

Biogeography and genetic diversity of the atlantid heteropods

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ABSTRACT

The atlantid heteropods are regularly encountered, but rarely studied marine planktonic gastropods. Relying on a small (< 14 mm), delicate aragonite shell and living in the upper ocean means that, in common with pteropods, atlantids are likely to be affected by imminent ocean changes. Variable shell morphology and widespread distributions indicate that the family is more diverse than the 23 currently known species. Uncovering this diversity is fundamental to determining the distribution of atlantids and to understanding their environmental tolerances. Here we present phylogenetic analyses of all described species of the family Atlantidae using 437 new and 52 previously published cytochrome c oxidase subunit 1 mitochondrial DNA (mtCO1) sequences. Specimens and published sequences were gathered from 32 Atlantic Ocean stations, 14 Indian Ocean stations and 21 Pacific Ocean stations between 35°N and 43°S. DNA barcoding and Automatic Barcode Gap Discovery (ABGD) proved to be valuable tools for the identification of described atlantid species, and also revealed ten additional distinct clades, suggesting that the diversity within this family has been underestimated. Only two of these clades displayed obvious morphological characteristics, demonstrating that much of the newly discovered diversity is hidden from morphology-based identification techniques. Investigation of six large atlantid collections demonstrated that 61% of previously described (morpho) species have a circumglobal distribution. Of the remaining 39%, two species were restricted to the Atlantic Ocean, five occurred in the Indian and Pacific oceans, one species was only found in the northeast Pacific Ocean, and one occurred only in the Southern Subtropical Convergence Zone. Molecular analysis showed that seven of the species with wide distributions were comprised of two or more clades that occupied distinct oceanographic regions. These distributions may suggest narrower environmental tolerances than the described morphospecies. Results provide an updated biogeography and mtCO1 reference dataset of the Atlantidae that may be used to identify atlantid species and provide a first step in understanding their evolutionary history and accurate distribution, encouraging the inclusion of this family in future plankton research.

1. Introduction
Zooplankton are a vital component of open ocean food webs. However, plankton species living close to the ocean-atmosphere boundary, where CO₂ dissolves into the ocean and direct warming occurs, may be particularly vulnerable to ocean changes (Hays et al., 2005). The most vulnerable holozooplankton to changing ocean chemistry are the calcium carbonate shell-

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