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Frontiers of Biogeography

Title

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Permalink

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Journal

Frontiers of Biogeography, 3(4)

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Publication Date

2012

DOI

10.21425/F5FBG12443

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workshop summary

Atlantic fishes as a model for the study of biogeography and phylogeography

Workshop on the biogeography and phylogeography of Atlantic fishes – Lisbon, Portugal, 26-27 November 2011

I am not all that fond of the folklore and mystique that surrounds famous scientists, yet I often wonder how meetings used to be run in the old days. The 1911 Solvay Physics meeting with Marie Curie, Albert Einstein, and Max Planck must have been quite something. The 1952 Royaumont meeting with Jim Watson, Jacques Monod, François Jacob, and Sydney Brenner would have been its Natural Sciences equivalent. Besides the presence of such icons and luminaries, the essence of the meetings was to genuinely exchange ideas and discuss science. Funding, publications, impact factors, and job advertising were not at the forefront of the agendas, as they unfortunately are now. How much time do we spend trying to figure out which talk we are going to miss because of concurrent sessions? How often does a session chair need to cut short an interesting discussion because of conflicting schedules? The recent *Workshop on the biogeography and phylogeography of Atlantic fishes* organized in Lisbon, Portugal, by Vitor Almada, Rita Castilho, and André Levy was a pleasure to attend because it gave the participants full opportunity to discuss the science, a precious commodity these days. Participants would interrupt speakers when points needed to be clarified, talks did not have a preset time limit and discussions were simply as long as needed. If just for that, the meeting was not to be missed.

The biogeography and phylogeography of Atlantic marine organisms share the same issues, pitfalls and successes as for any other region of the world. They also have their own peculiarities that make the region uniquely interesting. Two talks focused on the general issues of biogeography and phylogeography. W. Stewart Grant and Cliff Cunningham addressed the issues of molecular clock calibrations, loss of signal, and significance of ancestral polymorphisms. Both borrowed from examples of phylogeographies from the north Pacific and the north Atlantic. Grant com-

pared them, arguing that some significant loss of signal occurred during the last glacial maximum, resulting in potentially major misinterpretation of molecular clock data. Cunningham underscored other important drawbacks, first by showing the biasing effects of extinctions followed by secondary invasions and later by pointing to a seldom considered problem generated by the presence of ancestral polymorphisms. Generally used divergence based methods of calibrating molecular clocks are vulnerable to such problems, an issue that may be solved by different approaches, such as one proposed recently by Crandall et al. (2011), where population expansions are used as calibration points.

Two talks, by Vitor Almada and Sergio Floeter, provided new comprehensive background information on the biogeography of Lusitanian-Macaronesian and Atlantic fishes, respectively. Almada provided some original insights on the relative contribution of boreal and tropical faunas, and the role of potential refugia during glacial periods. The Lusitanian province being a unique entity that is not a simple meeting point of adjacent provinces. A thorough review of the literature showed that Macaronesia is clearly understudied compared to its biogeographic neighbours. Almada also presented an interesting meta-analysis of studies on population structure in fishes that span the Atlantic-Mediterranean and Atlantic-North Sea transitions. More studies showed structure in the former transition (81%) than the latter (60%), yet Almada argued that the lack of structure in many studies is an important result, because it is likely due to a direct effect of oceanic climate variability. Floeter presented a comprehensive review of the biogeographic situation of the Atlantic using state-of-the-art analysis of multiple phylogenetic approaches based on a large number of fish species. The main biogeographic barriers, represented by the Amazon outflow, the

Benguela current, and the mid-Atlantic divide manifest as concordance among a plethora of molecular phylogenies. Floeter was able to compile and synthesize those studies and provide statistical data to test the validity of those barriers. In addition, Floeter is compiling an original database of presence, distribution and abundance of reef fishes around the entire Atlantic Ocean. Such a database is essential to tease out the general models of divergence (dispersal versus vicariance) and also to test alternative hypotheses suggesting different routes of invasion: Tethys vicariance relicts, invasion via the Isthmus of Panama before its closure, recent invasion from the Indian Ocean via South Africa, Benguela vicariance, New World Origin, recent invasion from western Atlantic to eastern Atlantic, and recent invasion from eastern Atlantic to western Atlantic.

Three talks by Halvor Knutsen, Sophie von der Heyden and myself widened the discussion by encompassing the north (Knutsen), the south (von der Heyden), and the east (Bernardi). Knutsen presented a review of microsatellite analyses of fish populations present in northern Europe that recolonized the region after the retreat of the glaciers after the Last Glacial Maximum. As expected, founder effects, fast colonization and northward movement were seen. More surprisingly, ancient genotypes indicative of refugia and multiple routes of recolonization were uncovered. What most fascinated the audience was Knutsen's truly unique dataset on cod. Since 1919, 100 stations have been monitored yearly, with beach seines, to look for abundance of cod in Norwegian fjords. This information was then used to understand the present population structure of fjord and open water cod populations in the vicinity of those fjords. A combination of ecological, fisheries and molecular data were combined to provide a full picture of the species' population dynamics.

Sophie von der Heyden reviewed knowledge of the southern African transition between the Atlantic and Indian oceans, which meet where the cold Benguela and warm Agulhas currents collide. The meeting point is a shifting region between Cape Point and Cape Agulhas that forms a transition zone between fish assemblages and

populations. While some information is known, the region is clearly understudied and requires more work. Fortunately, pioneering work on a diverse array of marine organisms (including fish) by von der Heyden, is lifting some of the unknown from the region. Molecular work on clinids, gobies and invertebrates is revealing some general patterns that are fascinating. Some intertidal species, such as *Muraenoclinus dorsalis*, show extreme levels of population structure, with next to no gene flow between adjacent locales, while some invertebrates show higher levels of gene flow. Yet, overall, the region between Cape Point and Point Agulhas is generally a phylogeographic transition zone. While little is known about the detailed bathymetry and oceanography of the region, von der Heyden presented a convincing model of the effects of changes in sea-level. With lowering levels, available habitats for rocky species shrunk; with rising levels, as predicted with global climate change, available habitat will disappear even more. This is particularly true for the cold-adapted species, which would be moving poleward in other regions, but do not have anywhere to go in Southern Africa.

Bernardi presented information on Mediterranean species. In the Mediterranean, approximately 10% of the species are endemic. Bernardi argued that it is unlikely that any of them are true Tethys remnants and presented some genetic evidence on *Chromis chromis* that showed that it likely speciated within the Mediterranean after the Messinian Salinity Crisis, a hallmark of a true endemic. Bernardi then discussed the effects of a recent warming trend of the Mediterranean. This trend results in three major effects. First, the northward movement of warm adapted fishes that are traditionally seen in the southern portion of the Mediterranean. Second, the rate increase of biological invasions from the southern Atlantic fishes, best exemplified by the presence of *Parablennius pilicornis* and *Kyphosus*. Third, the rate increase of Lessepsian bioinvasions from the Red Sea via the Suez Canal. There are currently 70 Red Sea fish species that have been recorded in the Mediterranean, and the rate is rapidly increasing.

Finally, Rita Castilho presented an animated and passionate plea to use forward thinking in our new approaches. She reminded us of the proper path, pioneered by Knowles and Maddison (2002), to use a cogent framework to analyze marine phylogeography. It is due time to use strong testable hypotheses, and Castilho proposed to adapt methods of statistical phylogeography first proposed by Knowles and Maddison (2002), and later elaborated by Richards et al. (2007) to the marine realm. For example, the use of species distribution modelling combined with alternative molecular hypotheses could provide a strong framework to specifically predict a given distribution and phylogeographic pattern. In other words, it is time to move away from descriptive work and step into the testing phase of our field. Rita Castilho complained, however, that the vast amount of information now generated by next generation sequencing, that will provide the power to test those hypotheses, is still difficult to analyze due to the lack of simple analytical tools necessary to deal with the volume of inaccessible information newly generated.

After the meeting, some presenters went to the nearby city of Belem, where a map of the world, as seen by the ancient Portuguese mariners, is etched in marble on the plaza facing the monument to Henry the Navigator. Each presenter stood on the map at their study location for a moment. It was inspiring to see that places once explored by the Portuguese: Brazil, Angola, South Africa, Portugal, were again places of discoveries, places where marine molecular phylogeography was a new thread that brought together such a fine group of scientists.

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Edited by Michael N Dawson

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