

NEWS AND VIEWS

PERSPECTIVE

Niche diversification follows key innovation in Antarctic fish radiation

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Antarctic notothenioid fishes provide a fascinating evolutionary laboratory for the study of adaptive radiation, as their diversification is linked to both isolation in an extreme environment and a key innovation that allows them to exploit it. In this issue of *Molecular Ecology*, Rutschmann *et al.* (2011) evaluate how dietary niche differences have evolved in notothenioids: rarely, or repeatedly in multiple lineages. The authors use stable isotopes to measure species' use of benthic vs. pelagic resources and map resource use onto a molecular phylogeny. Their findings indicate that pelagic diets have evolved in multiple lineages in at least two families, indicating that dietary niche diversification has occurred repeatedly and in parallel.

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Most theories about why taxa undergo adaptive radiation – evolutionary divergence into a diversity of ecological forms – rely on some form of ecological opportunity. Ecological opportunity may arise from the extinction of competitors, diversification of available resources, acquisition of a 'key innovation' that allows the organism to use resources in a different way, or from colonization of a new habitat with available resources (Losos & Mahler 2010). The latter mechanism has received considerable attention, as our best-studied adaptive radiations occur either on islands (e.g. Caribbean anoles and Darwin's finches) or in island-like habitats such as lakes (e.g. African cichlids and threespine stickleback).

Notothenioids are a diverse and charismatic radiation of freeze-resistant marine fishes that at first glance may seem to be an exception to this common pattern of adaptive radiation into island-like habitats. Upon closer inspection, though, it's clear that they are an exception that proves the rule – the Southern Ocean, where notothenioids diversified,

is functionally similar to an island in many respects, so much so that its fish fauna is 97% endemic (Eastman & McCune 2000). This is because the establishment of the Antarctic Circumpolar Current led to dramatic cooling of the waters around Antarctica following its separation from South America approximately 30 million years ago. Much of the previous fish fauna became extinct following these environmental changes, but notothenioids were able to persist in part because they evolved a key innovation: antifreeze glycoproteins that allow them to survive in subzero temperatures (Matschiner *et al.* 2011).

The key innovation of antifreeze proteins explains the persistence of notothenioid fish in the inhospitable Antarctic waters, but not necessarily their diversity; with 96 species, they comprise almost half the fish fauna. The ecological opportunity hypothesis predicts that such diversity should arise hand-in-hand with the evolution of diverse ecological niches. Rutschmann *et al.* (2011) investigate the dynamics of dietary niche diversification, an important aspect of ecological divergence in many fish radiations. Previous studies have shown that in one family (Nototheniidae), multiple species have independently evolved from their ancestral state as a benthic (bottom-feeding) fish into open-water feeders that consumed zooplankton and pelagic fishes (Klingenberg & Ekau 1996). Rutschmann *et al.* (2011) expanded the scope of this inquiry to test for parallel dietary niche evolution in multiple families across the entire radiation. The authors mapped resource use, measured using stable isotopes, onto a molecular phylogeny, and revealed that similar transitions to pelagic feeding had occurred multiple times in at least one other family, the Channichthyidae.

Previous tests of the ecological opportunity hypothesis have largely examined macroevolutionary patterns of cladogenesis or trait evolution, but the inferences from such studies may be limited because species diversity and trait diversity are not always closely related to the diversity of resources used. Rutschmann *et al.* (2011) take a more direct approach by using stable isotope analysis, which can measure species' resource use because of the predictable change in the ratio of heavy to light isotopes when matter is transferred from a resource to a consumer (Newsome *et al.* 2007). Nitrogen isotope ratios increase with each such transfer and thus provide a measure of trophic level, while carbon isotope ratios are most often used to measure reliance on alternative carbon sources. In aquatic systems, both isotopes tend to distinguish between smaller zooplankton and larger benthic prey, and thus provide a measure of species' positions on the key benthic–pelagic diet axis. Isotope ratios from tissue samples yield a time-averaged assay of a consumer's diet, and thus provide a valuable complement to traditional, 'cross-sectional' stomach

content analyses. Given the clear link between isotopes and species' niches, and the growing interest in the role of the niche in diversification, we anticipate that stable isotope analysis will be increasingly applied to evolutionary as well as ecological questions (Newsome *et al.* 2007). In notothenioids, the patterns of trophic niche evolution implied by the isotope data paint a picture of extensive convergence along the benthic–pelagic axis (Fig. 1), indicating remarkable ecological lability during diversification.

Although the patterns uncovered here add support to an influential recent model for ecological diversification, this study raises as many new questions as it answers. A key unanswered paradox is the pattern that notothenioids apparently underwent two nearly synchronous bouts of parallel diversification on the benthic–pelagic axis in the same region (Fig. 1; additional lineages also provide examples of convergence upon certain niches). If ecological opportunities sparked this radiation in general, why should two lineages diversify in parallel along the same resource axis, rather than the diversification of one lineage precluding the diversification of the other? One possibility is that the apparent dietary similarity of species from different clades is an artefact of the low resolution of stable isotope analysis; species might consume different prey types that happen to have similar isotope signatures. For example, channichthyids are generally thought to consume more fish than nototheniids regardless of where they occur in the water column (La Mesa *et al.* 2004), and it is possible that such a difference plays a role in niche partitioning despite not manifesting in isotope differences between groups. Alternatively, lineages may be sufficiently different in other niche dimensions that they do not compete strongly despite sharing dietary resources. Finally, dietary specialists may have evolved while the lineages were geo-

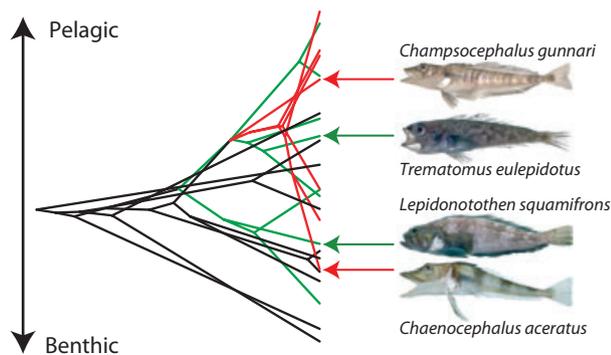


Fig. 1 'Traitgram' demonstrating the extent of trophic niche convergence between distinct lineages of notothenioid fish. The vertical position of the tips of the phylogeny shows the isotope data (fig. 5 in Rutschmann *et al.* 2011), converted to a single principal component benthic–pelagic axis. Vertical positions of interior nodes show estimated ancestral states over time (Ackerly 2009), although it should be noted that the ancestral notothenioid is thought to have been very benthic. Two key clades are highlighted – channichthyids in red and 'core' nototheniids in green – and representative benthic- and pelagic-like fish from each lineage are displayed (Photographs by Malte Damerau).

graphically isolated from one another and may co-occur following secondary contact despite niche similarity. Sympatric parallel adaptive radiations have only rarely been reported (e.g. Kozak *et al.* 2009) and it remains unclear why they should occur. Future work on the ecology of diversification in notothenioids may help to provide an explanation for this phenomenon.

This study places the notothenioid radiation in a firm position to help answer key questions about ecological diversification. For example, does morphological diversification follow a similar parallel pattern to the isotopic niche data, or do different lineages use distinct morphological adaptations to exploit pelagic resources? It would also be fascinating to study the ecological interactions between sympatric members of the channichthyid and nototheniid radiations. How do species from these parallel radiations with similar trophic niches partition resources, and what effect, if any, have these lineages exerted upon one another during diversification? There is much we do not know about how species interactions influence the course of adaptive radiation, but this study has further highlighted Antarctic fishes as a fantastic system in which to ask these questions.

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