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**DIVERSIDADE FUNCIONAL COM BASE NA
MORFOLOGIA DE POLIQUETAS:
UMA ANÁLISE ESPACIAL INTERESPECÍFICA E INTRA-
ESPECÍFICA**

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RESUMO

Os poliquetas ocupam grande parte dos ambientes marinhos disponíveis e são frequentemente os componentes dominantes do macrobentos em número de espécies e indivíduos. Este fato se deve à longa história evolutiva que permitiu uma elevada diversidade de formas e modos de vida. A relação entre forma e função é geralmente evidente na biologia das espécies e variações nos aspectos morfológicos resultam em diferenças no papel que os organismos desempenham no ambiente e, conseqüentemente, no funcionamento do ecossistema. Neste trabalho foram utilizadas e testadas características morfológicas de poliquetas para avaliar variações na estrutura funcional em diferentes níveis de interações biológicas. Neste contexto, os objetivos deste trabalho foram: (1) avaliar a morfologia funcional de assembleias de poliquetas marinhos e (2) avaliar a morfologia funcional de *Phragmatopoma caudata* ao longo do Atlântico Sul. Para o estudo interespecífico foram selecionados os atributos morfológicos dos poliquetas e categorias. A eficiência da categorização foi testada utilizando comparações entre ambientes lamoso e arenoso e em escala local e regional. Além disso, as características determinadas foram contrastadas com a diversidade taxonômica e diversidade funcional baseada em BTA (*biological traits analysis*). As características morfológicas mostraram padrões de variação distintos para cada ambiente e foram consistentes nas escalas espaciais investigadas. A resposta da análise morfológica foi muito semelhante às outras duas,

porém com uma porcentagem de explicação maior, o que significa que a morfologia fornece uma abordagem robusta para estudar a funcionalidade ecológica dos sistemas bentônicos marinhos. A abordagem intra-específica enfatizou os diferentes níveis hierárquicos de atributos morfológicos de *Phragmatopoma caudata* (tamanhos de corpo, opérculo, brânquia, tentáculos e órgão construtor) em relação à temperatura. Os atributos mostraram diferentes respostas à temperatura com distintas adaptações ótimas, sendo observado um padrão de distribuição unimodal para os atributos de nível hierárquico superior (tamanho do corpo e opérculo) e multimodal para os atributos de nível inferior (tamanho de brânquias e tentáculos). O órgão construtor não mostrou uma relação clara com a temperatura. Estes resultados fornecem importantes evidências da percepção e inclusão de atributos de diferentes níveis hierárquicos em análises e pesquisas com diversidade funcional.

Palavras-chave: Atributos biológicos, Diversidade funcional, Morfologia, *Phragmatopoma caudata*, Polychaetes, Temperatura.

ABSTRACT

The polychaetes occupy much of the available ecological niches in the marine environment and often are the dominant components of the macrobenthos in number of species and individuals. This fact is due to the long evolutionary history that allows a high diversity of forms and ways of life. The relationship between form and function is usually evident in the biology of the species and morphology variations resulting in differences in the role that the organisms play in the environment and, consequently, in the ecosystem functioning. In this study we were used and tested morphological characteristics of polychaetes to assess changes in the functional structure at different levels of biological interactions. In this context, the objectives were: (1) assess the functional morphology of marine polychaete assemblages, and (2) assess the functional morphology of *Phragmatopoma caudata* along the Southern Atlantic Coast. The efficiency of categorization was tested using comparisons among muddy and sandy environments at local and regional scales. Furthermore, the determined characteristics were contrasted with taxonomic diversity and functional diversity based-BTA (biological traits analysis). The morphological characteristics show different patterns of variation for each environment and were consistent in spatial scales investigated. The response of the morphological analysis was very similar of the other two, but with a higher percentage of explanation. This means that the morphology provides a robust approach to study the ecological functionality of benthic

marine systems. The intraspecific approach emphasizes the different hierarchical levels of morphological traits of *Phragmatopoma caudata* (body, opercular crown, branchiae, tentacles and building organ sizes) in relation to temperature. The traits showed different responses to temperature with distinct optimal adaptations, with a pattern of unimodal distribution for the higher level traits (body and opercular crown sizes) and multimodal to lower hierarchical level traits (branchiae and tentacles sizes). The building organ showed no clear relationship with the temperature. These results provide important evidence of perception and inclusion of traits from different hierarchical levels in analysis and research with functional diversity.

Keywords: Biological traits, Functional diversity, Morphology, *Phragmatopoma caudata*, Polychaetes, Temperature.

INTRODUÇÃO GERAL

Diversidade Funcional

A diversidade biológica é um termo muito utilizado atualmente que se refere à variedade de vida na terra em todos os níveis biológicos, incorporando os processos ecológicos e evolutivos a ela associados e compreendendo desde níveis mais abrangentes como os ecossistemas até a diversidade de genes (Magurran 2004). Assim, a diversidade biológica se torna um conceito complexo em vários aspectos (Purvis & Hector 2000). Durante muito tempo, a quantificação da diversidade biológica centrou-se na medida de diversidade taxonômica (Magurran 2004). No entanto, a diversidade taxonômica fornece informações limitadas sobre as propriedades do ecossistema (Díaz & Cabido 2001), pois esse critério descreve apenas quais e quantos táxons estão presentes no sistema, mas não sua relevância funcional para o ambiente (Pacheco et al. 2011). Assumir que todas as espécies são igualmente distintas, sem considerar suas relações de proximidades ou distâncias, que são expressas numa abordagem funcional ou filogenética, pode resultar em sobre-estimação ou subestimação da diversidade (Pillar & Orlóci 1993, Dornelas 2010).

A diversidade funcional teve maior repercussão após os primeiros trabalhos publicados por Tilman e colaboradores em 1997 e 2001 e eles a definiram como os componentes da biodiversidade que influenciam como um ecossistema opera e funciona, avaliado

por meio dos valores e variação de atributos dos táxons analisados. Mais recentemente, o termo foi sendo ampliado e definido como uma medida que informa o nível de funcionamento de um sistema (Hillebrand & Matthiessen 2009) ou, também, explica e prevê o impacto dos organismos nos ecossistemas, fornecendo um *link* mecanicista entre os dois (Petchey & Gaston 2006). A relação entre biodiversidade e funcionamento dos ecossistemas tem sido um dos temas centrais da ecologia contemporânea (Tilman et al. 1997, Hillebrand & Matthiessen 2009, Song et al. 2014), uma vez que, a diversidade funcional se torna uma ferramenta de extrema importância ecológica, pois é o componente da diversidade que influencia a dinâmica dos ecossistemas, a estabilidade, a produtividade, o balanço de nutrientes e outros aspectos do funcionamento do ecossistema (Tilman et al. 2001). Esta abordagem funcional foi incorporada em estudos que avaliam os impactos causados pelo homem e a consequente perda de biodiversidade. As atividades humanas têm alterado extensivamente os ambientes, que estão sujeitos à exploração da pesca, atividade extrativista, poluição química e enriquecimento de nutrientes (Sherman 1994, Bremner 2005). Como resultado dessas atividades intensas e extensas, a biodiversidade é perdida em escala global a uma velocidade cada vez maior (Díaz et al. 2006), ameaçando os processos e serviços ecossistêmicos (Díaz & Cabido 2001).

O enfoque funcional pode ser usado conforme duas abordagens distintas, mas complementares, que consideram as variações dos atributos em escala interespecífica e/ou intra-

específica. A abordagem interespecífica compreende um enfoque nas características dos táxons da comunidade ou assembleia estudada. Uma forma de avaliar o funcionamento ecossistêmico neste tipo de abordagem é a partir de análise de atributos biológicos (*analysis of biological traits - BTA*), cuja premissa é que o ambiente determina as assembleias e comunidades por meio da seleção de características dos táxons existentes (Southwood 1977, Bremner 2006). Já a abordagem intra-específica tem ganhado espaço devido ao reconhecimento da importância da variabilidade fenotípica e dos efeitos evolutivos modelando a organização das comunidades e populações (Carlucci et al. 2015, Laughlin et al. 2015, Laughlin & Messier 2015). A abordagem baseada na variação funcional entre indivíduos de uma mesma população, leva em consideração a plasticidade fenotípica dos atributos dentro dos indivíduos de uma mesma espécie (Cianciaruso et al. 2009). A inclusão destas métricas permite um conhecimento mais completo da realidade do ecossistema (de Bello et al. 2011) considerando a existência de interações entre os indivíduos e deles com o ambiente (Cianciaruso et al. 2009, Berg & Ellers 2010, Paine et al. 2011).

Atributo biológico

Historicamente, o termo atributo (*traits*) tem sido utilizado como um preditor do desempenho dos organismos e sua aptidão, conforme o proposto por Darwin (1859). Mais recentemente, em estudos de ecologia de comunidade e ecossistema o conceito de

atributos está sendo genericamente expandido para além de seus limites originais. O termo atributo é agora utilizado em estudos que vão desde o nível de organismos até ecossistemas. Diversos tipos de atributos são, portanto, utilizados para avaliar os componentes envolvidos na explicação dos processos ecológicos em níveis mais elevados de organização (Violle et al. 2007). A fim de evitar confusão e esclarecer futuros trabalhos, foi definido que atributo é qualquer característica morfológica, fisiológica, fenológica e comportamental mensurável Na escala do indivíduo, desde o nível celular até ao nível do organismo (*whole-organism level*), sem qualquer referência ao ambiente ou qualquer outro nível de organização (Arnold 1983, Violle et al. 2007, McGill 2015).

Os atributos apresentam diferentes níveis de organização hierárquicos e, apesar de um nível não ter maior importância que o outro, estes devem ser estabelecidos a princípio (McGill 2015). Alguns podem estar em níveis hierárquicos considerados baixos, como por exemplo, a taxa de reação enzimática (Irschick et al. 2008) ou um valor específico mensurado do organismo tais como seu comprimento ou largura. Estes são chamados de atributos na escala do órgão - *organ-level*. Por outro lado, tamanho do corpo e capacidade de locomoção do organismo são considerados atributos de níveis hierárquicos superiores (Perry et al. 2004, Mowles et al. 2010). Estes são chamados de atributos na escala do organismo – *whole organism*. Embora estejam em níveis distintos e mostrem o desempenho do organismo e sua aptidão, os atributos nem sempre estão relacionados uns com os outros e suas respostas não são

necessariamente a mesma frente ao mesmo distúrbio ambiental (Craine et al. 2001, Marks 2007).

A temperatura é considerada um dos principais fatores que determina a distribuição dos atributos, sejam eles de níveis inferiores ou superiores. Atributos na escala do organismo tendem a apresentar distribuição unimodal ao longo do gradiente de temperatura, com uma única adaptação ótima (Johnson & Goodall 1979). A temperatura diminui do equador aos pólos e o tamanho do corpo dos organismos tende a aumentar na direção oposta, seguindo a Regra de Bergmann (Bergmann 1947). Indivíduos que vivem em ambientes de temperaturas baixas acumulam biomassa mais facilmente em seus corpos devido ao gasto energético ser menor (Brown et al. 2004). Em contrapartida, atributos na escala do órgão apresentam distribuição multimodal, com múltiplas adaptações ótimas ao longo do gradiente de temperatura (Laughlin et al. 2012). Isso se deve ao fato de que atributos de níveis inferiores também são susceptíveis as variações locais do ambiente (Marks 2007).

A medida individual do atributo reflete com exatidão a variabilidade do atributo em questão, uma vez que, cada organismo presente na amostra/local tem sua medida particular. Nesse sentido, os indivíduos são entidades discretas dentro das populações e é essa variabilidade interna que as mantêm e regula (Giacomini 2007, Uchmanski 2000). Entretanto, tendo em vista a necessidade de monitoramentos e avaliações da biodiversidade frente aos distúrbios causados, em sua maioria, pelo homem e a compreensão de como estas respostas podem interferir na funcionalidade dos ecossistemas,

são necessários métodos mais efetivos para monitoramentos e avaliações de impactos. Desta forma, existem métodos que utilizam atributos em potenciais em vez de atributos medidos no nível de indivíduo. Nesta abordagem, os táxons (*e.g.* espécies, gêneros e famílias) são unidades discretas e os atributos - e sua funcionalidade - são pertinentes aos táxons estudados (Moretti et al. 2009). A classificação do atributo, neste caso, pode ser obtida por meio da literatura existente e de consultas/informações de especialistas da área. O uso de atributos em potenciais baseia-se no pressuposto de que a variabilidade entre táxons será superior àquela encontrada dentro deles (Podgaiski et al. 2011).

Poliquetas - objeto de estudo

Os poliquetas são considerados um dos grupos de invertebrados dominantes em habitats bênticos em número de espécies e de indivíduos (Grassle & Maciolek 1992; Ward & Hutchings 1996) e por isso, são os que mais contribuem para os padrões de diversidade da comunidade bêntica (Olsgard et al. 2003). Habitam grande parte dos ambientes marinhos, desde regiões entremarés de praias arenosas e rochosas, manguezais até zonas abissais (Fauchald 1977). São mais comuns no bentos, embora muitas larvas e indivíduos adultos de algumas famílias habitem a coluna de água (Paiva 2006). Isto se deve à longa história evolutiva (Fauchald 1974; Butterfield 1990), permitindo uma elevada diversidade de formas e modos de vida. Além disso, o grupo é

considerado um dos mais importantes em biomassa e produtividade no meio marinho (Rouse & Pleijel 2001) e desempenha papéis ecológicos essenciais ao funcionamento deste ambiente, pois é responsável ativo pela bioturbação, retrabalhando, reciclando e transportando oxigênio e material dissolvido nos sedimentos (Hutchings 1998). Também desempenha um papel importante nas cadeias alimentares marinhas, uma vez que, os poliquetas são uns dos principais itens da dieta de invertebrados e vertebrados marinhos comerciais da costa do Brasil (Amaral & Migotto 1980; Petti et al. 1996).

Sabellariidae é uma das famílias que compõem o grupo dos poliquetas e os organismos desta família são comumente chamados de *vermes favo de mel* ou *vermes castelo de areia*, pois constroem tubos com grãos de areia cimentados uns aos outros formando uma forte estrutura tridimensional. Além de prover proteção contra predadores, tais estruturas fornecem refúgio e alimento para uma gama de outras espécies de invertebrados, sendo riquíssima a fauna associada a esses recifes de areia (Capa et al 2012). Espécies pertencentes a esta família são sensíveis a perturbações no ambiente e podem sofrer deformações no corpo, o que pode ser monitorado em estudos de dinâmica populacional em larga escala espacial (Zale & Merrifield 1989). A espécie *Phragmatopoma caudata* ocupa extensas áreas na costa do Brasil (Kirtley 1994). Vivem de modo gregário normalmente em regiões entremarés e são considerados engenheiros de ecossistema por criar, modificar e manter complexos habitats (Coleman & Williams 2002).

As funções ecológicas desempenhadas pelos poliquetas fazem deles excelentes objetos de investigação com foco funcional. Além de exercerem importantes papéis e contribuem para os padrões de diversidade e abundância da comunidade bêntica, sua intrínseca relação com as condições ambientais permite usá-los como ferramentas para estudar a funcionalidade ecológica de sistemas e aplicá-los como indicadores de mudanças do ambiente. Assim, é de grande valia sua incorporação em estudos de diversidade funcional, tanto com uma abordagem para o grupo todo como para espécies que o compõem, como neste caso a espécie *Phragmatopoma caudata*.

OBJETIVOS

Objetivo geral

O objetivo geral deste trabalho foi investigar o papel da morfologia de poliquetas e suas funções em diferentes níveis de interações biológicas e sanar lacunas nos métodos e interpretações de análises usadas em estudos funcionais, com vista a fornecer uma visão mais compreensível a respeito da funcionalidade ecológica dos sistemas bentônicos marinhos.

Objetivo dos capítulos

Capítulo I: Propor uma nova classificação funcional baseada em características morfológicas de poliquetas; avaliar a consistência das respostas dos poliquetas em tipos distintos de sedimento com base na diversidade morfológica, taxonômica e de atributos biológicos em escalas locais e regionais.

Hipótese: Assumindo que o substrato e os processos físico-químicos estão entre os principais fatores que direcionam a composição das assembleias de poliquetas e que a taxonomia está altamente correlacionada à morfologia e função, nós esperamos uma resposta similar em relação aos poliquetas entre as três abordagens. Nós também esperamos que assembleias de poliquetas nos ambientes lamosos e arenosos nas três metodologias sejam semelhantes em escalas locais e regionais.

Capítulo II: Avaliar o papel da temperatura e outras variáveis ambientais sobre a distribuição de medidas de tamanho de corpo de *Phragmatopoma caudata* ao longo de um gradiente latitudinal da costa do Atlântico Sul e comparar o tipo de distribuição dessas medidas ao longo do gradiente de temperatura.

Hipótese: Como há uma relação entre tamanho de corpo e temperatura, nós investigamos se distintas medidas de tamanhos de corpo de *Phragmatopoma caudata* têm diferentes distribuições

modais ao longo do gradiente de temperatura. Se os padrões de respostas diferem entre tamanhos de atributos na escala do organismo e na escala do órgão, nós hipotetizamos que: (1) variações nos tamanhos de atributos na escala do organismo (nível hierárquico superior) têm a sua adaptação ótima de acordo com o gradiente de temperatura; (2) variações nos tamanhos de atributos na escala do órgão (nível hierárquico inferior) têm alternativas ótimas e, embora influenciado pela temperatura, não seguem o gradiente de temperatura; e (3) nossos dados não suportam a existência de múltipla dimensionalidade ou uma hierarquia dos atributos.

**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.

Keywords: Morphology, biological traits, polychaetes, soft-bottom, functional diversity

1. Introduction

Similarities among organisms' 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 & 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 & Wainwright 1994, Adams et al. 2004). The relationship between form and function can be evident (but see ecological role of

cryptic species; Sáez & Lozano 2005, Bickford et al. 2006) and may reflect causal relationships in ecological interactions and assemblage studies (Miles & 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 & 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 & 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 2012). The association between the structure of benthic assemblages and the texture of the sediments is well-known (Sanders 1958, Gray 1974, Snelgrove et al. 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 (Appendix A). 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 benth*” 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 & Jumars 1979, Fauchald & Rouse 1997, Rouse & Fauchald 1997, Beesley et al. 2000, Rouse & Pleijel 2001, Bartolomaeus & Purschke 2005, Tzetlin & Purschke 2005, Jumars et al. 2015). We found 176 features, therefore grouped into 14 themes (see Appendix A). 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 either 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 & 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 & 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).

To build the morphology-based matrix and biological-based matrix we first used the fuzzy-coding procedure (Chevenet et al. 1994), in which the polychaete families were coded for categories within each trait using only adult characteristics. The scores ranged from 0 to 3: 0 means no affinity to a trait category; 1 means *no affinity* with some exceptions in the family; 2 means *affinity* with some exceptions in the family; and 3 means *total affinity*. The level of affinity was determined by the literature we surveyed and Polytraits database. Then, the categories within each trait were weighted by the abundance of each family per sample. Finally, we calculated the sum of the category scores multiplied by the abundance of each family and divided by the total invertebrate abundance of each category and each sample (Thioulouse et al. 1997). All multivariate analysis and graphs were performed on the R software (R Development Core Team 2009) using the package ADE-4 (Thioulouse et al. 1997).

3. Results

3.1 Characteristics and related categories in morphology-based BTA and traditional BTA

For the morphology-based BTA, nine morphological characteristics were identified according to the proposed four steps, namely: pharynx complexity, jaws presence, feeding palps, head appendages, body appendages, body support structures, branchiae regionalization, body regionalization, and number of segments. Two to four categories were established for each morphological characteristic, with a total of 24 categories. Accordingly, each definition and their categories are shown in Table 1. Following the classification based on morphological characteristics, all of the categories for the 37 polychaete families were coded after the fuzzy-coding procedure (Appendix B).

Similarly, nine biological traits were identified for the traditional BTA: feeding mode, mobility, body design, maximum size, bioturbation, habitat, substrate preference, reproductive, and larval development. Differently from morphological, fifty biological

traits/families were not coded in the fuzzy-coding produce. Of the set of nine biological traits, half had at least one category with no coding (e.g. larval development, reproductive, substrate preference, size, and bioturbation – in decreasing order of number of uncoded categories).

Table 1 – Morphological characteristics with respective definitions and categories.

Morphological characteristics	Definitions	Categories (label)
Pharynx complexity	The pharynx is referred to as the buccal organ and is restricted to the muscular regions of the foregut. These structures have been classified as ventral pharynx, axial non-muscular and muscular pharynx, and absence of a buccal organ (Tzetlin & Purschke 2005) that assist in feeding and show where the organism lives.	Absence (PH.ab) Ventral (PH.vp) Axial non-muscular (PH.nm) Axial muscular (PH.am)
Jaws presence	Jaws are cuticular structures that assist in feeding and defense. They are formed on the surface of specialized epithelial cells and usually are sclerotized parts of the pharyngeal cuticle, which may be highly mineralized (Tzetlin & Purschke 2005). These structures to resource capture	Absence (JA.ab) Presence (JA.pr)

show where the organism lives.

Feeding palps	Feeding palps are long peristomium appendices, provided with a ciliated groove that assists in feeding. They are referred to as palps, tentacles, or a radiolar crown, and have been considered homologous (Rouse & Pleijel 2001). These structures to resource capture show where the organism lives.	Absence (FE.ab) Single pair palps (FE.pp) Multiples palps (FE.mp)
Head appendages	The head of polychaetes accumulate a variety of sensory stimuli showing a wide range of sensory structures for defense and feeding, such as antenna, sensorial palps, peristomial cirri, and anterior cirri (Rouse & Pleijel 2001).	Absence (HA.ab) Only one structure (HA.os) Multiple structure (HA.ms)
Body appendages	Beside the head, polychaetes are capable of perceiving stimuli all around the body for defense and feeding, using lateral organs, statocysts, dorsal organs, and parapodial cirri (Purschke 2005).	Absence (BA.ab) Presence (BA.pr)
Body support structure	The stout structures, such as uncini parapodium with similar rami and aciculae provide support to the body and help with locomotion (Beesley et al. 2000).	Uncini (BS.un) Parapodia with similar rami (BS.ps) Aciculae (BS.ac)

Branchiae regionalization	Branchiae are responsible for gaseous exchanges that provide the energy spent in locomotion and feeding. These structures can be located at the ends or along the body (Rouse & Pleijel 2001).	Absence (BR.ab) Regionalized (BR.re) Not regionalized (BR.nr)
Body regionalization	The body can be heteronomous (divided into thorax and abdomen) or homonomous (without regionalization) (Beesley et al. 2000). The regionalization can improve body mobility.	Regionalized (BO.re) Not regionalized (BO.nr)
Number of segments	The body is divided into metameres, of few or many segments. Body size has a primary role in defining ecological niche (Wilson 1975) and determines life strategies and biomass (Prevedelli & Simonini 2003).	≤ 100 (SE.100) ≥ 101 (SE.200)

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

As expected, there was a pattern of two distinct polychaete assemblages distributed along muddy and sandy habitats, consistent in both local and regional spatial scales (Figs. 1 to 6). In the two spatial scales, richness of families was higher in sandy (31 and 33

families for the local and regional scales, respectively) than in muddy habitats (18 and 30 families for the local and regional scales, respectively).

Likewise, faunal responses were consistent between the three methods, morphology-based BTA and traditional taxonomic and BTA. In other words, the structure of assemblages in sandy and muddy habitats was clearly distinct in terms of both morphology and taxonomical patterns. Nevertheless, the CA and FCA showed that the morphological method was generally more effective in explaining variability patterns than the taxonomical and biological methods (Figs. 1 to 6).

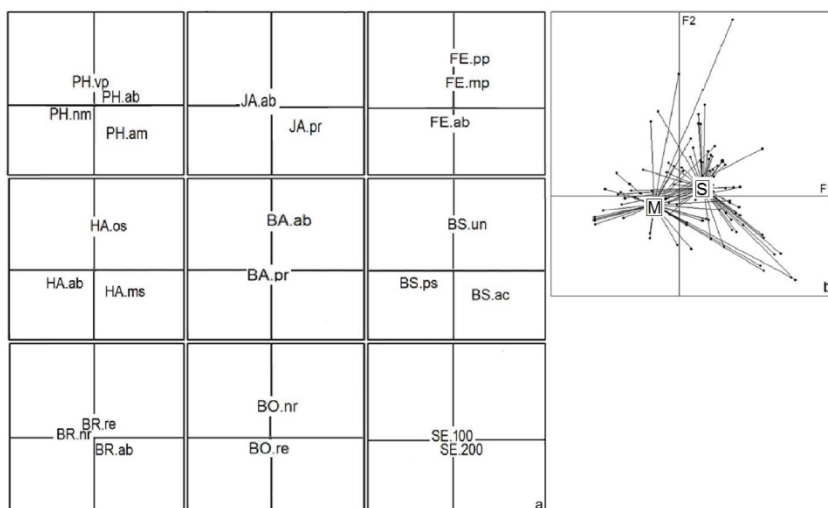


Figure 1 - Fuzzy correspondence analysis (FCA) of all morphological characteristics weighted by the abundance of families on the local scale: (a) factor map showing the distribution of categories within the 9 morphological characteristics and (b) factor map of sediment samples (M mud and S sand). For trait labels see Table 1.

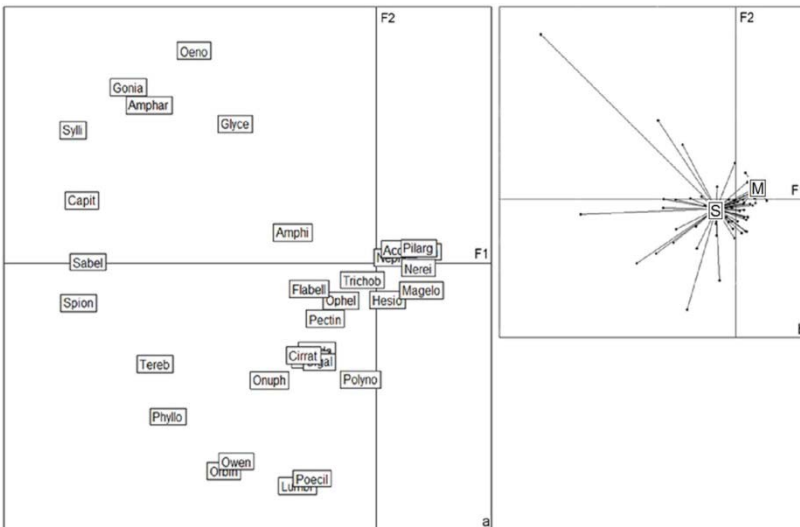


Figure 2 - Correspondence analysis (CA) of abundance of families on the local scale: (a) distribution of polychaete families on the factor map and (b) factor map of sediment samples (M mud and S sand). Each site label was positioned at the weighted average of its samples. Capit Capitellidae, Malda Maldanidae, Ophel Opheliidae, Orbin Orbinidae, Parao Paraonidae, Cossu Cossuridae, Nepht Nephtyidae, Nerei Nereididae, Gonia Goniadidae, Sigal Sigalionidae, Hesio Hesionidae, Sylli Syllidae, Glyce Glyceridae, Lumb Lumbrineridae, Onuph Onuphidae, Phyll Phyllodocidae, Amphi Amphinomidae, Polyn Polynoidae, Acoet Acoetidae, Oeno Oeonidae, Pilar Pilargidae, Oweni Owenidae, Sabel Sabellidae, Ampham Ampharetidae, Magel Magelonidae, Spion Spionidae, Cirra Cirratulidae, Flabe Flabelligeridae, Pecti Pectinoridae, Tereb Terebelidae, Poeci Poecilochaetidae, Trich Trichobanchidae.

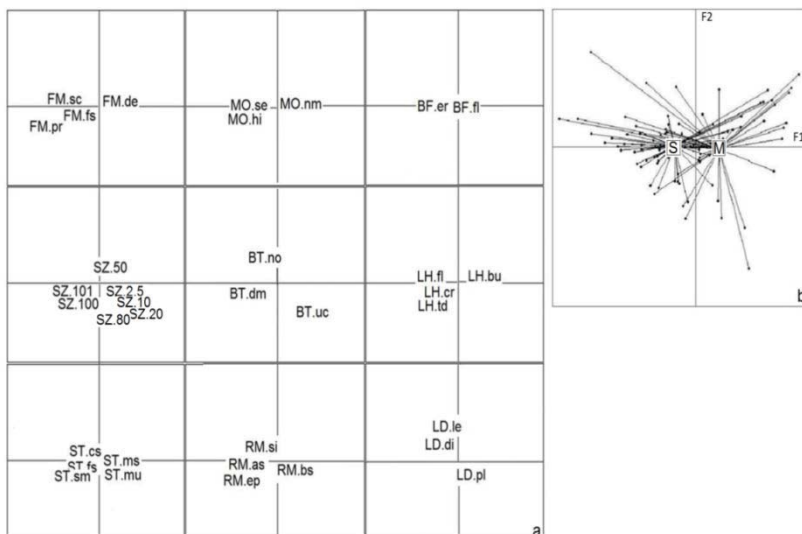


Figure 3 - Fuzzy correspondence analysis (FCA) of all biological traits weighted by the abundance of families on the local scale: (a) factor map showing the distribution of categories within the 9 biological traits and (b) factor map of sediment samples (M mud and S sand). Biological trait labels: Feeding Mode FM, deposit feeder FM.de, filter-suspension feeder FM.fs

scavenger FM.sc, predator FM.pr, Mobility MO, highly mobile MO.hi, non-mobile MO.nm, sedentary MO.se, Body Form BF, flat BF.fl, mound BF.mo, erect BF.er, Size SZ, <2.5mm SZ.2.5, 2.5-10mm SZ.10, 11-20mm SZ.20, 21-50mm SZ.50, 51-80mm SZ.80, 81-100mm SZ.100, >100mm SZ.101, Bioturbation BT, diffusive mixing BT.dm, upward-downward conveyor BT.uc, none BT.no, Living Habit LH, tube-dweller LH.td, burrow LH.bu, crevice LH.cr, free-living LH.fl, Substrate Type ST, coarse sand ST.cs, fine sand ST.fs, sandy mud ST.sm, muddy sand ST.ms, mud ST.mu, Reproductive Method RM, sexual internal RM.si, asexual RM.as, sexual external broadcast spawner RM.bs, epitoki RM.ep, Larval Development LD, planktotrophic LD.pl, lecithotrophic LD.le, direct LD.di.

At the local spatial scale, the first two axes of the FCA on the morphological data explained 66.4% of the overall variability. On the other hand, the two axes of the CA on the taxonomical data accounted for only 26.1% of the total variability and the two axes of FCA on the biological traits data explained 58.3% of the variability. The ordination of polychaete morphological characteristics along the axes of the FCA showed that muddy habitats (M) were mainly dominated by: presence of axial non-muscular pharynx and ventral pharynx, absence of jaws, feeding palps, and head appendages, presence of body appendages, non-regionalized branchiae, parapodium with similar rami and regionalized body, with less or a maximum of 100 segments. Moreover, sandy habitats (S) were associated to: presence of axial muscular pharynx or absence of pharynx, presence of jaws, feeding palps and head appendages, absence of body appendages, absence or regionalized branchiae, presence of parapodium with uncini and aciculae and non-regionalized bodies, with 200 or more segments (Figs. 1.a and 1.b). The CA on the array of family abundances discriminated two groups, which were either negative on F1 and positive/negative on F2 or

positive on F1 and positive/negative on F2 (Fig. 2.a). The projection of samples on the graph showed a clear correspondence to the sandy (S) and muddy (M) habitats (Fig. 2.b), formed by many families. In the last methodological approach, the ordination of biological traits along the axes of the FCA showed that muddy habitats (M) were mainly dominated by: deposit-feeders, non-motile, size with 2.5 to 80 mm, bioturbation upward conveyor, burrow, broadcast spawner, external reproduction, and plankthotrophic larvae. Moreover, sandy habitats (S) were associated to: predator, scavenger, filter-feeders, highly-motile, sessile, erect body, with 100 mm or more size, diffusion mixer and non-bioturbation, free-living, crevice and tube-dweller, sexual internal and epitoki reproduction, and lecithotrophic and direct larval development (Figs. 3.a and 3.b).

At the regional spatial scale, the analyses showed distribution patterns very similar to those found at the local scale, with separated faunal groups corresponding to each type of sedimentary habitat (Figs. 4 to 6). Again, the morphological method explained a larger proportion of the data in the FCA than the taxonomical and biological methods in the CA (58.4%, 26.4% and

43.1 for the first two axes, respectively). In the FCA, the differences in the pattern of distribution of morphological characteristics were the presence of ventral pharynx and non-regionalized branchiae associated with sandy habitat (Figs. 4.a and 4.b). The CA on the abundance of families also discriminated two faunal groups, of either negative on F1 and positive/negative on F2 or positive on F1 and positive/negative on F2. However, the projection of samples showed an inverted correspondence to the sedimentary habitats, muddy (M) to the first group and sandy (S) to the second (Figs 5.a and 5.b). In the biological approach, the difference in the pattern of traits distribution were the size 2.5 mm and epitoki reproduction associated with sandy habitat and broadcast spanner reproduction with associated with muddy habitat (Figs. 6.a and 6.b).

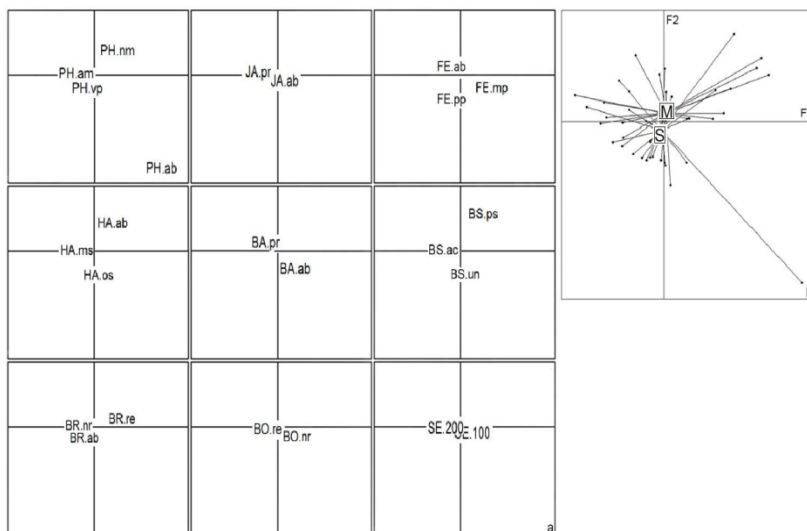


Figure 4 - Fuzzy correspondence analysis (FCA) of all morphological characteristics weighted by the abundance of families on the regional scale: (a) distribution of categories of the 9 morphological traits on the factor map and (b) factor map of sediment samples (M mud and S sand). For trait codes, see Table 1.

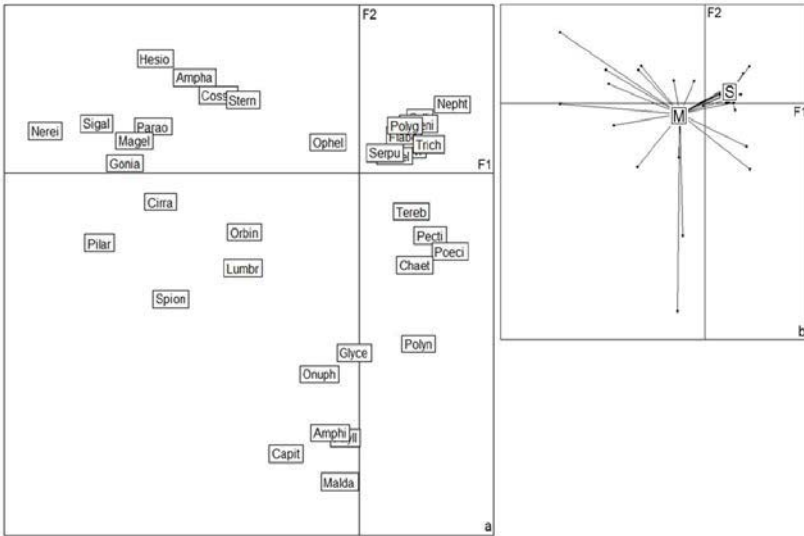


Figure 5 - Correspondence analysis (CA) of abundance of families on the regional scale: (a) distribution of polychaete families on the factor map and (b) factor map of sediment samples (M mud and S sand). Each site label was positioned at the weighted average of its samples. Capit Capitellidae, Malda Maldanidae, Ophet Opheliidae, Orbin Orbiniidae, Parao Paraonidae, Cossu Cossuridae, Nepht Nephtyidae, Nerei Nereididae, Gonia Goniadidae, Sigal Sigalionidae, Hesio Hesionidae, Sylli Syllidae, Glyce Glyceridae, Lumbr Lumbrineridae, Onuph Onuphidae, Phyll Phyllodocidae, Amphi Amphinomidae, Polyn Polynoidae, Dorvi Dorvilleidae, Pilar Pilargidae, Oweni Owenidae, Sabel Sabellidae, Ampha Ampharetidae, Magel Magelonidae, Spion Spionidae, Cirra Cirratulidae, Flabe Flabelligeridae, Pecti Pectinariae, Tereb Terebellidae, Poeci Poecilochaetidae, Trich Trichobranchidae, Chaet Chaetopterae, Poly Polygordiidae, Serpu Serpulidae, Stern Sternaspidae.

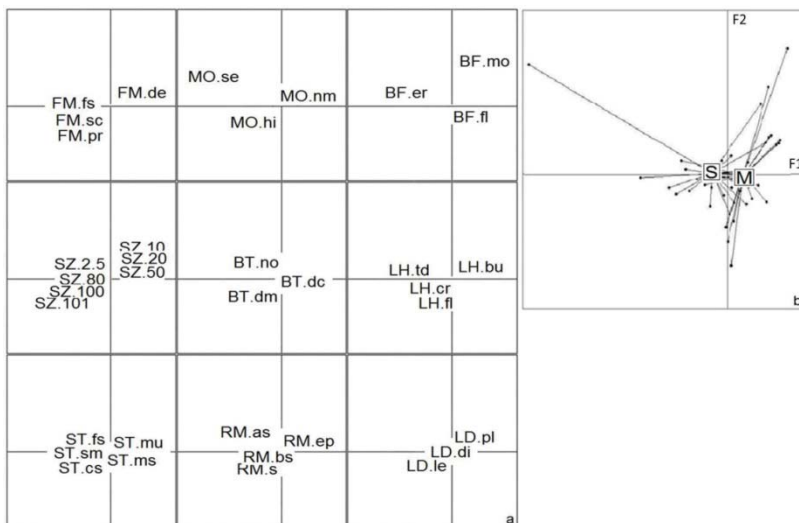


Figure 6 - Fuzzy correspondence analysis (FCA) of all biological traits weighted by the abundance of families on the regional scale: (a) distribution of categories of the 9 biological traits on the factor map and (b) factor map of sediment samples (M mud and S sand). Biological trait labels: Feeding Mode FM, deposit feeder FM.de, filter-suspension feeder FM.fs scavenger FM.sc, predator FM.pr, Mobility MO, highly mobile MO.hi, non-mobile MO.nm, sedentary MO.se, Body Form BF, flat BF.fl, mound BF.mo, erect BF.er, Size SZ, <2.5mm SZ.2.5, 2.5-10mm SZ.10, 11-20mm SZ.20, 21-50mm SZ.50, 51-80mm SZ.80, 81-100mm SZ.100, >100mm SZ.101, Bioturbation BT, diffusive mixing BT.dm, upward-downward conveyor BT.uc, none BT.no, Living Habit LH, tube-dweller LH.td, burrow LH.bu, crevice LH.cr, free-living LH.fl, Substrate Type ST, coarse sand ST.cs, fine sand ST.fs, sandy mud ST.sm, muddy sand ST.ms, mud ST.mu, Reproductive Method RM, sexual internal RM.si, asexual RM.as, sexual external broadcast spawner RM.bs, epitoki RM.ep, Larval Development LD, planktotrophic LD.pl, lecithotrophic LD.le, direct LD.di.

Discussion

While habitat-animal relationships have been traditionally explored using a taxonomical approach based on taxa abundance and composition, we proposed here to go further assessing changes in the functional structure of assemblages based exclusively in polychaete morphology. Our novel method allowed for a standardization of existing traits data into morphological characteristics of one of the most expressive benthic groups in marine soft sediments. This standard format eliminates major subjectivities in the analytical process, such as the problem caused by gaps of knowledge and information about functional traits in the literature. Some characteristics such as fecundity, reproduction and dispersal are likely to be partially or completely unknown at the species taxonomical level (Tyler et al. 2012). These knowledge gaps are usually solved by extrapolating the unknown characteristic to a congeneric species or to the family level (Tillin et al. 2006, Papageorgiou et al. 2009). The use of extrapolation may result in biased classifications of codes within traits, and lead to the

overgeneralization of biology and eventually of the ecological role of the taxon. Morphological characteristics can be easily measured and hold the potential for broad comparisons between habitats, regions and higher taxa (Ricklefs & Travis 1980). Besides, this method is perfectly adaptable to other benthic groups, even to smaller phylums or widely unknown or neglected taxa like oligochaetes, bryozoans, and sipunculans.

The three methods, either the traditional BTA, morphology-based BTA or taxonomical, revealed similar benthic patterns of variation according to all multivariate analyses results. These findings support the idea that the traditional taxonomy-based approach and functional diversity in general are correlated, as established by many previous authors (Bremner et al. 2003b, Micheli & Halpern 2005). However, despite the similar patterns, our results indicated that the novel morphological approach increased the analytical capability explaining the data variability, which means the distinction between sandy and muddy habitats, especially in comparison to the taxonomic approach (more than two-fold). This shows the indicative value of morphology-based functional responses

of polychaete assemblages, mainly related to the decreased number of categories applied to the entire data set. The 24 categories used in our morphological method were more inclusive and sensitive to sediment-type changes than the taxonomical method with more than 30 categories. In this sense, general trends in the ecological functioning of polychaete assemblages cannot be revealed using taxon identities alone. Functional changes related to morphological characteristics may indeed be important indicators of the sediment condition, as previously recognized in the literature (Papageorgiou et al. 2009). The improvement in the percentage of explanation of faunal trends with morphology-based BTA was more discrete but still evident against the traditional BTA approach. This is possibly related to the partial absence of codification in the classic BTA. Some polychaete categories could not be coded due to lack of available information, and the missing data may have caused some loss of robustness in the analysis. We have incorporated five of eight fundamental traits for polychaetes, with restricted information availability in the current literature (Tyler et al. 2012). These traits are commonly used for the benthic community in general and are

amongst the most problematic for its lack knowledge, even in the family taxonomical level. The absence of information on biological traits for the polychaete fauna resulted in missing data, which may cause distortions in the statistical output (Nakagawa & Freckleton 2008). This is at least an important signal of the need of further assessments to increase the value of the trait-based approach in ecology.

The improvement on the percentage of explanation of faunal patterns in the morphology-based BTA was outstanding against the taxonomical approach, while more discrete when compared to the classical BTA. This suggests a straight link between the morphological traits and their functionality. Morphological characteristics have founded functional approaches to biodiversity assessments and are an integrative approach with regard to the form and function of organisms in their relationships to the environment (Bock 1994, Tellería et al. 2013). Although some particular phenotypic features may be neutral or have no functional role (Radinsky 1992), similarities in morphological characteristics among taxonomically different groups of polychaetes are still evident (Struck et al. 2011),

suggesting that habitat may have an intimate connection to morphological adaptations. In our results, sandy and muddy bottoms were inhabited by morphologically and functionally different polychaete assemblages, which may reflect different levels of ecosystem functioning. The polychaete morphological characteristics predominant in the muddy habitat were more related to deposit feeding and low mobility, which may play an important role in promoting the physical change of habitat by altering the efficiency of nutrient fluxes and stability of sediments (Meysman et al. 2006). Sediment reworking translocate sediments from deeper layers to the surface and vice-versa (Pearson 2001), optimizing the oxygenation and irrigation in these cohesive environments (Sigala et al. 2012). On the other hand, the morphological characteristics predominant in the sandy habitat were more diverse, with sedentary filter-surface feeders and motile carnivores carrying specialized structures to perceive, gasp and assist on active foraging (Amieva & Reed 1987, Shimeta & Koehl 1997, Jayaraj et al. 2007, Beesley et al. 2000). This could be related with more a heterogeneous environment, once complex substrates tend to support richer and more diverse

assemblages and allow for the establishment of different kinds of taxa with different feeding habits (Simboura et al. 2000). This variety of animals and diets can maintain recycling and availability of nutrients to the environment. The linking between functional roles and habitat have been previously shown, with burrowers and low motile fauna associated to human-impacted sites, such as intensive fishing, while filter feeders and high motile fauna prevailed in less impacted sites (Bremner 2008). Thus, assessments of variations and implications in the relationships between traits and different sedimentary habitats could predict environmental changes and, therefore, its functioning (Tillin et al. 2006).

Herein consistent faunal patterns of variation along muddy and sandy habitats were also found between local and regional spatial scales. Nevertheless, differences between both spatial scales using the morphological method were lower, emphasizing that a functional approach allowed for more concise results. Regardless of the scale, the role of sediment type is a main factor determining patterns of faunal composition of communities but this relationship is still considered ambiguous and not yet well understood (de Bello et

al. 2009, Dimitriadis et al. 2012). Our results corroborate recent evidence on biological trait structure suggesting that ecological functioning might be primarily driven by small, local-scale processes that can also operate at larger geographical scales (Bremner et al. 2006b). The morphological approach can also be implemented in biological trait analysis as useful tools to assess trends in ecosystem functioning at larger scales that are not practical using taxon composition analysis.

Our results provide a convincing demonstration of the use of morphology to assess changes in the functional structure of polychaete assemblages at local and regional spatial scales. The incorporation of morphology in biological traits eliminates subjectivity and clarifies the analytical process, providing more substantial information on the ecological role of polychaetes along muddy and sandy habitats than the taxonomical approach. Moreover, a functional approach based in morphology allowed for more consistent responses between different spatial scales. The morphological method provides a robust approach for studying the ecological functionality of systems and could be applied to directly

indicate important shifts in response to diverse source of impacts such as contamination, dredging and trawling, as well as establishing conservation strategies in coastal systems worldwide.

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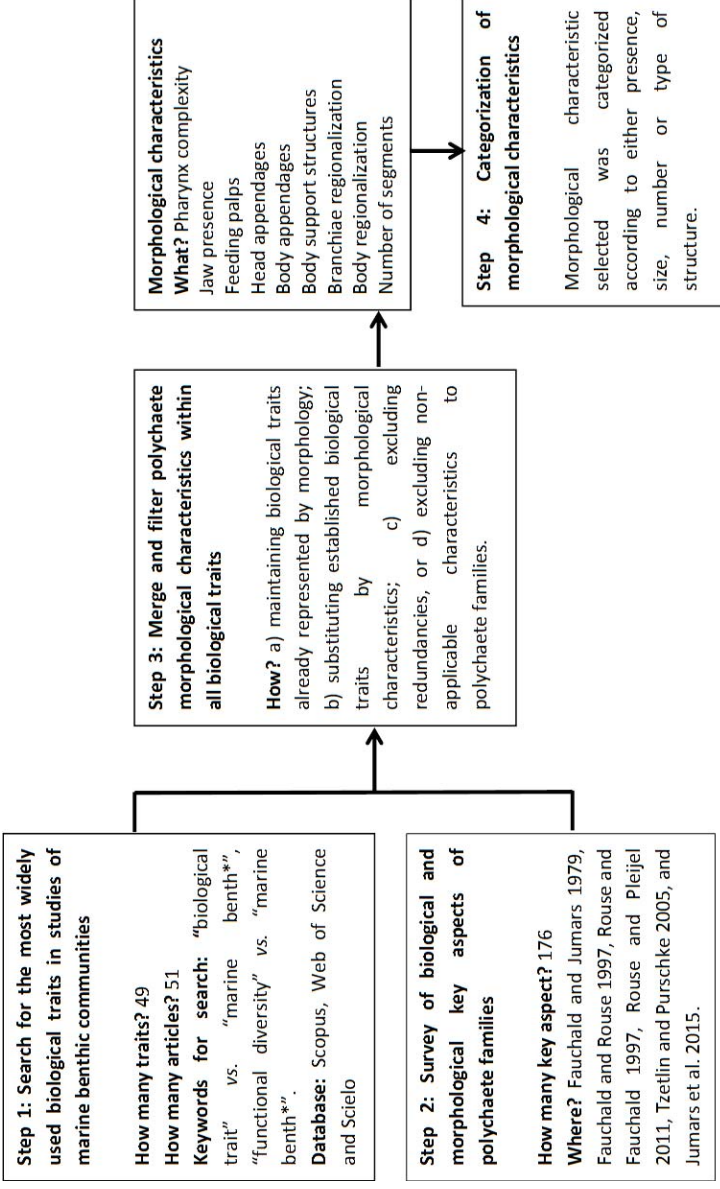
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Appendix A - Flow diagram with four steps to determine the morphological characteristics of polychaetes.



Step 1: search for the most widely used biological traits in studies of marine benthic communities.

Number	Year	Reference
1	2006	Aberhan, M., Kiessling, W., Fürsich, F.T., 2006. Testing the role of biological interactions in the evolution of mid-Mesozoic marine benthic ecosystems. <i>Paleobiology</i> , 32(2):259-277.
2	2012	Aberhan, M., Nürnberg, S., Kiessling, W., 2012. Vision and the diversification of Phanerozoic marine invertebrates. <i>Paleobiology</i> , 38(2):187-204.
3	2014	Alves, A.S., Veríssimo, H., Costa, M.J., Marques, J.C., 2014. Taxonomic resolution and biological traits analysis (BTA) approaches in estuarine free-living nematodes. <i>Estuarine, coastal and shelf science</i> , 138:69-78.
4	2013	Atalah, J., Fitch, J., Coughlan, J., Chopelet, J., Coscia, L., Farrell, E., 2013. Diversity of demersal and megafaunal assemblages inhabiting sandbanks of the Irish Sea. <i>Mar. Biodiv.</i> , 43:121-132.
5	2010	Ayata, S., Lazure, P., Thiébaud, E., 2010. How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (North-East Atlantic). <i>Progress in oceanography</i> , 87:18-36.
6	2014	Bolam, S.G., 2014. Macrofaunal recovery following the intertidal recharge of dredged material: A comparison of structural and functional approaches. <i>Marine environmental research</i> , 97:15-29.
7	2014	Bolam, S.G., Eggleton, J.D., 2014. Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. <i>Journal of sea research</i> , 88:47-58.
8	2014	Bolam, S.G., Coggan, R.C., Eggleton, J., Dising, M., Stephens, D., 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. <i>Journal of sea research</i> , 85:162-177.
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Step 1: biological traits were grouped into the themes of general biology, distribution and habitat, reproduction/life history and larvae/juveniles.

Themes	Biological traits	Reference by number
General Biology	Living habitat	4/6/7/8/9/11/12/13/17/19/20/25/26/28/29/30/32/36/38/39/40/ 41/42/47/49/50
General Biology	Life habit	1/6/7/8/9/14/19/20/21/22/23/24/25/27/28/29/30/34/36/37/38/39/ 40/42/46/47/50
General Biology	Life strategy	3/35
General Biology	Feeding mode	1/3/4/6/7/9/10/11/12/13/14/15/16/17/19/20/21/22/23/24/25/26/ 27/28/29/30/32/33/34/36/ 37/38/39/40/41/42/43/44/45/46/47/48/49/50/51
General Biology	Food type	9/10/15/16/19/22/25/28/33/36/46/48
General Biology	Feeding apparatus	9/22/25/28/35/47
General Biology	Predated	25
General Biology	Bioturbation	6/7/16/18/19/20/22/24/25/27/29/30/37/41/42/49
General Biology	Mobility	1/4/6/7/8/9/10/11/12/13/14/16/17/19/20/21/22/25/26/28/29/30/ 32/34/36/37/38/39/40/41/43/ 44/45/46/47/49/50/51
General Biology	Relative weight	12/13/23
General Biology	Growth form	36/41
General Biology	Maximum size	4/6/7/8/9/10/14/17/19/20/21/23/24/25/26/27/28/29/30/34/35/36/

		37/38/39/40/44/46/47/48/49/50/51
General Biology	Maximum growth rate	9
General Biology	Longevity (years)	4/6/7/8/9/11/12/13/16/19/20/23/25/26/27/28/29/32/34/36/37/ 38/39/41/46/47/48/49/50/51
General Biology	Body desing	3/4/6/7/8/9/11/12/13/17/19/20/21/26/28/29/30/32/35/38/39/40
General Biology	Body protection	10
General Biology	Skeletal composition and thickness	14
General Biology	Respiration-Energy transfer	9/28
General Biology	Fragility	19/32
General Biology	Sociability	4/9/11/12/13/14/19/25/28/32/51
General Biology	Attachment	4/9/11/12/13/17/19/26/28/32/38/39
General Biology	Degree flexibility	4/9/11/12/13/19/28/32/49
General Biology	Ornamentation	1
General Biology	Visual capabilities	2
General Biology	Means of stabilization	1
Distribution and Habitat	Biogeographic range	36
Distribution and Habitat	Depth range	25/36

Habitat		
Distribution and Migration		4/9/12/13/25/28/33/51
Habitat		
Distribution and Substratum preference		17/25/28/32/41
Habitat		
Distribution and Biozone		36
Habitat		
Distribution and Tolerance		19/20/25/34/49
Habitat		
Distribution and Physiographic feature		25
Habitat		
Reproduction/Life History	Reproductive	4/9/10/11/12/13/14/19/20/25/28/29/32/33/34/36/37/38/39/40/41/46/47/49
Reproduction/Life History	Reproductive frequency	25/34/36/37/38/46/47/48
Reproduction/Life History	Reproductive season	20/25/29/38/48
Reproduction/Life History	Fertilisation type	25/36
Reproduction/Life History	Developmental technique	25/47
Reproduction/Life History	Sexual differentiation	4/12/13/46
Reproduction/Life History	Time to maturity	4/12/13/25/47

History		
Reproduction/Life History	Fecundity	9/19/25/28/46
Reproduction/Life History	Eggs size	25/48
Reproduction/Life History	Dispersal	9/19/27/38/44/47
Reproduction/Life History	Regenerative ability	32/36
Larval/Juveniles	Larval duration	5
Larval/Juveniles	Larval development	5/8/17/20/25/26/29/31/37/38/41/49/50/51
Larval/Juveniles	Larval mortality	5
Larval/Juveniles	Larval dispersal	48
Larval/Juveniles	Larval development location	6/7/25/31
Larval/Juveniles	Feeding type of juvenile and larvae	25

Step 2: survey of biological and morphological key aspects of polychaete families.

Letters	Year	Reference
A	1979	Fauchald, K., Jumars, P. A., 1979. The diet of worms: a study of Polychaetes feeding guilds. Oceanography and Marine Biology an Annual Review. 17, 193-284.
B	1997	Fauchald, K., Rouse, G., 1997. Polychaetes systematics: Past and present. Zoologica Scripta. 26, 71-138.
C	1997	Rouse, G.; Fauchald, K., 1997. Cladistics and polychaetes. Zoologica Scripta. 26, 139-204.
D	2001	Rouse, G.W.; Pleijel, F., 2001. Polychaetes, Oxford, New York.
E	2005	Tzvetlin, A., Purschke, G., 2005. Pharynx and intestine. Hydrobiologia. 535/536, 199-225.
F	2015	Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. Annual Review of Marine Science. 7, 497-520.

Step 2: morphological characteristics were grouped into the themes of feeding mode, feeding palps, head features, head appendages, sensory organs, mobility, support structures, body regionalization, respiration, circulatory system, excretory system, reproductive, larval development, and behavior.

Themes	Key aspects	Reference by letters
Feeding mode	Macrophagous modes	A
Feeding mode	Herbivores	A
Feeding mode	Carnivores	A
Feeding mode	Microphagous modes	A
Feeding mode	Filter-feeders	A/D
Feeding mode	Surface deposit-feeders	A
Feeding mode	Non-selective deposit feeders	D
Feeding mode	Selective deposit feeders	D
Feeding mode	Burrowers	A
Feeding mode	Raptorial feeding	D
Feeding structures	No buccal organ	C/D/F
Feeding structures	Unarmed pharynx	A/F
Feeding structures	Simple axial proboscis	D/E/F
Feeding structures	Ventral buccal organ (simple)	D/F

Feeding structures	Jawed pharynx	A/F
Feeding structures	Ventral muscular proboscis	D/E/F
Feeding structures	Muscular axial proboscis	D/E/F
Feeding structures	Grooved palps	A/C/F
Feeding structures	One pair palps	D
Feeding structures	Multiple palps	D
Feeding structures	Prostomial grooved palps	C
Feeding structures	Peristomial grooved palps	C
Feeding structures	Prostomial paired palps	C
Feeding structures	Prostomial multiple palps	C
Feeding structures	Prostomial palps form a crown	C
Feeding structures	Peristomial paired palps	C
Feeding structures	Peristomial palps multiple	C
Feeding structures	Digestive tract	B
Feeding structures	Gut with lateral folds	C
Feeding structures	Gut with side branches	C
Feeding structures	Gut occluded	C
Feeding structures	Gut with a straight tube	C
Feeding structures	Mucous devices	A
Feeding structures	Stomodaeum	B

Feeding structures	Stomodaeum, axial, hypertrophied	C
Feeding structures	Stomodaeum, ventral buccal bulb	C
Feeding structures	Stomodaeum, disappears	C
Feeding structures	Stomodaeum, ventral hypertrophied	C
Feeding structures	Stomodaeum, axial simple	C
Feeding structures	Axial hypertrophied stomodaeum with jaws	C
Feeding structures	Axial hypertrophied stomodaeum one lateral pair of jaws	C
Feeding structures	Axial hypertrophied stomodaeum one or two D-V pairs of jaw	C
Feeding structures	Axial hypertrophied stomodaeum jaws form a cross or circle	C
Feeding structures	Ventral buccal bulb not eversible	C
Feeding structures	Ventral buccal bulb eversible	C
Feeding structures	Ventral hypertrophied stomodaeum ridged	C
Feeding structures	Ventral hypertrophied stomodaeum with jaws	C
Feeding structures	Ventral hypertrophied stomodaeum jaws prionognath	C
Feeding structures	Ventral hypertrophied stomodaeum jaws labidognath	C
Feeding structures	Dorsolateral folds	C
Feeding structures	Gular membrane	B/C

Head features	Head features	B
Head features	Prostomium clearly demarked by a distinct groove	C
Head features	Prostomium fused to the peristomium, but distinct	C
Head features	Prostomium fused to the peristomium, and limited	C
Head features	Prostomium on peristomium, frontal edge fused	C
Head features	Peristomium forms a distinct ring	C
Head features	Peristomium forms two distinct rings	C
Head features	Peristomium elongate	C
Head features	Peristomium forms rings and a collar	C
Head features	Peristomium limited to lips only	C
Head appendages	Antennae	D/F
Head appendages	Prostomial antennae	C
Head appendages	Median prostomial antenna	C
Head appendages	Pair of prostomial antennae	C
Head appendages	Peristomial cirri	D
Head appendages	Sensory palps	D/F

Head appendages	Anterior cirri	D
Head appendages	Prostomial sensory palps	C
Head appendages	Prostomial sensory palps ventral	C
Head appendages	Prostomial sensory palps ventro-lateral	C
Head appendages	Eyes	D/F
Head appendages	Statocysts	D
Sensory organs	Sensory organs	B
Sensory organs	Nuchal organs	C/D/F
Sensory organs	Nuchal organs as pits or grooves	C
Sensory organs	Nuchal organs form posterior projections	C
Sensory organs	Nuchal organ as caruncle	C
Sensory organs	Dorsal cirri	C
Sensory organs	Dorsal cirri cirriform	C
Sensory organs	Dorsal cirri include elytra	C
Sensory organs	Dorsal cirri foliaceous	C
Sensory organs	Dorsal cirri limited	C
Sensory organs	Tentacular cirri	C
Sensory organs	Ventral cirri	C
Sensory organs	Lateral organs	C/D

Sensory organs	Dorsal cirrus organs	C
Sensory organs	Dorsal organs	C
Sensory organs	Epidermal papillae	C
Sensory organs	Pygidial cirri	B
Sensory organs	Pygidial cirri, One pair	C
Sensory organs	Pygidial cirri, Two or more pairs	C
Sensory organs	Parapodial cirri	D
Mobility	Motile	A/F
Mobility	Discretely motile	A/F
Mobility	Sessile	A/F
Support structure	Uncini	C
Support structure	Aciculae	C/D
Support structure	Parapodia	C
Support structure	Parapodia with similar rami	C/D
Support structure	Parapodia with projecting neuropodia	C
Support structure	Parapodia in part with tori	C
Support structure	Parapodia in part notopodial ridges	C
Support structure	Parapodia spiomorph	C

Support structure	Chaetae	B/C/D
Support structure	Calcareous chaetae	C
Support structure	Chaetal inversion	C
Support structure	Compound chaetae	C
Support structure	Compound chaetae with two ligaments	C
Support structure	Compound chaetae with one ligament	C
Support structure	Compound chaetae with a fold	C
Support structure	Compound chaetae taper	C
Support structure	Compound chaetae falcate	C
Support structure	Compound chaetae dentate	C
Support structure	Compound chaetae hooked	C
Support structure	Capillary chaetae	C
Support structure	Fine silk notochaetae	C
Support structure	Spines in one anterior chaetiger	C
Support structure	Spines generally	C
Support structure	Hooded chaetae	C
Support structure	Falcate hooks	C
Support structure	Dentate hooks	C
Body regionalization	Thorax	D

Body regionalization	Abdomen	D
Body regionalization	Trunk structures	B
Body regionalization	Segmentation	C
Body regionalization	1st segment indistinct	C
Body regionalization	1st segment similar to those following	C
Body regionalization	1st segment surrounds head	C
Body regionalization	1st segment fused to head	C
Body regionalization	1st segment dorso-lateral around head	C
Body regionalization	1st segment elongate	C
Body regionalization	1st segment appendages same as following	C
Body regionalization	1st segment appendages/chaetae absent	C
Body regionalization	1st segment tentacular cirri only	C
Body regionalization	1st segment with notopodia only	C
Body regionalization	1st segment with neuropodia only	C
Body regionalization	1st segment with arthropod appendages	C
Body regionalization	Four or five longitudinal muscle bands	C
Respiration	Respiration	D
Respiration	Branchiae regionalization	D
Respiration	External gills	B

Respiration	Parapodial branchiae	C
Respiration	Dorsal simple branchiae	C
Respiration	Dorsal flattened branchiae	C
Respiration	Dorsal branchiae in a few anterior chaetigers	C
Circulatory system	Circulatory system	B
Circulatory system	Circulation structures	D
Circulatory system	Proventricle	C
Circulatory system	Circulatory system limited or absent	C
Circulatory system	Closed circulation	C
Circulatory system	Ostiate heart	C
Circulatory system	Blood and the heart body	C/D
Excretory system	Segmental organs	B/D
Excretory system	Segmental organs restricted to a few middle segments	C
Excretory system	Adult metanephridia	C
Excretory system	Adult protonephridia	C
Excretory system	Mixonephridia	C
Excretory system	Metanephromixia	C

Excretory system	Protonephromixia	C
Excretory system	Coelomoducts and nephridia separate	C
Excretory system	Nephridia and coelomoducts in most segments	C
Excretory system	One pair of anterior excretory nephridia; posterior gonoducts	C
Excretory system	Anterior sterile nephridia and posterior gonoducts	C
Excretory system	Ciliophagocytal organ	C
Reproductive	Reproduction	D
Reproductive	Assexual	D
Reproductive	Sexual	D
Reproductive	Sperm with mitochondrial interpolation	C
Larval development	Larval development	D
Larval development	Planktotrophic	D
Larval development	Lecitotrophic	D
Behavior	Pelagic	F
Behavior	Epifaunal	F

Behavior

Infaunal

F

Behavior

Commensal

F

Step 3: Merge and filter polychaete morphological characteristics within all biological traits.

This step results in determining the morphological characteristics of polychaetes from the merge of biological and morphological key aspects of polychaete with biological traits used to marine benthic community.

Biological traits	Key aspects of polychaetes (biological and morphological)	Feature maintained	Morphological surrogate	Redundant features	Features not applicable	Morphological characteristics of polychaetes
Feeding apparatus	No buccal organ	X				Pharynx complexity
Feeding apparatus	Ventral buccal organ	X		X		Pharynx complexity
Feeding apparatus	Ventral muscular proboscis					Pharynx complexity
Feeding apparatus	Simple axial proboscis	X				Pharynx complexity
Feeding apparatus	Muscular axial proboscis	X				Pharynx complexity
Feeding apparatus	Unarmed pharynx	X				Jaw presence
Feeding apparatus	Jawed pharynx	X				Jaw presence
Feeding apparatus	One pair palps	X				Feeding palps
Feeding apparatus	Multiples palps	X				Feeding palps
Feeding apparatus	Grooved palps			X		Feeding palps
Feeding apparatus	Prostomial grooved palps			X		Feeding palps

Feeding apparatus	Peristomial grooved palps	X	Feeding palps
Feeding apparatus	Prostomial paired palps	X	Feeding palps
Feeding apparatus	Prostomial multiple palps	X	Feeding palps
Feeding apparatus	Prostomial palps form a crown	X	Feeding palps
Feeding apparatus	Peristomial paired palps	X	Feeding palps
Feeding apparatus	Peristomial palps multiple	X	Feeding palps
Body design	Antennae	X	Head appendages
Body design	Prostomial antennae	X	Head appendages
Body design	Median prostomial antenna	X	Head appendages
Body design	Pair of prostomial antennae	X	Head appendages
Body design	Peristomial cirri	X	Head appendages
Body design	Sensory palps	X	Head appendages
Body design	Prostomial sensory palps	X	Head appendages
Body design	Prostomial sensory palps ventral	X	Head appendages
Body design	Prostomial sensory palps ventro-lateral	X	Head appendages
Body design	Anterior cirri	X	Head appendages

Body design	Eyes			X	Head appendages
Body design	Sensory organs		X		Body appendages
Body design	Lateral organs	X			Body appendages
Body design	Parapodial cirri	X			Body appendages
Body design	Dorsal organs	X			Body appendages
Body design	Statocysts	X		X	Head appendages
Body design	Pygidial cirri			X	Body appendages
Mobility	Uncini	X			Body appendages
Mobility	Aciculae	X			Body support structures
Mobility	Parapodia with similar rami	X			Body support structures
Mobility	Discretely motile			X	Body support structures
Mobility	Sessile			X	Body support structures
Respiration-Energy transfer	Respiration			X	Branchiae regionalization
Respiration-Energy transfer	Branchiae regionalization	X			Branchiae regionalization

Growth form	Thorax	X	Body regionalization
Growth form	Abdomen	X	Body regionalization
Maximum size	Segmentation	X	Number of segments

Step 3: Remaining biological traits and key aspects of polychaetes that it was not possible to merge and non-applicable characteristics to polychaete families.

Biological traits	Key aspects of polychaetes (biological and morphological)	Features not applicable
Feeding mode	Macrophagous modes	X
Feeding mode	Herbivores	X
Feeding mode	Carnivores	X
Feeding mode	Microphagous modes	X
Feeding mode	Filter-feeders	X
Feeding mode	Surface deposit-feeders	X
Feeding mode	Non-selective deposit feeders	X
Feeding mode	Selective deposit feeders	X
Feeding mode	Burrowers	X
Feeding mode	Raptorial feeding	X
Reproductive	Reproduction	X
Reproductive	Assexual/Sexual	X
Larval development	Planktotrophic	X
Larval development	Lecitotrophic	X
Life habit	Pelagic	X
Life habit	Epifaunal	X
Life habit	Infaunal	X
Life habit	Commensal	X
Food type	-	X
Bioturbation	-	X
Longevity (years)	-	X

Maximum growth rate	-	X
Relative weight	-	X
Reproductive frequency	-	X
Reproductive season	-	X
Fertilisation type	-	X
Developmental technique	-	X
Sexual differentiation	-	X
Time to maturity	-	X
Fecundity	-	X
Eggs size	-	X
Dispersal	-	X
Regenerative ability	-	X
Larval duration	-	X
Larval mortality	-	X
Larval dispersal	-	X
Larval development location	-	X
Feeding type of juvenile and larvae	-	X
Living habit	-	X
Life strategy	-	X
Biogeographic range	-	X
Depth range	-	X
Migration	-	X
Substratum preference	-	X
Biozone	-	X

Body protection		X
Skeletal composition and thickness	-	X
Fragility	-	X
Sociability	-	X
Attachment	-	X
Degree flexibility	-	X
Ornamentation	-	X
Means of stabilization	-	X
Tolerance	-	X
Visual capabilities	-	X
Physiographic feature	-	X
Predated	-	X
	1st segment indistinct	X
	1st segment similar to those following	X
	1st segment surrounds head	X
	1st segment fused to head	X
	1st segment dorso-lateral around head	X
	1st segment elongate	X
	1st segment appendages same as following	X
	1st segment appendages/chaetae absent	X
	1st segment tentacular cirri only	X
	1st segment with notopodia only	X
	1st segment with neuropodia only	X
	1st segment with arthropod appendages	X

-	Four or five longitudinal muscle bands	X
-	Circulatory system	X
-	Circulation structures	X
-	Proventricle	X
-	Circulatory system limited or absent	X
-	Closed circulation	X
-	Ostiate heart	X
-	Blood and the heart body	X
-	Segmental organs	X
-	Segmental organs restricted to a few middle segments	X
-	Adult metanephridia	X
-	Adult protonephridia	X
-	Mixonephridia	X
-	Metanephromixia	X
-	Protonephromixia	X
-	Coelomoducts and nephridia separate	X
-	Nephridia and coelomoducts in most segments	X
-	One pair of anterior excretory nephridia; posterior gonoducts	X
-	Anterior sterile nephridia and posterior gonoducts	X
-	Ciliophagocytal organ	X
-	Sperm with mitochondrial interpolation	X

Body size distribution of a reef building polychaete along a temperature gradient in the Atlantic coast of South America

Mariana B.P. Otegui, Mariana S. Oortman, Paulo R. Pagliosa

Summary

1. Temperature is a key environmental factor affecting distribution of phenotypic traits, influencing the life functions of organisms through changes in physiological processes. Phenotypic traits exhibit different distribution patterns with optimum shifts along temperature gradients, but predictions linking multidimensional phenotypes and fitness to environmental changes are scarce.

2. As there is a strong body size-temperature relationship, we specifically investigated if distinct body sizes have different modal distributions along a South-American temperature gradient. We used the widely distributed polychaete *Phragmatopoma caudata* with well-defined and diversified morphological structures, which allow more reliable measurements.

3. Five body measurements (whole-organism, opercular crown, branchiae, tentacles and building organ sizes) were taken at nine sites along the latitude range (3°–28° S). Their relationships to the descriptor variables temperature, salinity, tidal range, wave height, and dissolved oxygen were assessed. Quantile regression splines models were applied to indicate the possible maximum values for each phenotypic trait along the temperature gradient.

4. The phenotypic traits showed dimensionally different responses to temperature with distinct optimal adaptations. We found a unimodal and asymmetrical distribution in whole-organism and

opercular crown, converging on a single optimum to the south-end of the temperature gradient, and a multimodal distribution for branchiae and tentacles with two optimums in the ends of the gradient.

5. The approach provides strong evidence of the sound importance of including different levels of traits which maximizes the understanding on body size-temperature relationships. Despite the strong influence of temperature, secondary factors operating at local scales as the effects of Amazon and la Plata river discharges also influence the trait distributions. This study not only provides a framework of individual species responses along a temperature gradient, but also exposed the value of a phenotypic trait as a possible predictor to changes in future climate scenarios.

Keywords: Morphology, Optimum adaptation, Organ-level, Performance traits, *Phragmatopoma caudata*, Unimodal curve, Whole-organism.

1. Introduction

Body size is the most ecologically integrative attribute of a species helping to understand the species-environment interactions (Allen et al. 2006). The body size distribution of individuals of a single species along an environmental gradient is usually represented by a unimodal-skewed curve (Johnson & Goodall 1979). Contrariwise, body size is a generic term referring to many and different body structures that may achieve different or multiple optimal adaptation in an environmental gradient formed by one or multiple variables (Marks 2007). Considering that organism traits are shaped by natural selection to achieve reproductive success (Stearns 2000), the many size variations within a species is a consequence of fluctuations in environmental characteristics, coexistences, and chance. The summed or unique effects of these three factors causing individual traits variability has been the base of a sort of methods and theories on community assembly rules and species range distribution (Gaston & He 2002; Pillar & Duarte 2010; Laughlin et al. 2012).

Temperature is a key environmental variable shaping the asymmetrical unimodal distribution of species body size (Witman & Roy 1992; Langlois et al. 2012). As temperature decreases from equator to poles, body sizes are expected to increase towards the poles (Bergman's rule; Bergmann 1947). That is, individual body size distribution tends to be left-skewed in the south hemisphere or right-skewed in north hemisphere. In both hemispheres, the largest size classes are the modal ones, meaning that large-sized individuals are restricted in their geographical occurrence while small-sized individuals are widespread distributed. As metabolism is greatly influenced by temperature (Brown 2014; Weber et al. 2015), one could expect that higher ambient temperatures result in higher metabolic demand. Therefore, individuals living in habitats of warmer temperatures (*i.e.*, low latitudes) are expected to live less than those living in habitats of lower temperatures (*i.e.*, high latitudes) due to the thermal advantage of their reduced surface-to-volume ratio (Brown et al. 2004). Organisms in high latitudes are more likely to accumulate body mass at a slower pace, increasing their body size (Watt, Mitchell & Salewski 2010).

Despite the species body size distribution being partially explained by the energetic model (Allen et al. 2006); the influence of the temperature in such pattern is paramount. The body size-temperature relationship has been reported from unicellular to multicellular forms of life, from terrestrial to marine habitats, and within the marine realm, for planktonic, nektonic, as well as for benthic organisms (Stillwell 2010; Kordas, Harley & O'Connor 2011; Takahashi et al. 2012; Garzke, Ismar & Sommer 2015; Kelley et al. 2015; Macheriotou et al. 2015). Nevertheless, many deviations from the main pattern of the unimodal-skewed distribution have been shown (Nicol 1964; Graus 1974; Roy & Martier 2001; Angielczyk, Burroughs & Feldman 2015) arousing that a more detailed mechanism could be acting. In fact, not all body size analysis is based on whole-organism measurements (*i.e.*, total length, total width, total height, total area, or total mass), but is related to the size of any particular organ or body structure. Thereafter, many measurements of body size might present phenotypic traits with independent dimensions and consequent distinct optimal adaptations to the temperature conditions (Marks 2007; Laughlin 2013). The

interaction between phenotype traits and environment could be used as a framework for mapping the adaptive value or fitness and predict species responses to environmental changes (Laughlin & Messier 2015). Furthermore, the traits could be hierarchically arranged, with variation in whole-organism traits (on top hierarchy) most closely related to processes acting on ecological scale. On the other hand, organ-level traits variations (on bottom hierarchy) are most closely related to evolutionary processes (Marks 2007).

While most studies on body size do not account for the intraspecific variation of phenotypic traits, herein we aim to assess and discuss the body size-temperature relationship considering whole-organism and many organ level measurements of the polychaete *Phragmatopoma caudata*. The genus *Phragmatopoma* is endemic to the Americas inhabiting the intertidal and shallow subtidal zones of the coast (Kirtley 1994). The range of occurrence of the species *P. caudata* crosses a natural gradient of temperature, from the tropics (Florida, Caribbean islands, and North of Brazil) to the warm temperate (South of Brazil). Furthermore, the species have well defined and diversified morphological structures that allow a

precise and discernible body size measurement: i- The building organ which secretes the cement used to build strong sand tubes that forms extensive reefs (Zale & Merrifield 1989). These characteristics yield them the status of ecosystem engineers by modifying, maintaining, and creating complex habitats (Coleman & Williams 2002); ii- The architecture of the oral tentacles is the most prominent morphological body structure of the species, used to accomplish a filter-feeding habit (Amieva & Reed 1987); iii- The numerous and discrete rows of thoracic branchiae are the energetic bomb of the species (Fanta 1968); iv- The opercular crown is a peculiar morphological structure of the sabellariids polychaetes and one of the most distinctive taxonomical character of the group (Dales 1952). In this study we have evaluated the role of temperature and other environmental variables on the body size distribution of *P. caudata* along a latitudinal gradient, from tropics to warm temperate, in the South Atlantic coast. As there is a strong body size-temperature relationship, we investigated specifically if distinct body sizes measurements have different modal distributions along a temperature gradient. If patterns of responses differ among whole-organism size

and organ sizes, we hypothesize that: (1) variation in whole-organism body size, the top hierarchic trait, have its optimal adaptation in agreement with the gradient of temperature; whereas (2) variations in organ size levels, the bottom hierarchic traits, have alternative optima and despite influenced by the temperature they will not follow its gradient; and, if we found a matching pattern for the bulk of body size measurements, (3) our data will not support the existence of a multiple dimensionality or a hierarchy of traits and the body size distribution will have just one optimal adaptation that will be related with the temperature gradient.

2. Material and Methods

To entrust the environmental gradient throughout the *P. caudata* range of distribution, nine sites widely spaced (minimum of 233 km and maximum of 960 km) along a 25° of latitude range (3°–28° S) were sampled during the austral autumn, from March to June 2012 (Fig. 1; Appendix A). In intertidal areas of each site, we

sampled three different worm reefs with a core of 0.1 m² and 0.1 m high. The field work was carried out as quickly as possible to avoid worm scape and damage, and avoiding reefs with no evident physical disturbance and macroalgae or bivalves coverage. The reef samples were immediately preserved in ethanol 90%. In the laboratory, the polychaete worms were carefully removed from the tubes. To avoid ontogenetic variation only adult individuals were engaged in the investigation. Twenty unharmed specimens were randomly chosen from each sample (N = 540 individuals).



Figure 1. Sampled sites of *Phragmatopoma caudata* populations along the Atlantic coast of South America. For more information on the sampled sites see Appendix A.

2.1 Body size

In order to compare different hierarchical levels of traits we established five body size measurements for *P. caudata* (i.e., whole-organism length and the length of opercular crown, branchiae, tentacles, and building organ; Fig. 2). The whole-organism size corresponded to the body length taken from the opercular crown to the initial region of the cauda. The other four measurements were taken to represent many organ-level sizes. The opercular crown is a rigid structure in the anterior end of the body filled by a ring of paleas (Capa, Hutchings & Peart 2012). The length of the opercular crown was measured from the dorso-ventral axis of each animal. A pair of filamentous branchiae is present in each thoracic segment, except the first (Jorge, Petersen & Fanta 1969). For a better representation, the length of the first three filamentous branchiae in the thorax was measured and the average value was calculated for each individual. The thoracic region is composed of the tentacle filaments arranged in series of rows (Capa et al. 2012). We then measured the average length of three tentacle filaments of the last

row of multiple tentacles (closer to the thoracic region). For this purpose, the last row of multiple tentacles was removed and positioned upright in a lamina plate, allowing a more accurate measurement. The building organ is a U-shaped invagination located near the mouth in the thoracic region (Stewart et al. 2004). The size of the building organ was measured as the inner length from the anterior top to its lower base. For the total body size measurements we used an electronic digital caliper (Digimes; 10 μm precision). The bulk of organ size measurements were taken under a Zeiss optical stereoscope (Discovery V12; 270 to 480 μm precision) coupled to a digital camera (AxioCam MRc 5).

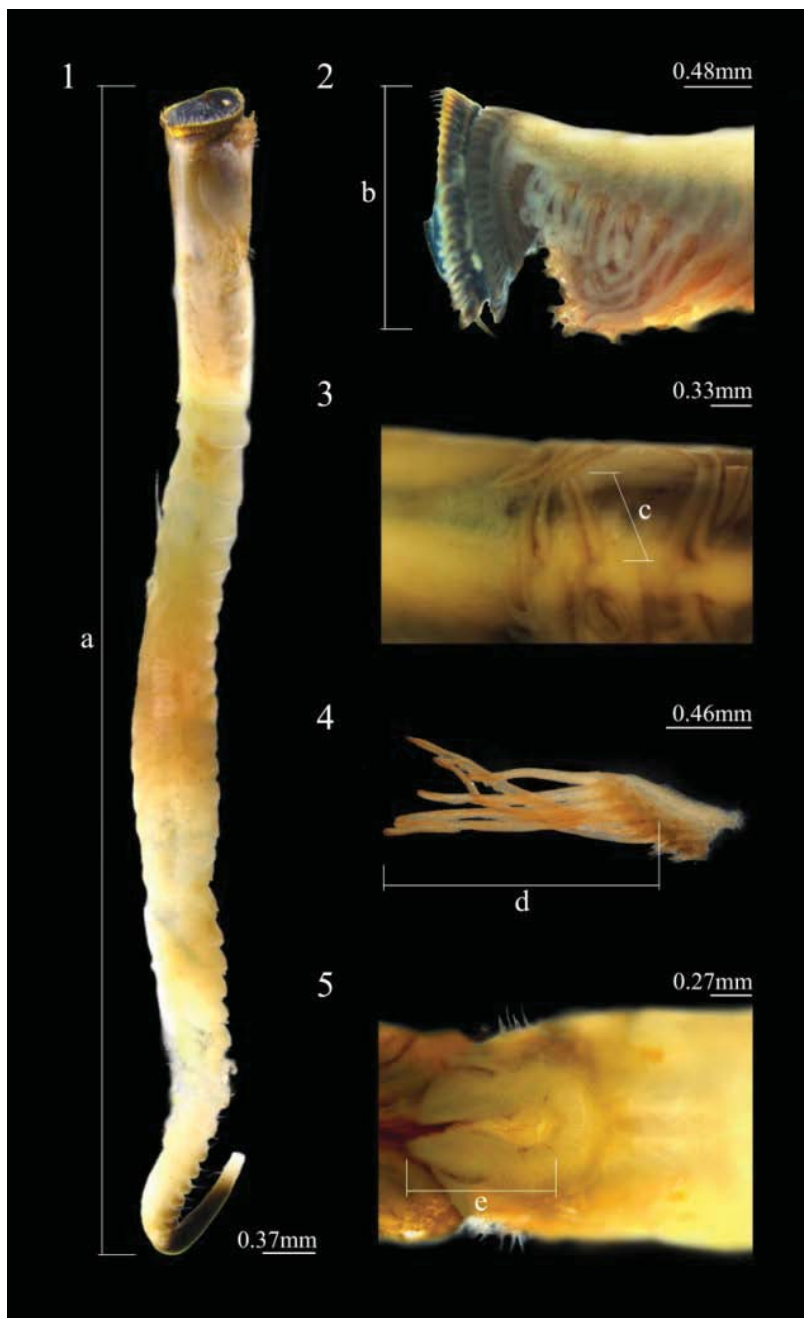


Figure 2. Phenotypic traits of *Phragmatopoma caudata*: (1) view of the whole-organism (a) measure of total body length, except the caudal region; (2) lateral view of anterior region and (b) measure of opercular crown size; (3) lateral view of thoracic and parathoracic regions and (c) measure of branchiae size; (4) view of the last row of multiple tentacles and (d) measure of tentacles size; (5) ventral view of the thorax region and (e) measure of building organ size. Recalling that were measured the first three branchiae and three tentacles of each specimen and the average value was calculated by each individual.

2.2 Temperature and other environmental variables

The environmental variables used in our analyses were pre-selected based on their relevance to an intertidal species, which are subjected to geophysical (e.g. tidal range, wave height, and salinity) and biogeochemical (e.g. dissolved oxygen) forces, along with regional climate (temperature). These variables were extracted from different sources considering the geographical position (latitude and longitude) of each of our study sites. The average temperature of the three coldest months of the year (°C) was extracted from the WorldClim database for the period 1950-2000 (Hijmans et al. 2005). The data were generated through interpolation of average monthly climate data from weather stations on a 30 arc-second resolution grid

($\sim 1 \text{ km}^2$ resolution). The salinity (psu) and dissolved oxygen (mL/L) data were taken from BioOracle database for the periods 1961-2009 and 1898-2009, respectively (Tyberghein et al. 2012). Interpolated data of salinity and dissolved oxygen were developed from oceanographic *in situ* surface measurements gathered from the World Ocean Database 2009 (WOD09; Boyer et al. 2009). The tidal range (\approx MHWS - MLWS) was calculated using the tidal atlas of finite element solutions FES2012 (Carrère et al. 2012). On a grid of 0.0625 degree resolution, were chosen the greatest values of the sum of the two major tidal constituents (*i.e.* semidiurnal amplitude $M2 + S2$ or diurnal amplitude $K1 + O1$). The final amplitude values were doubled to take the tidal range output (cm). Finally, the wave height data were obtained from the latest global atmospheric ERA-Interim reanalysis produced by the European Centre for Medium-Range Weather Forecasts ECMWF (Dee et al. 2011). The global average wave height data (m) on 0.125 degree resolution ranged from January 2005 to December 2013 using the maximum month estimates based on 6-hourly altimeter measurements (Envisat, Jason-1, and Jason-2).

2.3 Data analysis

To verify the influence of the environmental variables on the distribution of body size we applied a distance-based linear model analysis (DistLM) to model the relationships between lengths of the whole-organism, opercular crown, branchiae, tentacles, and building organ against temperature, salinity, tidal range, waves and dissolved oxygen. DistLM analyzes the relationship between a multivariate data cloud, and one or more predictor variables in order to detect which of the potential predictors explained most of the variability of the response variables. The models were fitted using step-wise selection and the most parsimonious model was chosen using a modified Akaike information criterion (AICc; Anderson, Gorley & Clarke 2008). Afterwards, in order to examine the relationships between body sizes with only temperature across the sites, we applied a canonical analysis of principal coordinates (CAP). The strength of associations between the variables was indicated by the square canonical correlations (δ^2) with 9999 number of permutations. The advantage of the CAP is that it is specifically designed to find an axis through the multivariate cloud of data which has the strongest

relationship with the environmental variables of interest (Anderson 2008). All multivariate analyses were based on Bray-Curtis dissimilarities calculated from untransformed data and with the PERMANOVA+add-on package for PRIMER v6 (Anderson et al. 2008).

Finally, in order to assess and compare the optimal adaptation of each body size to the temperature gradient we built curve distributions using quantile regression spline models based on the 95th percentile. Quantile regression splines indicate possible maximum values for each phenotypic trait along the environmental gradient (Konecker & Basset 1978). The three possible modal distributions are non-modal or straight line, unimodal-skewed, and multiple modal patterns. The appropriate model for each phenotypic trait was selected using the small-sample-correction version of AICc (Anderson 2008). The model which has the smallest AICc value out of the set of models having polynomial of degree 1, 2, 3, or 4 was chosen. The analysis and graphs were performed on the R software (R Development Core Team 2009) using `quantreg` and `splines` packages (Hastie 1993; Koenker 2007).

3. Results

Taking into account the macroscale of the study and the latitudinal gradient sampled, the environmental variables temperature, salinity, dissolved oxygen, tidal range, and wave height were found to be significant and together explained a great amount (27%) of the variability in the body size distribution of *P. caudata* (DistLM; AICc = 3614.8; Table 1). However, the magnitude of the contribution of each environmental variable to the model was quite dissimilar, with temperature explaining 9 to 15 fold more than any other variable individually. Temperature alone (20% of explained variance) explained more than the double of the sum of all other environmental variables, indicating the sound body size-temperature relationship for the reef building polychaete.

Table 1. Results of a distance-based linear model (DistLM) relating phenotypic traits of *Phragmatopoma caudata* with environmental variables in step-wise selection procedure.

Variable	AICc	Pseudo- <i>F</i>	P	Prop.
Temperature	3656.5	135.06	0.001	0.200
Tidal range	3642.2	16.49	0.001	0.023
Salinity	3632.2	12.12	0.001	0.017
Waves	3621.9	12.31	0.002	0.017
Dissolved oxygen	3614.8	9.152	0.001	0.013

Prop. = proportion of explained variance; Cumul. = cumulative proportion of explained variance.

When analyzing the bulk of body size measures constrained by only temperature data we observed two main trends in the spatial distribution of samples (CAP; Fig. 3). First, there was a forthright correlation with temperature ($\delta^2 = 0.70$; $p = 0.004$), evidencing that the body sizes change in a predictable way along the temperature gradient. In general, the body sizes tend to decrease with increased temperature. Second, three groups of sites were observed along the gradient, each one limited to a range of five degrees of temperature (between 15-20°C; 20-25°C, and 25-30°C). Such highlighted trends of variation could indicate that all body sizes are changing in

response to temperature or that each body size is showing a different spatial trend along to temperature gradient.

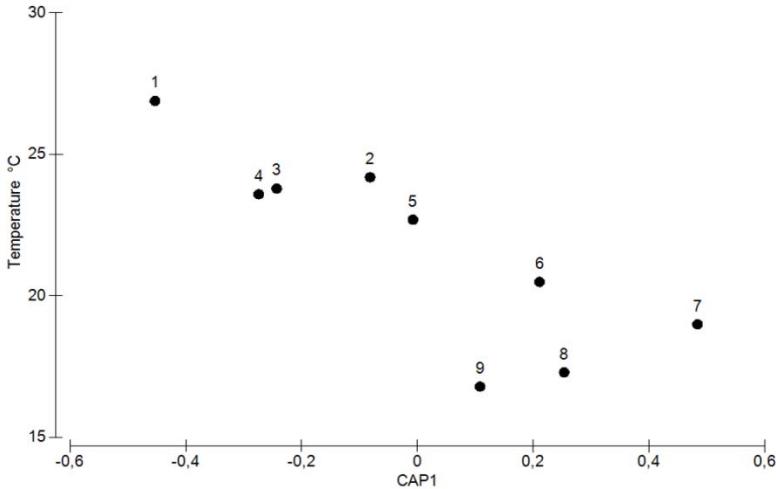


Figure 3. Constrained canonical correlation (CAP) of the *Phragmatopoma caudata* phenotypic traits (whole-organism, opercular crown, branchiae, tentacles, and building organ sizes) with temperature gradient. For more information on the sampled sites see Figure 1 and Appendix A.

To disentangle the question whether the body size-temperature relationship for *P. caudata* is a matter of unique or multiple optimal adaptations of phenotypical traits, we analyzed the modal curve distribution for each phenotype separately. The

scatterplots of whole-organism and organ-level body sizes showed similar and alternative patterns of modal distributions along the temperature gradient (Fig. 4). The model for whole-organism size showed a clear unimodal and asymmetrical distribution, converging on a single optimum around 19°C (Splines; AICc = 1425.4; Polynomial degree = 3). In the same way, the data on opercular crown length showed a unimodal left-skewed distribution, converging on a single optima adaptation around 19°C (Splines; AICc = 556.1; Polynomial degree = 3). Oppositely to the patterns previously presented, the curve distributions for branchiae and tentacle sizes showed a bimodal distribution, with highest values at both ends of the temperature gradient and lowest values in the middle of the gradient. Despite the multimodality of the curves for these two phenotype traits, their modal intensity was quite different. The branchiae tended to be larger in low temperatures (modal around 18°C) than in high temperatures (modal around 26°C) (Splines; AICc = 257.7; Polynomial degree = 4). The tentacles showed similar amplitude of sizes in both modal around 18°C and modal around 26°C (Splines; AICc = 974.4; Polynomial degree = 4). The building

organ sizes showed a slight tendency of increase from higher to lower temperatures with no clear modal pattern, just a smooth sharp in the curve around 21°C (Splines; AICc = 224.4; Polynomial degree = 4).

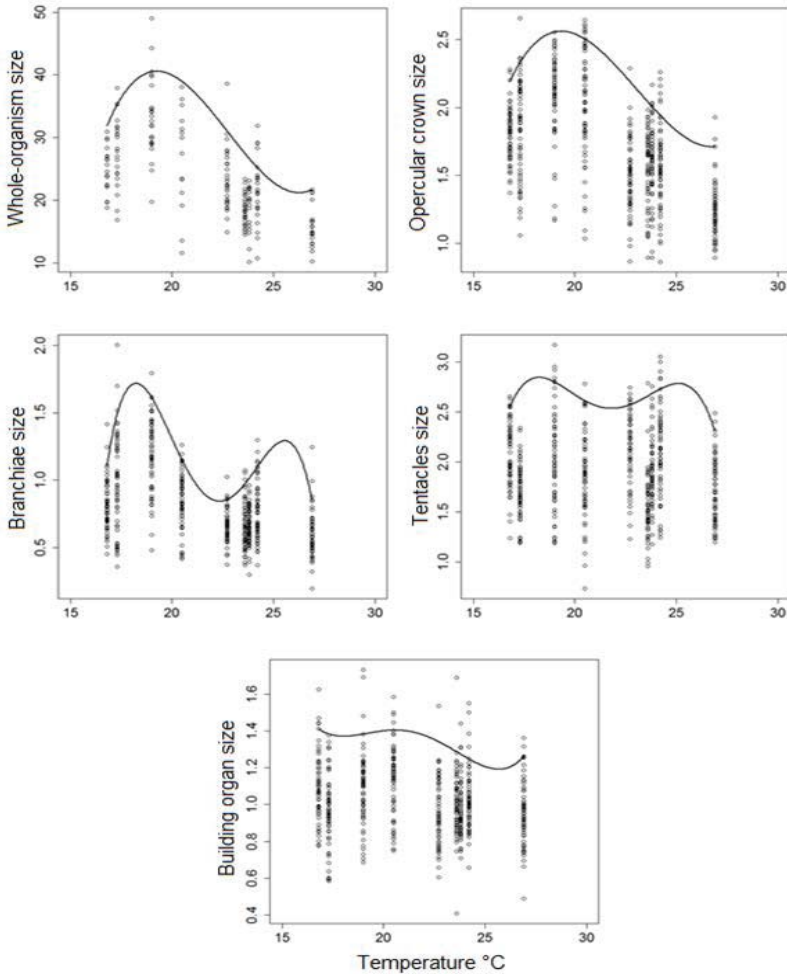


Figure 4. Relationship between individual phenotypic traits of *Phragmatopoma caudata* and temperature from nine sites along the Atlantic coast of South America, emphasizing the type of the distribution curve (unimodal or multimodal). The regression spline model shows the distribution of the traits for the 95th percentile indicated by a vertical line.

4. Discussion

Our results demonstrate that the body sizes of *P. caudata* are strongly influenced by the temperature gradient along its geographical range of distribution in the South American Atlantic coast. We found a clear multidimensionality for the five phenotypic traits studied indicating alternative optimal adaptations of body sizes to the temperature conditions. The optimal adaptation of phenotypic traits, as described by the modal curve distribution, followed a unimodal left-skewed pattern for the size of both whole-organism and opercular crown, a multimodal curve for tentacles and branchiae sizes, and a non-modal or increasing distribution along the temperature gradient for building organ size. The phenotypic plasticity of the genus *Phragmatopoma* is largely known in many

aspects, with exception to the relationships with temperature. Patterns of oogenesis and oocyte development (Faroni-Perez & Zara 2014), fecundity, size of eggs and adults (McCarthy, Young & Emson 2003) and even increases in the number of abdominal segments (Kirtley 1994) are tightly related with wave activity, habitat type, day length, and availability of reef constructing material. In this sense, the plasticity in body sizes of *P. caudata*, represented by their many alternative dimensional responses, could reflect the multiple facets of the organism and provide numerous ways to its establishment in a variable environment (Laughlin 2013) mainly driven by the temperature.

The thermal sensitivity of most biological processes in *P. caudata* seem to operate within the ranges of critical temperatures (Kingsolver & Huey 2008) and following the Bergmann's rule. At lower temperatures, with decreased metabolic rates, *P. caudata* could spend more energy in body growth and consequent biomass increase. In contrast, higher temperatures could accelerate the metabolic demand (*i.e.*, for reproduction, productivity, feeding, mortality, avoiding predation), requiring a compensation from other phenotypic

traits. These compensation mechanisms could reflect a hierarchy of traits with alternative optimal adaptations. The whole-organism body size will be in the top of the hierarchy and then directly related to temperature, while the bottom of the hierarchy is represented by organ sizes that are related with temperature and secondarily with others environmental variables (Marks 2007).

The opercular crown size showed a unimodal distribution similar to the pattern found for the whole-organism. This response was expected because of the known strong relationship between these two traits, as the size of the opercular crown is widely used as a proxy for the total length in biometric analysis and age classes studies (Occhioni, Brasil & Araújo 2003; Faroni-Perez 2014). The correlation between whole-organism size and opercular size is largely related to its early ontogenetic development along with the anterior region of body. In fact, the operculum and the building organ are developed from the first segment (Dales 1952). The building organ size presents a non-modal curve but with a slight decrease trend towards the highest temperatures, like opercular size and whole-organism size. The mucus secreted as a cement in tube

building is made by lysozyme-like enzymes with increasing molecular diameter in high temperatures (Stabili et al. 2009). The resultant increased volume of mucus with minor demands to the building organ together with a generalized small organism size may ground organ compensation to a small size.

On the contrary, the multimodal curve distribution found for sizes of both branchiae and tentacles could indicate a secondary influence of other environmental variables (besides temperature) in the efficiency of the respiration and feeding, two of the main activities to energy supply and maintenance of polychaetes' life (Rouse & Pleijel 2001). Despite the influence of the temperature gradient in the present case of *P. caudata*, the multimodal curves for the distribution of branchiae and tentacles sizes suggest relationships with the other environmental variables. The peaks of highest values of sizes coincide geographically with the presence of the Amazonas River at the upper limit and of the Plata River at the lower limit of the spatial range of our study. The plume of low-salinity, nutrients, suspended and dissolved material in the waters of both rivers might reach the polychaete reefs at the extreme sampled sites (Möller et al.

2008; Moller, Kampel & Novo 2010). The plumes of the rivers could promote an alternative dimensionality and multiple optimal adaptations to tentacles and branchiae sizes.

Both branchiae and tentacles sizes similarly showed multimodal patterns of distribution, but with different peaks. The size adaptations of the respiratory and feeding structures could allow *P. caudata* to tolerate low oxygen and low food availability caused by the plumes of the rivers. The tentacles sizes tend to increase symmetrically in both extremes of the reef-worm distribution, indicating that the tentacles performance and size are equally susceptible to the low food availability caused by the turbidity of the plumes (Riisgard & Ivarsson 1990; Riisgard & Nielsen 2006). On the other hand, the branchiae showed an asymmetrical multimodal curve with larger sizes more concentrated at south than at north. The branchiae performance and size in the extreme of the geographical distributions of species could be differently affected by the general diminishing concentration of dissolved oxygen in water caused by the plumes (Yokoyama & Tamai 1981; To-orn, Sato-Okoshi & Paphavasit 2015) and, additionally, by the natural seasonality in

temperature at the south which change the oxygen solubility in water (Nagy et al. 2002; Willig et al. 2003; Piola et al. 2005).

The body size-temperature relationship has been brought up to the center of ecological responses to climate change, especially global warming (Daufresne, Lengfellner & Soomer 2009). There is substantial evidence that global warming might have far-reaching consequences by promoting smaller body sizes and shorter life spans (Sheridan & Bickford 2011) linked to the change of the optimum adaptation of the population curves. Additionally, climate change may reduce the mean fitness of many species as environmental temperatures exceed the optimal temperatures of the animals (Kingsolver & Huey 2008). Although we can construct mechanistic models to predict the thermal Bergman's rule, like in the present study, species manipulations have shown that rapid changes can weaken or even break the rule (Kingsolver 2009). In fact, many marine species with faster life cycles and smaller body sizes have been experiencing distribution shifts (Perry et al. 2005). All these recent evidences could have implications to the reef-building polychaete *P. caudata* and their associated community. As

ecosystem engineers (Coleman and Williams 2002) multiple responses to temperature changes can lead to sound alterations in both marine benthic biodiversity and ecosystem functioning.

Overall, our results support a very convincing demonstration that phenotypic traits of *P. caudata* responded differently to temperature variations in a large spatial scale and the temperature as the main factor determining the modal distribution of these traits. The distribution pattern of whole-organism size was represented by a unimodal and asymmetrical curve as long as organ-level sizes showed a multimodal curve with peaks at two extremes of the temperature range, matching the species geographical distribution range. The temperature may accelerate many biological processes and consequently influence the life history of *P. caudata* in different ways. This requires a compensation relationship between performance traits and temperature causing an intraspecific variation influencing the function of organisms. The results provided evidences of the significance of including different levels of traits with unique information in analysis to better understand the body sizes-temperature relationships. Furthermore, this study not only

provides a framework of individual species responses along a temperature gradient, but also exposed the value of a phenotypic trait as a possible predictor to changes in future climate scenarios.

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Appendix A. Information on the sampled sites of *Phragmatopoma caudata* populations along the Atlantic coast of South America.

Sites	Latitude	Longitude	States	Location
1	2°54' S	41°50' W	Piauí	Cajueiro Beach
2	5°52' S	35°59' W	Rio Grande do Norte	Ponta Negra Beach
3	8°20' S	34°56' W	Pernambuco	Calheta Cabo Beach
4	13°1' S	38°28' W	Bahia	Buracão Beach
5	20°16' S	40°16' W	Espírito Santo	Camburi Beach
6	22°58' S	43°2' W	Rio de Janeiro	Itaipu Beach
7	23°58' S	46°20' W	São Paulo	Santos Beach
8	25°53' S	48°33' W	Paraná	Guaratuba
9	27°26' S	48°31' W	Santa Catarina	Daniela Beach

CONCLUSÃO GERAL

Os resultados do presente trabalho fornecem uma visão mais compreensível e integrada a respeito do papel da morfologia de poliquetas e suas funções em níveis de interações biológicas intra-específica e interespecífica. Além disso, tendo em vista os crescentes danos causados ao meio ambiente e os inúmeros esforços e maneiras de avaliar e monitorar esses impactos, nós pretendemos com este trabalho explorar e melhorar as ferramentas para estudos com foco funcional. Com os dois capítulos da tese buscou-se sanar lacunas nos métodos e interpretações de análises usadas nesses estudos.

Analisando mais a fundo cada Capítulo, o primeiro mostrou que as características morfológicas selecionadas para os poliquetas indicaram a predominância de grupos funcionais distintos para os ambientes lamoso e arenoso e este padrão foi consistente nas escalas locais e regionais. Além disso, as abordagens mostraram respostas semelhantes, porém a análise morfológica apresentou uma porcentagem de explicação maior que as abordagens clássicas taxonômicas e de atributos biológicos, o que reforça o uso da morfologia em abordagem funcional.

Em relação ao segundo capítulo, os atributos fenotípicos de *Phragmatopoma caudata* mostraram diferentes respostas à temperatura com distintas adaptações ótimas, sendo observado um padrão de distribuição unimodal para tamanho do corpo e opérculo e multimodal para tamanho de brânquias e tentáculos. Estes resultados

forneem importantes evidências da inclusão de atributos de diferentes níveis hierárquicos em análises e pesquisas com diversidade funcional. Além disso, apesar da expressiva influência da temperatura (aproximadamente 75% de explicação da variabilidade), fatores secundários locais, como a vazão dos Rios Amazonas e la Plata, também podem influenciar na distribuição dos atributos fenotípicos de *P. caudata*.

Para finalizar, uma consideração importante é que a incorporação da morfologia em atributos biológicos elimina a subjetividade e clarifica o processo analítico, fornecendo informações mais substanciais sobre o papel ecológico de poliquetas nos ambientes. Além disso, esta abordagem pode ser perfeitamente empregada a outros grupos bentônicos, mesmo para aqueles grupos menores ou amplamente desconhecidos ou negligenciados, tornando a comparação entre trabalhos funcionais mais eficazes.

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