of degraded areas (e.g., implementation of artificial reefs) (Bohnsack, 1991; Charton & Ruzafa, 1999). Therefore, misuse of concepts may lead to serious consequences in empirical context and conduct managers to wrong decisions.

From an extensive literature review, the present study performed a quantitative and qualitative analysis of the most used concepts in the context of HS in marine ecosystems and provides the current scenario of the use of these terms. The aim of this study was to investigate the disagreement in the use and empirical application of *complexity* and *heterogeneity*, and if different patterns of use of these terms would be observed in studies that investigated different marine habitats. Moreover, a conceptual clarification was also performed, taking in account the different dimensions of the concepts (Pickett & Cadenasso, 2002), in order to provide robust definitions aiming to allow comparisons of studies addressing different aspects of HS.

## Materials and methods

### Literature survey

A search was conducted in the ISI Web of Science platform database (considering a temporal scale of 13 years, 2003–2015) using the following keywords: *habitat heterogeneity*, *spatial heterogeneity*, *habitat complexity*, *spatial complexity*, *structural heterogeneity*, and *structural complexity*. Additionally, the search was refined according Web of Science categories: (i) Ecology, (ii) Marine Freshwater Biology, (iii) Environmental Sciences, (iv) Oceanography, (v) Biodiversity Conservation, (vi) Zoology, (vii) Fisheries, (viii) Evolutionary Biology, (ix) Behavioral Sciences, and (x) Water Resources. During the search, the following studies were not considered: (i) from freshwater and terrestrial environments, (ii) reviews, and (iii) that did not address habitat physical structure (e.g., articles that considered heterogeneity or complexity as environmental conditions as temperature, pH, and wave exposure or as stratification of water layers).

The search resulted in 181 empirical publications that used *complexity* and *heterogeneity* examining the influence of HS on marine communities (e.g., biodiversity, interaction rate between predator and prey, population oscillations) from different habitats. For each study analyzed, the following information was recorded: (i) type of marine habitat, (ii) year of publication, (iii) terms used to characterize the HS (i.e., complexity, heterogeneity or both), (iv) definition of terms (here literally registered), and (v) reference of the terms (studies cited, in the surveyed articles, as reference for the definition).

## Data analysis

The use of the terms complexity and heterogeneity was analyzed and classified for all studies surveyed as: (i) complexity (only); (ii) heterogeneity (only); (iii) complexity and heterogeneity as synonymous; and (iv) complexity and heterogeneity, both used as non-synonymous. Marine physical HS studies encompass almost exclusively benthic habitats, and studies were categorized accordingly to which benthic habitat it was done: Coral reef, Rocky intertidal, Seagrass, Mussel bed/Oyster reef, Rocky subtidal, Kelps, Mangrove, Soft bottom, Macroalgae, Coastal water, Deep ocean, Salt marsh, Rhodolith bed, Laboratory experiments (Lab), and More than one habitat (MTOH) (Table 1).

Hierarchical cluster analysis was performed (group average method) to analyze the similarity between the habitat categories based on the number of articles that use the terms in different ways (i.e., heterogeneity, complexity, heterogeneity, and complexity as synonymous, heterogeneity, and complexity as non-synonymous) and did not consider the definition of the terms. In this analysis, habitat categories that contain 90% of all sampled articles were considered (Coral reef, Rocky intertidal, Seagrass, Mussel bed/Oyster reef, Rocky subtidal, MTOH, Kelps, Soft bottom and Deep ocean), and the software PRIMER 6.0 (Clarke & Warwick, 2001) was used.

## Conceptual clarification

Conceptual clarification of *complexity* and *heterogeneity* was performed with the surveyed articles that presented definitions ($n = 31$), following the methodology of Pickett & Cadenasso (2002). The clarification considered two conceptual dimensions: (1) the core concept, i.e., the most general definition of each concept; and (2) the model, i.e., how the concepts are operationalized in the context of the HS in marine ecosystems. The core concept is essential to understand the main meaning of the terms complexity and heterogeneity that must drive their uses in ecology to facilitate the communication between different fields of knowledge.

**Table 1** Comments about the habitat categories analyzed

| Habitat category | Comments |
|---|---|
| Coral reef ($n = 39$) | |
| Rocky intertidal ($n = 29$) | |
| Seagrass ($n = 20$) | |
| Mussel bed/Oyster reef ($n = 13$) | Bottoms with the presence of shells |
| MTOH ($n = 13$) | MTOH corresponds to the papers that investigated more than one habitat category in the same study, for example seagrass and coral reef or rocky intertidal, coral reef, and mangrove |
| Rocky subtidal ($n = 13$) | Rocky reef and artificial reef |
| Coastal water ($n = 11$) | Coastal areas that do not have typical structural elements (estuaries, lagoons, continental shelf waters), or in which structures were added for experiments (e.g., rock, vegetation, artificial structure) |
| Soft bottom ($n = 8$) | |
| Kelps ($n = 8$) | |
| Deep ocean ($n = 8$) | Slopes and reefs of deep ocean |
| Mangrove ($n = 6$) | |
| Salt marsh ($n = 4$) | |
| Lab ($n = 4$) | Manipulative studies performed in laboratory |
| Macroalgae ($n = 3$) | |
| Rhodolith bed ($n = 1$) | |

A survey of the terms *complex*, *complexity*, *heterogeneous*, and *heterogeneity* was conducted in two main dictionaries of English language (The Oxford and Cambridge English Dictionaries) in order to identify the most general definition of the concepts, i.e., core concepts. Additionally, to understand how the concepts are operationalized, the central ideas of the definitions were analyzed and grouped in order to build a scheme. In the present review, definitions were organized as synonymous or not, and in two kinds of classification. The first classification was: (i) multidimensional measurement, that corresponds to more than one space dimension (e.g., *complexity* or *heterogeneity* as topography, rugosity, tridimensional surface) or more than one characteristic of the HS (e.g., number, density and composition of structural elements); or (ii) unidimensional measurement, that corresponds to one characteristic of the HS (e.g., *complexity* as density or number of HS). The second classification was: (i) quantitative (e.g., density and/or number of distinct structural elements), (ii) qualitative (e.g., composition/type of structural elements), and iii) quali-quantitative measurements (e.g., number and composition of structural elements). Therefore, only multidimensional definitions of *complexity* or *heterogeneity* could be classified as quali-quantitative measurements. Definitions that do not fit clearly into these classifications and/or present vague ideas have been presented as *unclear definitions*.

## Results

### Uses and definitions of *complexity* and *heterogeneity*

There has been an increase in the number of publications discussing the role of HS on marine ecosystems over the last 13 years, especially using the term complexity (Fig. 1). In general, the use of *complexity* was the most frequent case (55.2% of all publications) compared with the other kinds of use and increased from 2003 to 2015. The second most common approach was the use of *complexity and heterogeneity as synonymous* (30.9%) (Fig. 1).

Overall, the five ecosystem categories that represented 70% of all publications (Coral reef, Rocky intertidal, Seagrass, Mussel bed/Oyster reef, Rocky subtidal, and MTOH) showed that the term *complexity* presented the greatest use and both terms as *synonymous* was the second greatest use observed, except Rocky subtidal category that the greatest use was both terms as *synonymous* (Fig. 2).

Cluster analysis indicated two major groups of clustering of habitat categories considering different use of *complexity* and *heterogeneity* (Fig. 3). In the Soft bottom and Deep ocean categories (Group A), both terms were mainly used as *synonymous*. The second group (B), studies on all other habitats, mostly used *complexity* and with low occurrence of the other uses (heterogeneity, complexity, and heterogeneity as synonymous and non-synonymous). Moreover, the Group B was clustered in two subgroups: B1) Seagrass, Coral reef, and Rocky intertidal, that showed higher proportion in the use of terms as *non-synonymous* than B2) Rocky subtidal, Kelps, Coastal Water, MTOH, and Mussel bed/Oyster.

Around 80% of all publications did not define the terms used to characterize the HS (Fig. 4). Mangrove and Rocky intertidal categories had the highest number of papers with definitions considering the total of publications belonging to each category (around 33% and 26%, respectively). In addition, of the 181 articles collected, 88% had no references for the definitions presented.

The reference most cited by studies surveyed that defined the terms *complexity* and/or *heterogeneity* was McCoy & Bell (1991) (63% of publications with citation). Other references cited in the studies surveyed to define the terms used were Gee & Warwick (1994), Beck (2000), Loehle (2004), Dunn & Halpin (2009), Meager et al. (2011) and Tokeshi & Arakaki (2012). Beck (2000), Dunn & Halpin (2009), and Meager et al. (2011) did not present their own definitions (Table 2). Beck (2000) and Meager et al. (2011) are empirical studies that cited the definitions of *complexity* and *heterogeneity* developed by McCoy & Bell (1991). Besides, Dunn & Halpin (2009) is also empirical and did not define *complexity* (Table 2).

### Conceptual clarification of *complexity* and *heterogeneity*

The meanings of *complex* and *complexity* showed that the core of these concepts includes the connection between different parts (Online Resource 1), observed as "many different and *connected* parts," "quality of being *intricate*" and "many parts *related* to each

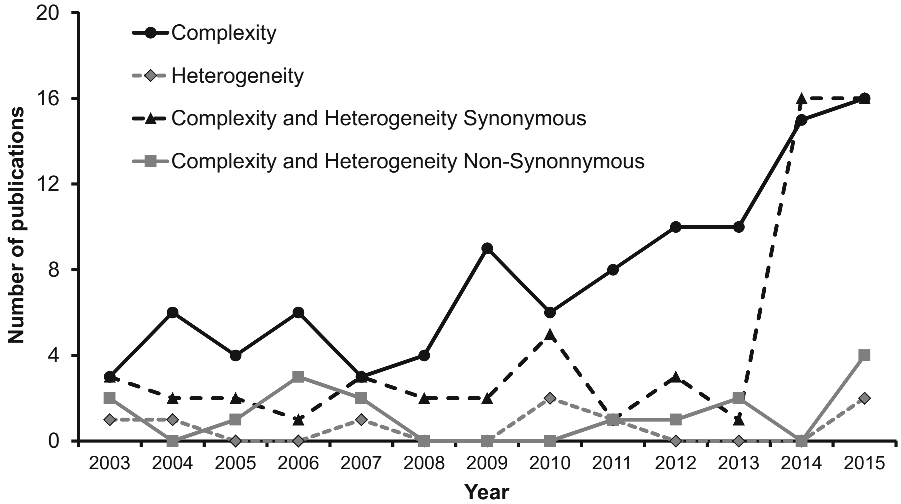


**Fig. 1** Number of publications documenting the use of the terms complexity and heterogeneity isolated, as synonymous and non-synonymous over time, in the context of HS in marine studies ($n = 181$)

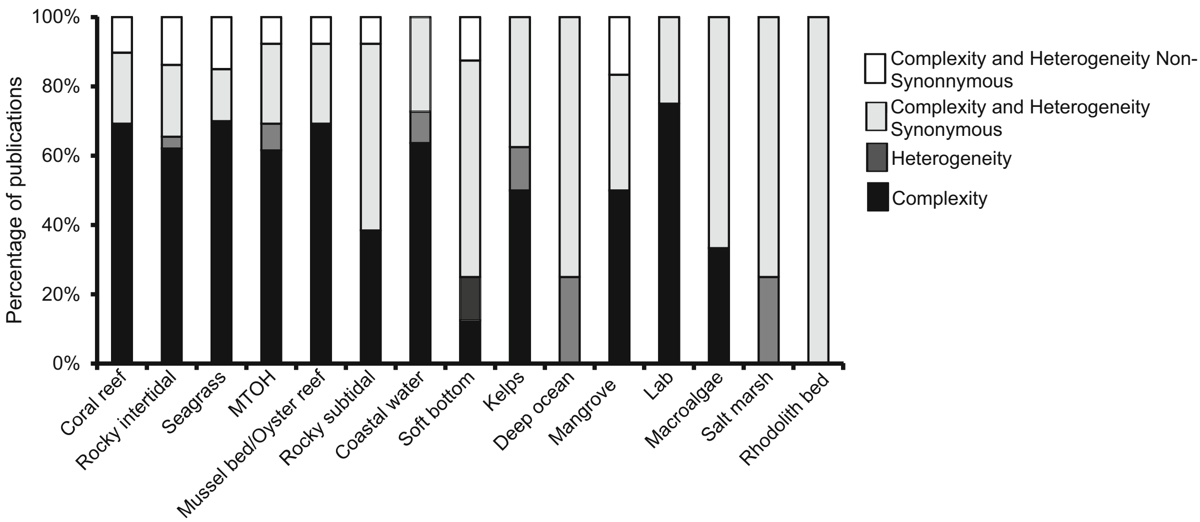


**Fig. 2** Percentages of publications that used the terms complexity and heterogeneity isolated, as synonymous and non-synonymous in context of HS for each marine habitat categorized ($n = 181$)

other." In addition, meanings of *heterogeneous* and *heterogeneity* indicated that the core concept includes the existence of different types of *things* and the quotes "*diverse* in character or content" and "*different parts or types*" make this clear.

In the context of HS in marine ecosystems, *complexity* was frequently used alone, in a multidimensional approach and as a quantitative measure (Fig. 5; Online Resource 2). Moreover, the majority of definitions of *heterogeneity* were classified in unidimensional approach and as a quantitative measure (Fig. 5; Online Resource 2). No definition of complexity and/or heterogeneity was found in the surveyed studies that could be classified only as a qualitative measure in the multidimensional approach.

## Discussion

In the last decade, empirical studies dealing with the influence of HS on biological communities in marine environments were mostly done on benthic habitats.

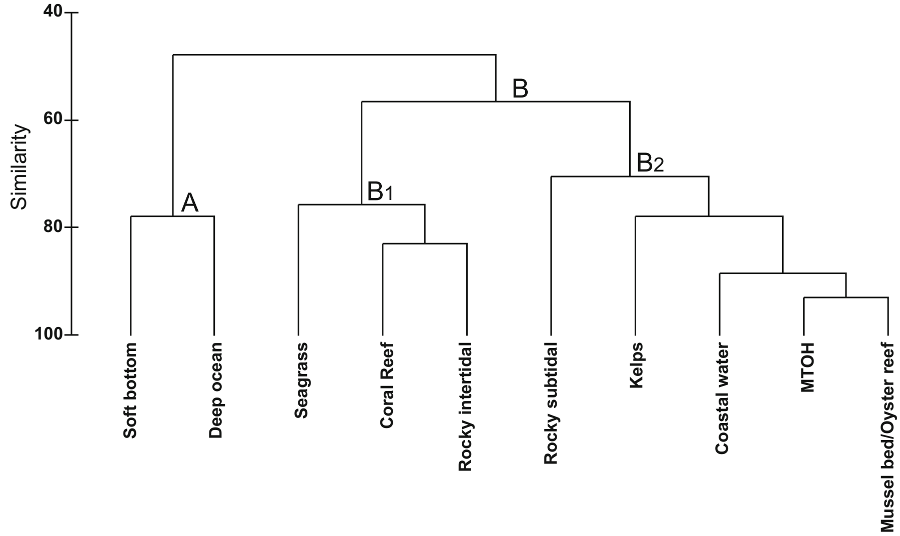


**Fig. 3** Cluster analysis of the number of publications considering the use of terms complexity and heterogeneity in habitat categories of the marine studies that contain 90% of all publications. *A* and *B* represent clustering groups, as well as *B1* and *B2* represent the subgroups clustered for group *B*

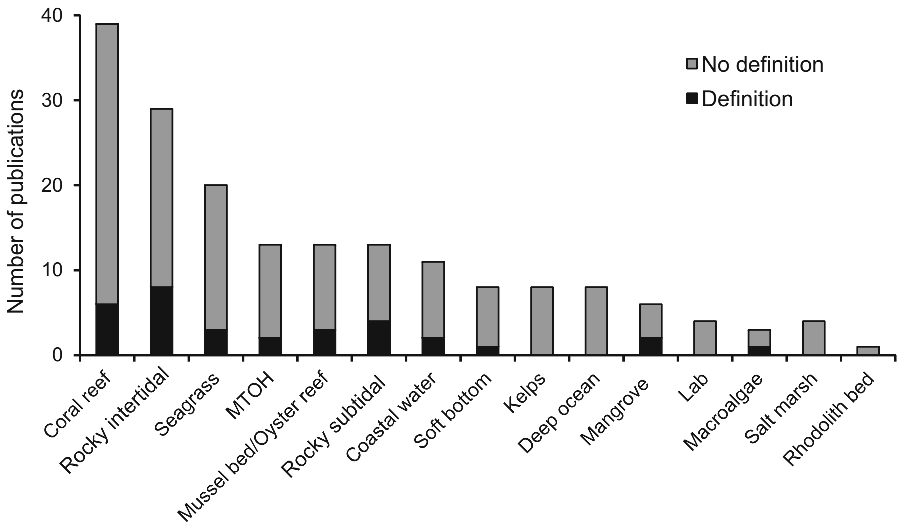


**Fig. 4** Number of publications surveyed that defined and not defined the terms complexity and heterogeneity in context of HS in marine studies ($n = 181$)

These studies showed the disagreement in the use and application of the terms *complexity* and *heterogeneity*. The occurrence of different uses of the terms on studies performed in distinct habitats (e.g., coral reefs, mangroves, rocky intertidal and subtidal shores, seagrasses, mussel beds) blurs the understanding of the effect of HS in marine ecology. However, a small overlap in central ideas of the concepts of *complexit*y and *heterogeneity* was observed between the definitions found in the surveyed articles and in the core meanings of terms (dictionaries definitions). Considering the breadth of the core meanings, this slight overlap could be the starting point for clarification of *heterogeneity* and *complexity* concepts in the context of HS. Clarification is necessary to formulate clear general definitions that will help comparison between different studies in marine environments.

**Table 2** Terms and definitions from references cited in the publications surveyed by this study

| Reference | Term | Definition |
|---|---|---|
| McCoy & Bell (1991) | Complexity | "…encompasses variation attributable to the absolute abundance (per unit area or per unit volume) of individual structural components" |
| | Heterogeneity | "…encompasses variation attributable to the relative abundance (per unit area or per unit volume) of different structural components" |
| Gee & Warwick (1994) | Complexity | "…is concerned with the small-scale characteristics of a habitat such as the size, shape, surface texture and degree of angularity of a substrate and their relationship to inter-substrate spaces" |
| Beck (2000) | Complexity | There is no own definition |
| | Heterogeneity | "McCoy and Bell (1991) offered a definition of habitat structure…proposes that it is composed of at least two major factors, complexity and heterogeneity" |
| Loehle (2004) | Complexity | "Tridimensional structure generated by the geometric aspects of the physical objects" |
| Dunn & Halpin (2009) | Complexity | There is no own definition |
| | | "Our use of 'rugosity' in the present paper refers to changes in the degree and direction of relief and does not fully encompass other measures of topographic or benthic complexity" |
| Meager et al. (2011) | Complexity | There is no own definition |
| | Heterogeneity | "Heterogeneity, the relative abundance of different structural features such as crevices and macrophytes within a habitat; and complexity, the physical architecture of a habitat (McCoy & Bell, 1991)" |
| Tokeshi & Arakaki (2012) | Complexity | "…the concept of habitat complexity implies the existence of different 'kinds' of elements that constitute a habitat" |

The marked increase in the number of publications that addressed HS in marine ecosystems reflects the importance of this topic for ecology, and the main habitat category responsible for this trend was coral reef. The number of publications documenting HS in coral reef is increasing since the 1960s (Graham & Nash, 2013). This habitat provides one of the most striking examples of the effect of HS on associated organisms, and presents pioneering studies in the quantification of HS in aquatic environment (Kovalenko et al., 2012). The tradition in research of coral reefs possibly influenced other research fields in the benthic marine environment, including the use of the term *complexity* in investigations of the effects of HS on different communities.

In empirical measurements of *complexity* and *heterogeneity*, scientists from distinct areas face different situations to evaluate the HS. For example, the kind of habitat in coral reefs and rocky intertidal (i.e., hard substrate) are clearly different compared to seagrass or kelp forests. The choice of measurements in empirical studies should consider the reality of study site (e.g., kinds of structural elements) and biological group faced in sampling or experimentation; however, there must be a general definition in order to allow comparison between different studies and ecosystems.

*Heterogeneity* to McCoy and Bell (1991), and to some studies surveyed here, corresponds to a quantitative measure, but its applicability usually refers to kinds of structural elements in some habitat (e.g., rocks, vegetation, crevices), i.e., composition. Then, the definition of *heterogeneity* used alone or as *non-synonymous* has a relation with the qualitative core meaning surveyed from the dictionaries (i.e., the existence of different types of *things*). Therefore, it is possible to define *heterogeneity* as a qualitative and unidimensional entity of HS that corresponds to types of structural components of the environment (e.g., rocks, crevices, shoots, sediment fractions).

Overall, *complexity* definition in the publications surveyed has been similar to its core concept (*many different and connected parts*), and these different parts in theoretical studies was discussed as different characteristics of structure (Loehle, 2004; Tokeshi & Arakaki, 2012). However, the idea of *connection between parts* expressed in the core meaning of the terms *complexity* and *complex* was not observed in

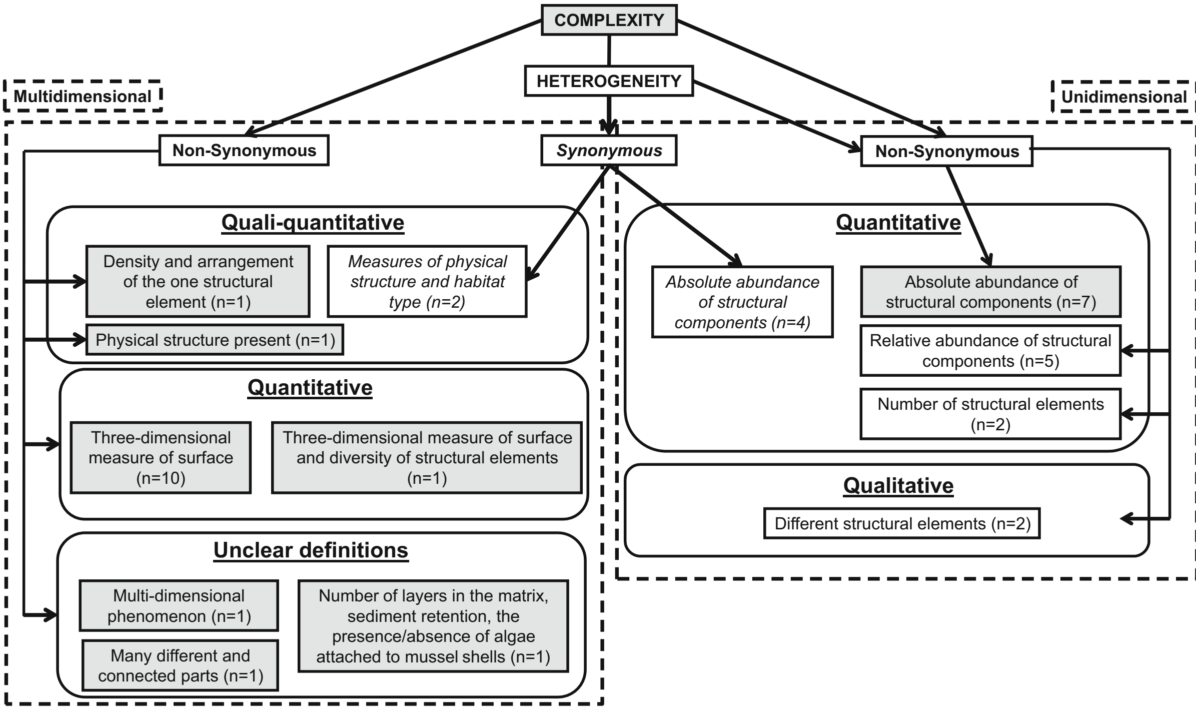


**Fig. 5** Scheme of the central ideas of *complexity* and *heterogeneity* definitions found in a subset ($n = 31$) of the 181 publications reviewed. Definitions of both terms used as non-synonymous in some publications was showed separated and the total of definitions in the scheme was 38. This scheme is organized in the multidimensional and unidimensional approaches of the concepts, and these were classified here as quantitative, qualitative, and quali-quantitative measures, as well as unclear definitions. Definitions for isolated use of complexity are represented by *boxes filled with gray*, isolated use of heterogeneity are showed in the *boxes with no fill* and for both terms as synonymous, definitions are represented by *boxes with no fill* and *italic font*

the surveyed studies. Ecological relationships are not restricted to isolated traits of a multidimensional variable, as HS, and more likely those traits (e.g., distinct dimensions of HS) interact with each other (Corning, 2000). Then, structural habitat complexity could be defined as a multidimensional entity that corresponds to a set of qualitative (e.g., composition or spatial arrangement of structural elements) and quantitative structural traits of habitat (e.g., number, size, and density of the different structural elements) that may interact and affect ecosystems at different levels.

Here is proposed an integrative and multidimensional perspective of HS in marine systems, similar to what was indicated by Tokeshi and Arakaki (2012). The *habitat complexity* corresponds to the variation of HS in a given place (i.e., the most structured habitats correspond to the most complex habitats) and *habitat heterogeneity* refers to one dimension (or trait) of structural habitat complexity.

## Conclusion

Review and conceptual clarification of use of the terms *complexity* and *heterogeneity* for HS studies in marine ecosystems demonstrated that they do not have a conventional use. Therefore, ecological empirical studies urgently need to make clear what concepts are behind the measurements performed and correctly cite them allowing closer communication between different areas of knowledge. This will contribute more robustly to generalizations, such as the positive influence of HS on the diversity of marine communities. The framework used here, which is addressing HS and the core meaning of the terms in marine empirical studies, indicated that the concept of *complexity* must be operationalized as a multidimensional measurement with parts that interact and consider *heterogeneity* as a part of the habitat complexity. Moreover, given the great importance of habitat complexity on functioning of ecosystems, further investigations addressing the influence of different traits of HS and the possible interaction of them on different levels of organization in marine ecosystems are required.

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