

Biogeography and phylogeography of the Atlantic

In recent years, the number of biogeographic and phylogeographic studies of marine species in the Atlantic Ocean has increased sufficiently that synthesis would be beneficial. In this issue, we present six papers promoted by a workshop dedicated to identifying processes affecting biogeographic patterns of Atlantic marine organisms. The talks at the workshop and the articles in this issue help to define new biogeographic hypotheses and provide research directions for better understanding biogeographic patterns in the Atlantic Ocean.

Contrary to recent proposals that warm temperate provinces be subsumed as parts of warm regions that include the tropics (Briggs & Bowen 2012), Almada et al. (2013) find that the Lusitania Province should be kept separate as evolution of its ichthyofauna since the Miocene has generated substantial endemism. Divisions also are apparent within the province, in the sharp separation between the ichthyofauna of the oceanic islands of Azores, Madeira and Canaries versus the mainland shores of western and southern Europe and Northwest Africa. Almada and colleagues also find that the Mediterranean emerges as a center of biological diversity which likely acted both as a refugium during glaciations and as a center of diversification for thermophilic fish.

That the north Atlantic biota has been affected dramatically by climate change, particularly during glaciations, also is emphasized by Provan (2013). In his paper, Provan reviews the historical factors that have determined current patterns of genetic variation across the ranges of northern North Atlantic sessile species. Because the loss of genetic diversity is thought to diminish the adaptive potential of species, geographic regions that contain unique genetic variation are important from a conservation viewpoint. The North Atlantic 'rear-edge' (southernmost) populations of nine species—a bryozoan, a mysid, a fish, a microturbellarian, two gastropods, three seaweeds—apparently were cryptic refugia for temperate marine organisms during the last glacial maximum of the Pleistocene, some 18,000 years ago. These refugia harbour unique genetic variation that is sometimes

also associated with high levels of genetic diversity. There are, as always, exceptions and some species have higher than expected genetic diversity at higher latitudes. These and other inconsistencies suggest that there may not be a general pattern fitting all marine species distributed on either side of the Atlantic. However, some groups of species show congruent patterns, and greater in-depth work on individual species will generate knowledge from which can be drawn a general picture of biotic factors that shape biogeographic responses to climate fluctuations.

Compilation of individual studies is the purview of comparative phylogeography, which can shed light on historical and contemporary population processes by providing independent and parallel datasets. The paper by Pereira and Almada (2013) presents a study on two migratory lampreys sympatric in western Europe, *Petromyzon marinus* (which also occurs in the western North Atlantic), and *Lampetra fluviatilis* (which is restricted to European watersheds). These two lampreys have contrasting levels of genetic diversity in Europe. *P. marinus* is much less genetically diverse than *L. fluviatilis*. Pereira and Almada argue that the probable causes for this difference include the relative recency of *P. marinus* in Europe, compared to the longer evolutionary history of *L. fluviatilis* in the region, and higher cold tolerance that enabled *L. fluviatilis* to survive in areas with low glacial temperatures.

Comparative phylogeographic analyses in other cases may highlight congruent genetic structures among species, which indicates biogeographic boundaries resulting from long-term barriers to gene flow or secondary contact between previously isolated lineages. In this issue, von der Heyden et al. (2013) use three phylogenetically related clinid fishes, which are co-distributed along South Africa's coast but inhabit different tidal heights. This study design provided an opportunity to test for the effects of intertidal height on genetic population structure. The species inhabiting high intertidal tide pools showed greater levels of population divergence than subtidal and shallow-water fishes, possibly because move-

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ment in intertidal fishes is restricted during low tide. The coast of southern Africa is at the crossroads of tropical and cold upwelling oceanic ecosystems, and has one of the highest levels of species diversity in the world. As this study shows this area provides a treasure trove of opportunity to explore the mechanisms influencing population structure.

The generation of marine diversity in many parts of the world is often associated with complex coastline topography. Yet, across the Atlantic-Indian Ocean boundary in south-western Africa, high levels of biodiversity exist even though the coastline is linear with low habitat diversity. Teske et al. (2013) propose a “range extension-divergence” model that involves a geographic extension into previously inhabitable areas during a period of climate warming, followed by isolation and adaptation of the new population. The authors posit three alternative mechanisms for the generation of genetic diversity: (1) isolation, by exposure of the continental shelf, (2) reduction in Agulhas Current intensity and (3) reduced sea surface temperatures and intensified upwelling leading to diversifying selection. As the authors acknowledge, the model can be challenged on several points, and this paper will trigger further research to validate the model.

The burgeoning possibilities for testing models, brought to phylogeography by massively parallel sequencing techniques, are discussed by Rocha et al. (2013). Different approaches and strategies are summarized, as well as their applications, benefits and limitations. This review may prompt researchers, who previously have used only the few genes available, to increase genome coverage to solve mysteries that have proven daunting in the past. But new challenges arise; the main constraint to biologists is the reliance on custom made bioinformatics tools to deal with the massive amounts of data that can now be generated. The development of new technologies to survey DNA variability will change the nature of biogeographic hypotheses that can be tested. While geographic surveys of 'neutral' markers have been influential in understanding the historical and contemporary genetic effects on populations, the ability to identify genes under selection has already broadened biogeographical hypotheses to include patterns of adaptation.

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Rita Castilho¹, W. Stewart Grant², and
Vítor M. Almada³

¹Center for Marine Sciences, CCMAR-CIMAR, University of Algarve, Portugal

²Alaska Department of Fish & Game, Commercial Fisheries Division, Anchorage, USA

³Eco-Ethology Research Unit at the ISPA Instituto Universitário, Lisbon, Portugal

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