

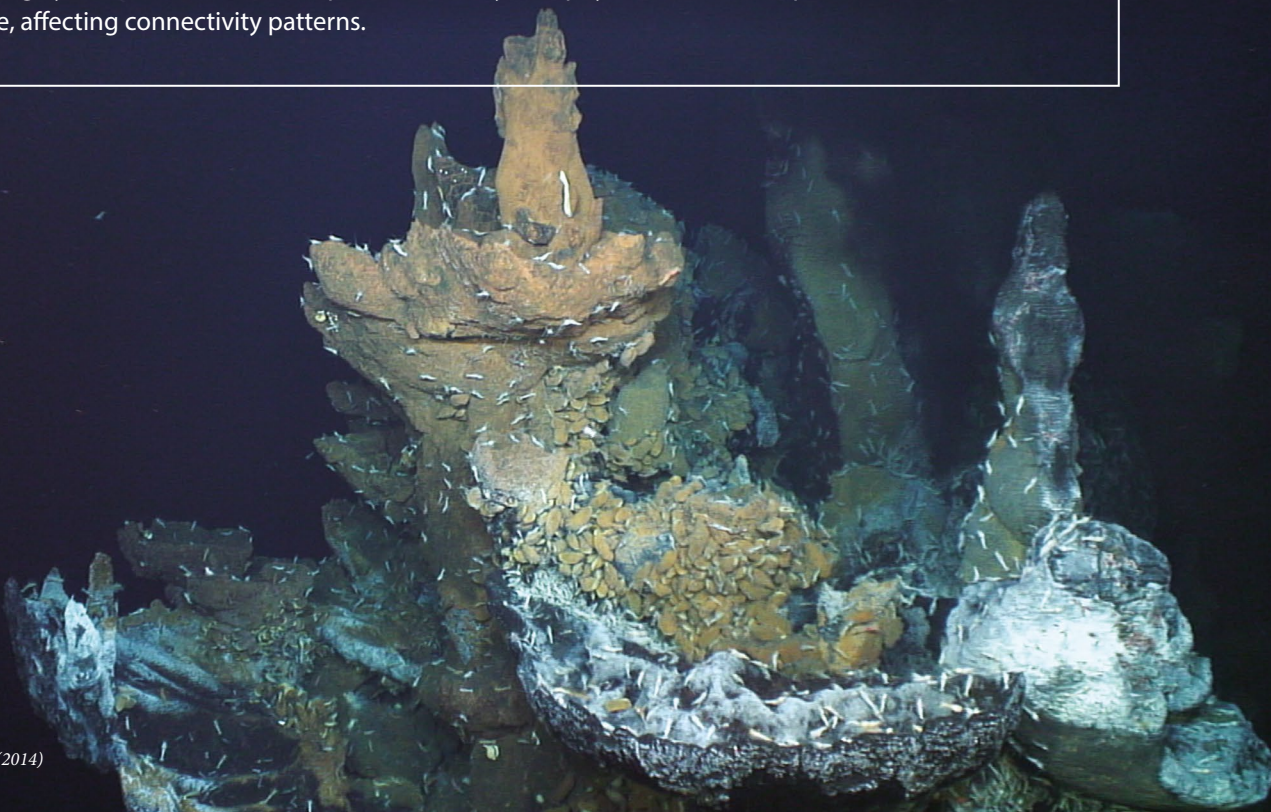
CONNECTING THE VENTS: USING GENETICS TO UNDERSTAND ECOSYSTEM CONNECTIVITY ALONG THE MID-ATLANTIC RIDGE

SUMMARY OF LATEST RESEARCH FROM THE iATLANTIC PROJECT

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KEY MESSAGES

- New work on population genetics of hydrothermal vent fauna on the Mid-Atlantic Ridge (MAR) has identified genetically different populations for several species. Specific vent sites along the MAR may play distinct roles (sources, sinks) for different species, with important implications for their management.
- Genetic data also identified a multi-species hybrid zone at 26-36°N on the MAR, formed by physical limitations on species dispersal, thus creating a sink area of greater genetic diversity.
- Different vent species have different dispersal abilities, affecting their resilience to disturbance and environmental change.
- To be biologically relevant, management strategies and protected area networks need to take a multi-species approach to account for different species' dispersal abilities, as well as considering temporal aspects: population connectivity may evolve through time, linked to natural variation in hydrothermal venting intensity and location at the seafloor.
- Ideally, the potential effectiveness of protected area networks and other measures related to the management of deep-sea mining activities should be tested beforehand (e.g. through modelling) and over time by monitoring biodiversity and connectivity through genetic data.
- This is especially relevant in the global change context since species ranges, ecosystem functioning, spawning cycles, survival and other parameters may abruptly alter as a consequence of environmental change, affecting connectivity patterns.



CONNECTING THE VENTS: USING GENETICS TO UNDERSTAND ECOSYSTEM CONNECTIVITY ALONG THE MID-ATLANTIC RIDGE

Along the Mid-Atlantic Ridge, the occurrence of specialised communities of vent fauna is controlled by the location of hydrothermal venting, which is highly patchy. The fate of species living in such a spatially isolated and dynamic environment depends on their ability to disperse and colonise new areas. Knowledge is needed on the distribution of populations and the exchanges between them as that determines the resilience of vent communities to environmental instability and fragmentation – including disturbance by human activities such as mining. Genetic data generated by the iAtlantic project provides new insights into ecosystem connectivity along the ridge, with important implications for the protection of these habitats.

Deep-sea hydrothermal vents: pristine but fragile environments

Seafloor polymetallic sulphide deposits are the target of increasing interest for deep-sea mineral exploration, with near-continuous exploration areas already licensed along the northern Mid-Atlantic Ridge (MAR). The potential future exploitation of these deposits represents a significant threat to the specialised fauna that live on and around deep-sea hydrothermal vents, such as mussels, shrimp and limpets. Mining will likely have deleterious effects on both the vent fauna and nearby abyssal fauna, resulting from short- and long-term damage to their habitats, notably through (1) habitat fragmentation, which increases local extinction risk and loss of biodiversity; (2) alteration of subsurface hydrothermal circulation, with fluctuations in venting activity that could affect species settlement and/or reproduction, and (3) creation of potentially toxic sediment plumes from mining wastewater discharge into the water column, which could alter animal physiology at vents and impact the pelagic ecosystem over large areas. These threats raise many questions about the protection of vent and neighbouring abyssal faunas, and the design (size, spacing) and establishment of protected areas.

Vent fauna and barriers to their dispersal

Vent fauna communities are usually distributed in small oases along the MAR, controlled by the highly fragmented and temporally unstable nature of hydrothermal activity along the ridge. The first studies on population connectivity on the MAR were carried out on two major components of vent fauna: shrimp swarms and mussel beds. Both mussels and shrimps have a long dispersive larval phase as plankton/nekton in the water column, suggesting that they can

migrate long distances and rapidly colonise the fragmented vent habitat. The ability to disperse far and wide to colonise new territories represents an evolutionary advantage for species living in transient and fragmented habitats – a paradigm first put forward some 40 years ago¹ to explain the persistence of vent fauna in such a spatially restricted and ephemeral environment.

Previous analyses of the genetic variation in *Rimicaris* vent shrimps^{2,3,4} supported the view of a single, freely exchanging population occurring along the whole MAR. Now, new genome-wide data generated by iAtlantic confirms strong genetic mixing between the different shrimp swarms sampled along the ridge, resulting in a unique population. Though further genetic information is required to confirm it, a similar dynamic was suggested for *Shinkailepas briandi*, a limpet that is found in abundance on MAR hydrothermal vent chimneys⁵.

Conversely, genetic data from vent mussels revealed that MAR mussel populations are geographically separated into four distinct species (two in the northern MAR, two in the southern MAR; Fig. 1) with some local hybridisation. This indicates a more pronounced isolation that could arise from mussels' greater difficulty in dispersing and establishing new colonies. Alternatively, these mussel species may have undergone genetic divergence elsewhere and subsequently independently colonised different spots along the MAR. In this case, the genetic differences developed during their previous isolation would likely have arisen due to restricted migration caused by physical barriers such as ridge topography or the long distance between sites. It is therefore difficult to determine whether these species have the capacity to rapidly recolonise the MAR hydrothermal environment after disturbance.

Left: The vent limpet *Leptodrilus atlanticus* encrusting vent mussels. Image © F. Lallier, IFREMER/Biobaz cruise.

Atlantic vent limpets are vulnerable low spreaders

iAtlantic undertook an extensive population genomics (ddRAD) study on several hydrothermal species, including two limpet species: *Lepetodrilus atlanticus*, which lives on the shells of vent mussels, and *Peltoispira smaragdina*, which lives on the walls of hydrothermal chimneys. The aim was to better understand their past and present population exchange dynamics between the main hydrothermal vent fields along the MAR.

Based on both mitochondrial DNA and thousands of nuclear genetic markers, three groups of *L. atlanticus* limpet populations were identified along the MAR (Fig. 1). The three northernmost populations (Azores Triple Junction, 36-37°N) show no genetic differentiation and the gene flow is almost non-existent between the three geographic venting regions (36-37°N, 29°N and 5°S), indicating very restricted dispersal of this limpet both northwards and southwards along the ridge. Based on this genetic information, this very abundant limpet can be considered as three distinct breeding

groups that could represent geographically isolated cryptic species (i.e., physically similar but genetically different). This contrasts significantly with vent shrimp, whose genetics indicate they can freely disperse along the MAR.

Results for *L. atlanticus* were compared with another abundant limpet, *P. smaragdina*. Mitochondrial DNA data from this second species indicates that individuals sampled along the ridge belong to a single large population with some local differentiation at the northern and southern limits of its range. In-depth genomic analysis from several thousand genetic markers suggests the population at the Moytirra vent field (the northern limit of the species range) may be completely isolated, with virtually no exchanges with populations further south. The southern populations (37°N, 29°N, 26°N and 23°N) are subdivided into two distinct genetic units, with a hybrid zone (where cohabitation and interbreeding of two genetic groups occurs) near the Rainbow vent site (36°N). These findings mirror genetic studies carried out on vent mussels *Bathymodiolus azoricus*

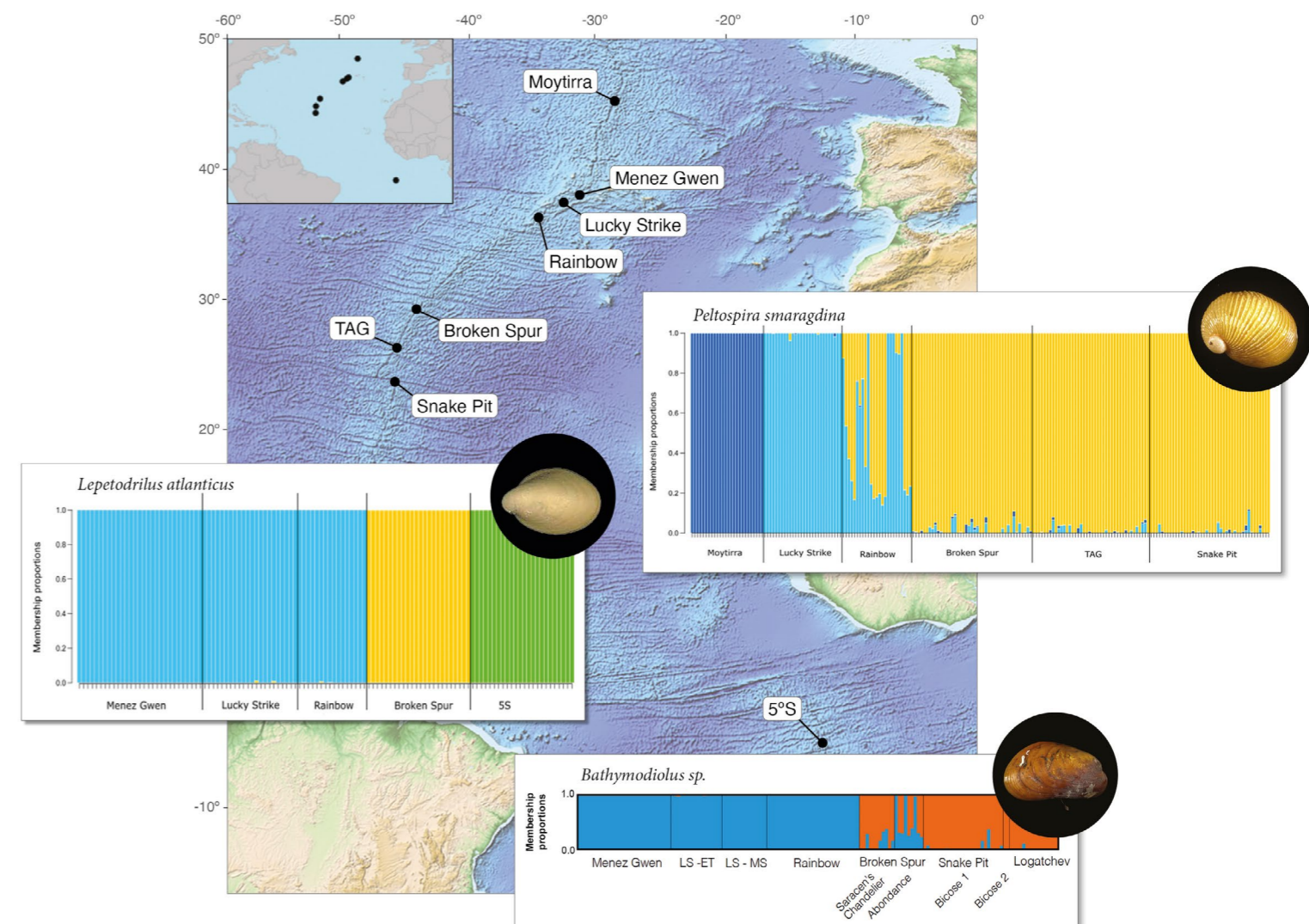


Figure 1: Population structure (graphs of the genetic composition of individuals (bars) associated with the different genetic units (colours) revealed by the analysis) of the vent limpets *P. smaragdina* (found on hydrothermal chimney walls) and *L. atlanticus* (found in mussel beds) and the two hybridising mussel species (*B. azoricus* and *B. puteoserpentis*) along the Mid-Atlantic Ridge.



Left: The vent limpet *Leptodrilus altanticus* encrusting vent mussels and rocky substrate. Image © F. Lallier, IFREMER/Biobaz cruise.

and *B. puteoserpentis*, where a hybrid zone around the Broken Spur vent site (29°N) was first discovered⁶, and is now extended to Snake Pit (23°N) based on the new genomic data from iAtlantic (Fig. 1).

With this second confirmed case, it is now possible to consider a multi-species hybrid zone on the MAR, most likely positioned between 26°N (TAG vent site) and 36°N (Rainbow vent site) and formed by physical limitations on species dispersal, thus creating a sink area of greater genetic diversity. Any natural or anthropogenic modification of hydrothermal activity in this extended zone could have major consequences for vent species, either by reinforcing their isolation or by creating bridges between previously isolated genetic units located further north or south.

Implications for management of Atlantic vent fauna

Although vent shrimp are able to exchange widely along the MAR and further afield, most other vent species have a long history of geographic isolation, indicating the need to manage vent communities based on their degree of spatial isolation and their potential as sources for other populations. This requires studies at a large (regional) spatial scale to enable local management of each genetic unit. iAtlantic's results suggest that only few migrants may be exchanged in both southward and northward directions, although the southward direction seems favoured, especially for the vent limpet *P. smaragdina*.

Differences in the genetic connectivity of hydrothermal vent

species may result from different larval dispersal capabilities and life history traits (i.e., reproduction, larval biology traits) and therefore warrant different conservation or management approaches. This has important implications for the resilience of hydrothermal ecosystems: if sites are tenuously connected for numerous vent species, communities may not be able to recover from mining-induced disturbances or any increase in the local natural extinction rate. This should be taken into account in the design of protected areas and in the authorisation of mining activity, particularly in areas of limited migration where both population replenishment and site recolonisation could be strongly attenuated. The introduction of external threats such as polymetallic sulphide mining could directly disrupt dispersal by increasing larval mortality, reducing adult fecundity or decreasing the success of larvae settling and growing at intermediate sites. In such a context, species would become isolated and their populations would shrink, increasing the risk of extinction for the most vulnerable species.

Based on these data, some sites may act as source for particular species (i.e. Snake Pit/TAG/Broken Spur for *P. smaragdina*) and sinks for other species (those same sites for *B. azoricus* mussels). To be biologically relevant, management strategies and protected area networks need to take a multi-species approach to account for the less dispersive species. Finally, temporal aspects must also be considered: population connectivity may evolve through time, linked to the natural variation in hydrothermal venting intensity and location at the seafloor. Such approaches would help to address known ocean protection challenges and shortcomings⁷ and consolidate the recognition of the northern MAR vent fields as ecologically or biologically significant by the UN Convention on Biological Diversity. Ideally, the effectiveness of protected area networks should be tested over time by monitoring biodiversity and connectivity through genetic data. This is especially relevant in the global change context since species ranges, ecosystem functioning, spawning phenology, survival and other parameters may abruptly change, affecting connectivity patterns.

The full results of this study have been submitted for publication: Portanier E. et al. (submitted) Genetic connectivity and demographic history of iconic hydrothermal vent gastropods along the Mid-Atlantic Ridge: insights using next-generation sequencing and conservation implications (submitted to *Conservation Biology*).

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