



Matching ecological functioning with polychaete morphology: Consistency patterns along sedimentary habitats



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ABSTRACT

The relationship between form and function is usually evident and reflect causal relationships in ecological interactions. However, the consistency of the taxonomical and functional approaches versus a morphological approach is yet to be assessed and applied to benthic-sediment relationships. Here, we propose a new functional classification based on morphological characteristics using polychaetes. To test the validity of the framework we assess the consistency between polychaete responses to distinct sedimentary environments using morphological, taxonomical and biological traits approaches, and comparing the patterns of polychaete responses at local and regional scales. The selected morphological characteristics were pharynx complexity, jaws presence, feeding palps, head appendages, body appendages, body support structures, branchiae and body regionalization, as well as number of segments, which were categorized according to presence, size, number or type of structure. The novel morphological method was successfully applied and all analyses showed consistent faunal patterns of variation along muddy and sandy habitats at the distinct spatial scales. Nevertheless, in the three case studies the morphological method explained more over the general variability and was more concise than the other two methods, emphasizing the reliability of a functional approach. The distinct set of morphological characteristics found in muddy and sandy habitats reflected two different ecological roles of polychaetes. Discretely motile, small sized and of low sensibility polychaetes prevailed in muddy habitats, while sandy sediments were dominated by organisms with richer and more heterogeneous characteristics. The responses of the morphological analysis were very similar to the taxonomical and biological traits analysis, but with a much higher explanatory power, meaning that morphology provides a robust approach for studying the ecological functionality of marine benthic systems.

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1. Introduction

Similarities among organism's traits within a community enable an arrangement that account for the role played by species in the environment. This functional classification emerged from the concept that the boundaries of species' niches are defined by resource availability, resource partitioning, and competition (Hutchinson, 1959; Keddy, 1992). Assessments of benthic communities functioning have been successfully made by means of biological traits analysis (BTA) and are useful to environmental impact assessments, as well as defining conservation strategies (Frid et al., 2008; Bremner et al., 2003a; De-Juan and Demestre, 2012; Rees et al., 2013).

The biological traits analysis detach from trait-based approaches mainly by the fact that the former usually uses a trait value previously established, which is a potential trait instead of a measured trait of an organism. In this sense, studies using a potential trait described at a

specific taxonomical level could be equivalent and comparable to studies using the same specific taxonomical level classification. Taxonomic and functional approaches have been compared in several studies (Törnroos et al., 2014; Strong et al., 2015). Nonetheless, the majority does not use equivalent information. Reliable comparisons should arise from balanced information of both components, such as data sets of the same hierarchical level (Mlambo, 2014). However, the use of the biological traits framework does not guarantee that all traits are indeed classified at the same taxonomical level. This simply reflects the many gaps in biological information so that one might classify trait potential using the nearest available classification of a taxon (i.e., genus, family, or a higher taxonomical group; Tillin et al., 2006).

One solution for reliable comparisons between functional and taxonomical classifications could be the usage of morphological instead of a myriad of biological traits. The anatomical features of organisms have been a central element in biology for centuries (Adams et al., 2004), and taxonomy itself was historically based on descriptions of morphology and, more recently, on a molecular basis (Reilly and Wainwright, 1994; Adams et al., 2004). The relationship between form and function can be evident (but see ecological role of cryptic species; Sáez and

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Lozano, 2005; Bickford et al., 2006) and may reflect causal relationships in ecological interactions and assemblage studies (Miles and Ricklefs, 1984; Losos, 1990). Thus, morphology allows the comparison of both taxonomical and functional approaches.

Furthermore, matching ecological functioning with morphology can reduce the uncertainty in analytical procedures. Biological traits approach result in a suitable understanding of environmental functioning, but less than a third of the biological characteristics of marine invertebrates are truly known (Tyler et al., 2012). Moreover, some trait categories are often subjective or unrated (e.g. small, medium, and large; see the example how to rate categories in Pacheco et al., 2011). Another difficulty may emerge when selecting biological traits since it is based on a trade-off between the contribution of each trait to patterns of ecological functioning and the time/effort required to gather information (Bremner et al., 2006a). On the contrary, more information concerning morphology is available in the literature as morphological characteristics have been extensively described.

Herein we used the polychaete families as the target assemblage in soft bottom benthic assemblages. The family taxonomic level has been previously recognized as able to show accurate and robust ecological patterns (Muniz and Pires-Vanin, 2005; Aguado-Giménez et al., 2015). Polychaetes typically contribute to a high percentage of the total macrobenthic community diversity, abundance, and biomass (Hutchings, 1998). They also occupy a large part of the available niches in the marine environment and dominate marine sediments (Rouse and Pleijel, 2001) in diversified forms and ways of life (Conway-Morris, 1979; Butterfield, 1990). Studies of soft sediment assemblages are fundamental in marine environmental monitoring and assessments of impacts from human activities (Oug et al., 2012). The association between the structure of benthic assemblages and the texture of the sediments is well-known (Sanders, 1958; Gray, 1974; Snelgrove and Butman, 1995; Rosenberg, 2001) but such relationships are rarely compared using taxonomical versus morphological approaches. Furthermore, patterns of assemblages' spatial variability tend to be masked by numerous additional sources of variation and are commonly unknown (Dimitriadis et al., 2012).

In this sense, our aims were to: (a) propose a new functional classification based on morphological characteristics using polychaetes; (b) assess the consistency between polychaete responses to distinct sediment types using the traditional taxonomical, BTA and morphology-based BTA approaches; and (c) compare the patterns of polychaete responses of the three methodological approaches at local and regional scales. Sediment patchiness and related physico-chemical (e.g. turbidity, salinity, temperature) and biological (e.g. benthic and pelagic primary production structure and dynamics, biotic interaction) processes are amongst the main factors driving the composition of polychaete assemblages, and that taxonomy is highly correlated to morphology and function, we expected distinct faunal structures between sandy and muddy habitats, and that this pattern would be congruent among the traditional taxonomic, BTA and morphology-based BTA approaches. We also predicted that faunal distribution patterns along muddy and sandy habitats would similarly vary at local and regional scales using the three methodological approaches.

2. Material and methods

2.1. Defining characteristics and related categories in morphology-based BTA and traditional BTA

To establish the characteristics in the morphology-based BTA and its relationships with ecological functioning, we followed four steps from a survey of references up to selection of morphological characteristics and categories (Supplementary material S1). We started by two complementary bibliographic surveys. Hence, the first step involved searching for the most widely used functional traits in studies of marine benthic communities. This review was carried out using the keywords

“biological trait” or “functional diversity” vs. “marine benthic” within Scopus, Web of Science, and Scielo databases. We listed 51 references with 49 biological traits, which were grouped into the themes of general biology, distribution and habitat, reproduction/life history and larvae/juveniles. These groups were defined according to the following databases: Polytraits (Faulwetter et al., 2014) and the Biological Traits Information Catalogue - BIOTIC (MarLIN, 2006).

The second step was a survey of biological and morphological key aspects of polychaete families, carried out according to a well-known literature on polychaete biology (e.g. Fauchald and Jumars, 1979; Fauchald and Rouse, 1997; Rouse and Fauchald, 1997; Beesley et al., 2000; Rouse and Pleijel, 2001; Bartolomaeus and Purschke, 2005; Tzvetlin and Purschke, 2005; Jumars et al., 2015). We found 176 features, therefore grouped into 14 themes (see Supplementary material S1). Hereafter, the list of features selected in the first two steps was merged in order to filter polychaete morphological characteristics within all functional traits. This third step or filtering process involved either: a) maintaining traits already represented by morphology (e.g., head appendages); b) substituting established traits by morphological characteristics (e.g., respiration by regionalization of the branchiae); c) excluding redundancies (e.g., maximum size and longevity) or d) excluding non-applicable characteristics to polychaete families (e.g., reproductive and larval aspects that are vague or not defined at the family level). Finally, in the fourth step each of the selected morphological characteristic was categorized according to presence, size, number or type of structure. At the end of these four steps, we established the polychaete morphological characteristics and the categories within them.

To establish the biological traits used in the classical BTA, we started from the same survey already carried out in step 1, consisting in the most widely used functional traits in studies of marine benthic communities. From this survey, we selected corresponding traits and categories in order to follow the same number of morphological characteristics for comparison purposes.

2.2. Comparing three methodological approaches: taxonomical, traditional BTA and morphology-based BTA

To assess the consistency of variations in polychaete structure along sandy and muddy habitats using the new morphology-based BTA, the traditional BTA and the taxonomical approaches, we applied the methods to the same polychaete data set, of local and regional spatial scales. We used data from the NONATObase (Pagliosa et al., 2014), a database for polychaetes comprising information from several authors in the southwestern Atlantic Ocean. At the local scale, the samples were taken from 120 subtidal plots along the North and South bays of Santa Catarina Island, 27°29'S 48°30'W (for details see Pagliosa, 2005). At the regional scale, the samples were taken from 48 plots in the shallow shelf (up to 50 m depth), within the latitudinal range of 23°22' to 35°30' S (for details see Lana, 1981; Montero, 1983; Paiva, 1990; Muniz et al., 1996; Venturini, 2007; Ferreira, 2008; Almeida and Vivan, 2011). In the datasets the sedimentary environments were established using samples with at least 61% of mud or sand (almost all >80%).

The distribution patterns of polychaete assemblages along sandy/muddy habitats in both local and regional spatial scales were analyzed by a correspondence analysis (CA) for the taxonomic method and by a fuzzy correspondence analysis (FCA) for the morphological and biological methods. Correspondence analysis is an unconstrained ordination method well adapted to assess the structure of taxa-by-samples data producing simultaneous ordination of rows and columns of any array (Hill, 1973; Dolédec and Chessel, 1991). The methods were applied to a set of 32 polychaete families at the local scale data set (N = 120) and of 35 families at the regional scale (N = 48). The CA was carried out with an abundance-based matrix (taxonomical method) and the FCA with a matrix based on the combination of morphological characteristics and abundances (morphological and biological methods).

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