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Diversidade de hidroides (Cnidaria) do Atlântico profundo sob uma perspectiva macroecológica

Diversity of deep-sea Atlantic hydroids (Cnidaria) under a macroecological perspective

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Resumo

A variação batimétrica nos oceanos e suas mudanças ambientais associadas impõem limites à distribuição de espécies, modulando a ocorrência de indivíduos com diferentes formas, funções e histórias de vida de acordo com a profundidade, e sendo, portanto, importante para o entendimento de padrões da biodiversidade marinha. Este estudo objetiva inferir padrões de distribuição de hidroides no Oceano Atlântico e mares árticos e antárticos adjacentes a mais de 50 m de profundidade, buscando contribuir para o entendimento da diversificação e estruturação associadas à variação batimétrica que propiciaram a ocupação dos diferentes ambientes pelo grupo. Apresentamos pela primeira vez inferências das amplitudes de distribuição batimétrica das espécies, da variação de características funcionais de indivíduos e espécies com a profundidade e da distribuição da composição de espécies ao longo da profundidade e da latitude. Em conjunto, os resultados indicam que a distribuição de hidroides no Atlântico profundo está relacionada a fatores históricos e a gradientes ambientais associados às variações latitudinal e batimétrica. Os tamanhos reduzidos e a baixa fertilidade em mar profundo sugerem que a colonização e a evolução de hidroides ao longo da profundidade são principalmente influenciadas pela disponibilidade de alimento e pelas baixas densidades populacionais. Ainda, a maior proporção de espécies e indivíduos solitários em mar profundo e o maior uso de substratos não-consolidados sugerem influência da disponibilidade de substrato. A proporção de espécies capazes de liberar medusas abaixo de 50 m é geralmente menor que em águas rasas costeiras, mas a proporção aumenta com a profundidade, principalmente abaixo de 1.500 m. A liberação de medusas seria desvantajosa em um ambiente com baixas densidades populacionais, por aumentar a incerteza da fecundação dada pela dispersão de gametas, e despender mais energia para reprodução em um cenário de poucos recursos alimentares. Amplas distribuições batimétricas sugerem capacidade de dispersão vertical e alta tolerância às mudanças ambientais associadas à variação batimétrica. Os resultados indicam também que a colonização de hidroides em mar profundo ocorre em um sistema de fonte-sumidouro, no qual as populações de mar profundo seriam sustentadas por imigração de águas mais rasas. Mostramos neste estudo que hidroides são importantes habitantes do mar profundo e que o entendimento da diversidade do grupo neste ambiente se beneficiará de investigações em áreas ainda pouco amostradas, como latitudes tropicais sul e profundidades abaixo de 1.000 m.

Palavras-chave: Macroecologia marinha, mar profundo, Hydrozoa

Abstract

The bathymetric variation in the oceans and associated environmental changes impose limits on the distribution of species, modulating the occurrence of individuals with different forms, functions and life histories according to depth, and is therefore important for the understanding of marine biodiversity patterns. This study aims to infer patterns of hydroid distribution in the Atlantic Ocean and adjacent Arctic and Antarctic seas at more than 50 m deep, seeking to contribute to the understanding of the diversification and structuring associated with the bathymetric variation that favored the occupation of the different environments by the group. We present for the first time inferences on the bathymetric ranges of distribution of the species, on the variation of functional traits of individuals and species with depth, and on the distribution of the species composition along depth and latitude. Together, the results indicate that the distribution of hydroids in the deep Atlantic is related to historical factors and to the environmental gradients associated with latitudinal and bathymetric variations. Reduced sizes and low fertility in deep sea suggest that colonization and evolution of hydroids along depth are mainly influenced by food availability and low population densities. Also, the greater proportion of solitary species and individuals in the deep sea and the greater use of unconsolidated substrates suggest influence of substrate availability. The proportion of species capable of releasing medusae below 50 m deep is generally lower than in shallow coastal waters, but the proportion increases with depth, especially below 1,500 m. The release of medusae would be disadvantageous in an environment with low population densities, by increasing the uncertainty of fertilization given by the dispersion of gametes, and expending more energy for reproduction in a scenario of few food resources. Wide bathymetric distributions suggest vertical dispersal capacity and high tolerance to the environmental changes associated to the bathymetric variation. The results also indicate that colonization of hydroids in the deep sea occurs in a source-sink system in which deep-sea populations would be sustained by shallower water immigration. We show in this study that hydroids are important inhabitants of the deep sea and that the understanding of the diversity of the group in this environment will benefit from investigations in areas still poorly sampled, such as southern tropical latitudes and depths below 1,000 m.

Keywords: Marine macroecology, deep sea, Hydrozoa

Introdução Geral

A macroecologia estuda a relação dos organismos com o ambiente onde vivem em grandes escalas espaciais, a partir da caracterização de padrões de distribuição da diversidade, como riqueza, abundância, amplitudes de distribuição ou tamanhos corporais (Brown & Maurer, 1989; Brown, 1995; Gaston & Blackburn, 2000; Witman & Roy, 2009; Keith *et al*., 2012). A distribuição atual da diversidade decorre de eventos históricos de origens, expansões, diversificações e extinções das espécies, e relaciona-se à capacidade de seus indivíduos e populações ocuparem diferentes nichos (Valentine, 1973; Jablonski *et al*., 1985, 2006; Sexton *et al*., 2009; Lomolino *et al*., 2017). Características funcionais dos organismos (= "*traits*" em inglês) estão relacionadas a suas respostas a fatores bióticos ou abióticos, afetando suas capacidades de crescimento, sobrevivência e reprodução em habitats distintos, assim influenciando diretamente a variação espacial na composição de espécies e podendo contribuir com o entendimento da seleção natural e do funcionamento de ecossistemas (Soininen *et al*., 2007; Violle *et al.,* 2007; Bremner, 2008; Connell & Irving, 2009; Webb *et al*., 2009; Brun *et al.,* 2016).

A variação batimétrica nos oceanos, com seus gradientes e mudanças ambientais associados, como queda de temperatura, luminosidade, disponibilidade de matéria orgânica e de substratos consolidados, e aumento da pressão hidrostática, impõem limites à distribuição de espécies (Somero, 1990, 1992; Smith *et al*., 1997; McClain & Hardy, 2010; Rex & Etter, 2010; Brown & Thatje, 2011; Talley *et al*., 2011; Jamieson, 2015), levando à ocorrência de indivíduos com diferentes formas, funções e histórias de vida de acordo com a profundidade (McClain, 2004; McClain *et al*, 2005; Rex *et al*., 2006; Ramirez-Llodra *et al.,* 2010). Por outro lado, o aumento da profundidade leva a condições ambientais mais homogêneas, reduzindo barreiras ao fluxo gênico e levando a uma maior uniformidade da fauna (McClain & Hardy, 2010; Rex & Etter, 2010). A variação ambiental no fluxo de matéria orgânica particulada para o bentos profundo é considerada um fator importante influenciando mudanças faunais ao longo da profundidade, e estruturando as comunidades em mar profundo (Carney, 2005; Rex & Etter, 2010; Wei *et al*., 2010; McClain *et al*., 2012; McClain & Rex, 2015; Woolley *et al*., 2016).

Hidroides, os estágios polipoides, geralmente bentônicos, das espécies de Hydroidolina (exceto Siphonophorae) (Cornelius, 1995; Cartwright *et al*., 2008; Schuchert, 2012), são ecologicamente diversos e apresentam grande variação intra e interespecífica de formas e tamanhos nos diferentes ambientes (Gili & Hughes, 1995; Cunha *et al*., 2016). Vivem desde

águas rasas até profundidades hadais (Kramp, 1956; Calder, 1996; 1998), alimentando-se de matéria em suspensão e usando seus nematocistos para capturar pequenos organismos planctônicos (Gili & Hughes, 1995). Geralmente colonizam substratos consolidados, mas também ocorrem em substratos não-consolidados (Gili & Hughes, 1995; Bouillon *et al*., 2006; Schuchert, 2012). Reproduzem-se sexuada e assexuadamente (Gili & Hughes, 1995). Suas espécies podem ou não liberar medusas ao longo dos ciclos de vida. Arquetipicamente, pólipos brotam medusas dioicas, portadoras dos gametas que, após fertilizados, desenvolvem-se em larvas plânulas, as quais se metamorfoseiam novamente em pólipos bentônicos (Cornelius, 1995). Há, porém, diferentes níveis de redução da fase de medusa nas diferentes linhagens, até sua completa supressão em ~74% das espécies (Gibbons *et al*., 2010), nas quais o pólipo porta os gametas em gonóforos fixos.

Os primeiros registros de hidroides em profundidades maiores do Atlântico foram obtidos por expedições do final do século XIX, a partir da coleta de novas espécies e também estendendo as amplitudes de distribuição de espécies de áreas mais rasas (*e.g.*, Allman, 1874; Smith & Harger, 1874; Verrill, 1874). No entanto, apesar da importância de compreender os efeitos da variação batimétrica na distribuição da biodiversidade marinha, há apenas inferências pontuais ou regionais da distribuição de hidroides de mares profundos, e com diferentes focos (*e.g.*, Calder, 1998; Henry *et al*., 2008). Na realidade, o conhecimento atual sobre os padrões de distribuição no mar profundo é escasso para a maioria dos táxons de invertebrados marinhos, com poucas sínteses do conhecimento de táxons superiores em oceanos como um todo (Allen & Sander, 1996; Rex *et al*., 1993, 2000, 2005, 2006; Rex & Etter, 2010; Woolley *et al*., 2016).

Objetivo Geral

Este estudo tem o objetivo de inferir padrões de distribuição de hidroides no Oceano Atlântico e mares árticos e antárticos adjacentes com mais de 50 m de profundidade, melhorando nossa compreensão da diversificação e estruturação associadas à batimetria que propiciaram a ocupação dos diferentes ambientes pelo grupo.

Organização da Tese

À parte esta introdução geral, essa tese é apresentada em 4 capítulos principais e uma seção de considerações finais.

O Capítulo 1 apresenta um extenso levantamento bibliográfico de registros de hidroides, em toda a área estudada, com o objetivo de descrever a distribuição batimétrica das espécies. Investigamos as relações das amplitudes de distribuição batimétrica com as regiões, latitudes e profundidades médias de ocorrência, assim como com a taxonomia do grupo. Por fim, examinamos a influência de fatores históricos nos padrões de profundidades de ocorrência sob um contexto filogenético.

O Capítulo 2 caracteriza a distribuição de uma série de características funcionais das espécies (= "*traits*") e indivíduos de hidroides ao longo da profundidade, contrastando-as com o conhecimento sobre a biologia do grupo e a ecologia de mar profundo.

No Capítulo 3 inferimos padrões de distribuição das espécies de hidroides em todo o Oceano Atlântico e mares polares circundantes considerando a variação batimétrica e latitudinal, buscando reconhecer limites e gradientes de distribuição.

O Capítulo 4 é um artigo publicado em resposta a Chaudhary *et al*. (2016), abordando a complexidade dos padrões de distribuição de espécies e o viés gerado pela heterogeneidade amostral nos dois hemisférios.

Considerações Finais

Este estudo é pioneiro nas inferências de padrões de distribuição da diversidade de hidroides no Oceano Atlântico e mares polares circundantes em relação às variações batimétrica e latitudinal. Foram estudadas as amplitudes de distribuição batimétrica das espécies (Capítulo 1), a variação de características funcionais de indivíduos e espécies com a profundidade (Capítulo 2), e a distribuição da composição de espécies ao longo da profundidade e da latitude (Capítulo 3). Os padrões indicam que a distribuição de hidroides no Atlântico profundo é mediada tanto por fatores históricos – conforme sugerido pelo isolamento da fauna Patagônica e Antártica e pelas diferenças em amplitudes de distribuição batimétrica entre táxons e regiões –, quanto por gradientes ambientais associados à variação latitudinal e batimétrica. Tamanhos reduzidos e baixa fertilidade em mar profundo sugerem que a colonização e a evolução de hidroides ao longo da profundidade são principalmente influenciadas pela disponibilidade de alimento e pelas baixas densidades populacionais, enquanto a maior proporção de espécies com indivíduos solitários em mar profundo e maior uso de substratos não-consolidados também por formas coloniais sugerem influência da disponibilidade de substrato (Ramirez-Llodra *et al*., 2010).

As amplas distribuições batimétricas e a tendência de maior uniformidade da fauna abaixo de 1.000 m de profundidade devem ser causadas pela grande capacidade de dispersão vertical e horizontal, assim como certamente inclui a tolerância às mudanças ambientais associadas à variação batimétrica (Young *et al*., 1997a, 1997b). Da mesma forma, maiores amplitudes de distribuição geográfica para espécies com maiores amplitudes de distribuição batimétrica também devem resultar de tolerâncias fisiológicas e capacidades dispersivas.

Os dados sugerem que a colonização de hidroides no Atlântico profundo ocorre em um sistema de fonte-sumidouro, no qual as populações de profundidade seriam sustentadas pela imigração de indivíduos de águas mais rasas (Rex *et al*., 2005). As extensões das amplitudes de distribuição das espécies, geralmente do raso para o fundo, com raras espécies estritamente batiais ou abissais, e a menor proporção de espécies férteis abaixo de 1.000 m de profundidade, apontam para taxas mais baixas de reprodução sexuada em estratos batimétricos profundos. Ainda, a proporção de espécies capazes de liberar medusa abaixo de 50 m é geralmente mais baixa do que em águas rasas costeiras – apesar de a proporção aumentar com a profundidade, principalmente abaixo de 1500 m. A liberação de medusa seria desvantajosa em um ambiente com baixas densidades populacionais, por diminuir a chance de fecundação devido ao aumento

da dispersão de gametas, e ainda despender mais energia para reprodução em um ambiente com poucos recursos energéticos. No entanto, apesar do aumento de grupos meroplanctônicos com o aumento da profundidade, seus baixos índices de fertilidade adicionam evidências para a hipótese de fonte-sumidouro (Rex *et al*., 2005).

Algo importante deste estudo é que lidamos com um esforço amostral desigual ao longo do Oceano Atlântico, menor em latitudes tropicais sul e em profundidades abaixo de 1.000 m. Dados estão disponíveis principalmente próximos às margens continentais, com um hiato no conhecimento nas extensas planícies abissais. Isso demonstra a necessidade de melhores amostragens no futuro. O maior número de registros profundos nas latitudes mais bem amostradas é a base para afirmar que há subestimativa de riqueza de dados biológicos associados para diversas áreas – ou pior, nenhuma área está, de fato, adequadamente amostrada. A alta diversidade que já é conhecida para o grupo em mar profundo pode revelar-se ainda maior com futuras coletas direcionadas às áreas menos estudadas e a diferentes habitats, como por exemplo os de substratos não-consolidados, que tem grande potencial de riqueza.

O caminho a seguir para o estudo de macroecologia de hidroides de mar profundo inclui maximizar o rendimento dos dados já coletados e um maior apoio e dedicação à amostragem de áreas profundas, principalmente do Atlântico Sul. Derivando diretamente desta tese, é de particular interesse um estudo que relacione as características funcionais de hidroides tanto com as amplitudes de distribuição batimétrica quanto com as variações latitudinais e batimétricas de composição de espécies, com o objetivo de revelar a influência de características funcionais, principalmente relacionadas ao tamanho e reprodução, na distribuição de espécies. Por fim, investigações futuras integrando variáveis ambientais e filogenias devem contribuir com o entendimento dos processos micro e macroevolutivos envolvidos nos padrões aqui observados (Leclère *et al*., 2007; Cartwright & Nawrocki, 2010; Fine, 2015).

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