

NEWS AND VIEWS

PERSPECTIVE

'Back to the future': How archaeological remains can describe salmon adaptation to climate change

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A strategy for species to survive climate change will be to change adaptively their way of life. Understanding rapid adaptation to climate change is therefore a priority for current research. In this issue, Turrero *et al.* (2012) use an original approach to unravel life history trait responses to climate change in two fish species (*Salmo trutta* and *S. salar*). Going against the flow, the authors adopt the strategy of going back to the future by investigating the responses of fish to the warming periods that followed the Last Glacial Period (approximately 30–20 000 years BP). To do this, they analysed *Salmo* vertebrae from well-dated archaeological sites in northern Spain in order to uncover key life history traits, which they then compared to those of contemporary specimens. They found that, as the climate got warmer, *Salmo* species tended to reduce the time spent in growing areas and reached spawning areas at a younger age; this tendency began approximately 15 000 years BP and accelerated in contemporary periods. The implication is a lower age at maturity and a lower reproductive success, which they tentatively related to recent declines in population growth rate. This innovative study demonstrates how changes in life history traits are linked both to the population growth rate and to the evolutionary rate under climatic constraints, which may serve as a basis for future conservation research.

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Species adaptation in an era of changing climate

Climate change is one of the most critical human-induced threats to biodiversity. Species develop several strategies for coping with such rapid changes, which may enable

them to survive drastic environmental changes. One such strategy consists of colonizing new environments as the climate warms, in other words, to follow the climate change front. Under this strategy, species typically expand their ranges northward as the climate gets warmer (Parmesan & Yohe 2003). Using long-term distributional data, several studies validated this pattern, notably in highly mobile organisms such as butterflies (Parmesan 2006; Chen *et al.* 2011). Another strategy consists of phenotypic adaptations. Adaptive changes can occur either through plastic changes ('ecological responses') or genetic changes ('evolutionary responses') (Gienapp *et al.* 2008). Traditionally, scientists have used long-term surveys or small-scale experiments to unravel patterns of adaptation to global warming (Parmesan 2006; Gienapp *et al.* 2008; Hoffmann & Sgrò 2011). Many examples of recent adaptations in response to climate change have been reported using these traditional means of unravelling current observed population trends (Visser 2008; Gienapp *et al.* 2008).

Apart from the debate between the plastic vs. genetic basis of species adaptation (reviewed in Gienapp *et al.* 2008), there is an urgent need to further appraise the long-term effectiveness of these adaptations, especially for adequately predicting the fate of biodiversity (Smith & Bernatchez 2008). By adopting an approach based on the analysis of faunal remains, Turrero *et al.* partially fulfil this objective.

Going 'back to the future': revisiting the past – a means of predicting the future

An African proverb states that 'when you don't know where you're going, look at where you came from'. This proverb is apt as many insights can be gained by probing historical environmental and ecological trends. Essentially, variations in the past climate have been unravelled through the analysis of sediments or archaeological data (Blanchet *et al.* 2009; Kuper & Kröpelin 2006). Reciprocally, the analyses of flora and fauna remains (i.e. pollen or vertebrae) have provided insightful information about the evolution of geographic ranges during periods of intense climate change. For instance, Graham *et al.* (1996) analysed fossil mammal fauna from North America and showed that most species shifted their range during the Late Pleistocene, but that individual species shifted differentially (in space and/or time) in response to Pleistocene climatic fluctuations. Similar species-specific responses to Pleistocene climatic changes have been revealed in woody plant species (Davis 2001). These studies are particularly valuable because the Pleistocene was a climatically dynamic period punctuated by more or less regular cold–warm cycles (Hofreiter & Stewart 2009). For instance, temperature increases of more than 10°C over a few decades have been reported

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(Rahmstorf 2002), a rate of warming dramatically higher than the current rate. Obviously, characterizing 'winners' and 'losers' and the determining processes within this climatic context is of prime importance.

Most previous studies (see Hofreiter & Stewart 2009 for examples) that used archaeological remains succeed in highlighting patterns of range shifts, but fail to unravel more complex processes that operate at the phenotypic level. The study by Turrero *et al.* is anchored within this palaeoecological framework, but it goes a step further by (i) revealing changes in life history traits under a period of intense climate change and (ii) combining palaeoecological data with genetic data to unravel relationships between these changes in life history traits and population dynamics.

Combining palaeoecological and molecular data to understand population dynamics

The two riverine fish species considered by Turrero *et al.* are widely distributed in the Northern Hemisphere and economically important (for aquaculture and angling). Although considered at a low risk of extinction by the IUCN, these two species are of principal concern from a conservation standpoint owing to their commercial value. *Salmo salar* is an obligatory anadromous species: it spawns in rivers where the juveniles spend few years before reaching the sea to grow and mature. They then return to their

natal rivers to spawn and die (most of the time). Their life cycle therefore encompasses two distinct phases: a marine phase that can be 1–3 years long and a freshwater phase that can be 1–6 years long. *Salmo trutta* is partially anadromous as some individuals are able to complete their life cycle in freshwater. The time spent in marine and freshwater, as well as the age at reproduction, can be inferred from solid structures such as scales, otoliths or vertebrae. An increment ring (circulus) is added more or less concentrically and regularly to these solid structures, the distance between two circuli being positively proportional to the individual's growth rate. Growth rate is generally lower during winter, stress periods, as well as in freshwater, which make circuli useful for inferring key life history parameters (see Fig. 1). These key life history parameters are generally inferred from contemporary specimens and are useful, for instance, to test the ecological causes and evolutionary consequences of variation in life history traits (e.g. Aubin-Horth & Dodson 2004).

The originality of Turrero *et al.*'s study is that they used these solid structures to infer life history traits of specimens from several Pleistocene subperiods and then compared these to those of contemporary specimens. Specifically, they analysed archaeological remains from sites corresponding to three distinct Palaeolithic periods, namely the Solutrean (20–16 000 years BP), the Magdalenian (16–12 000 years BP) and the Azilian/Asturian (12–6000 years BP). Roughly, the Solutrean was character-

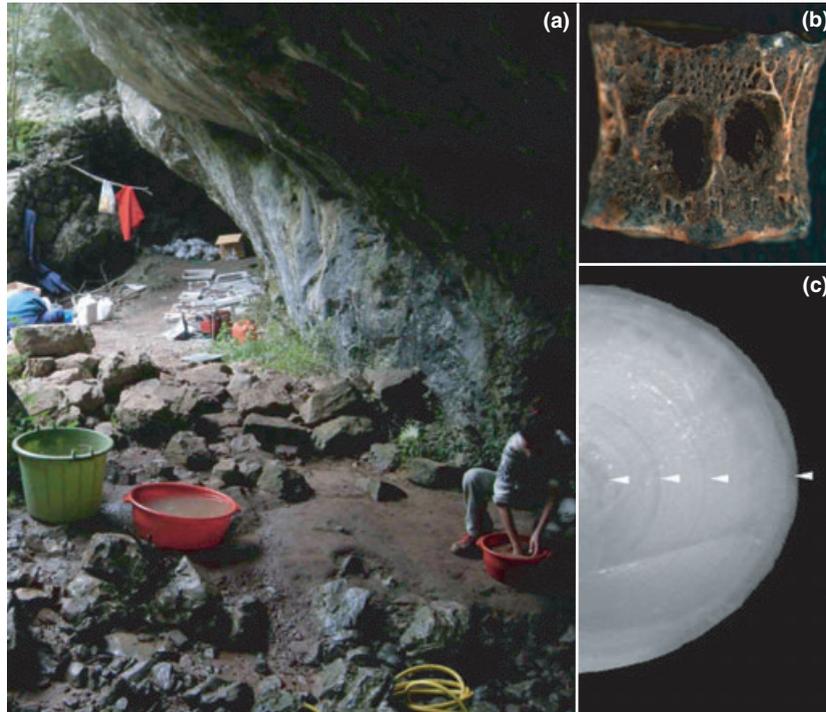


Fig. 1 Pictures from (a) an archaeological site from which old vertebrae were excavated (La Güelga, northern Spain); (b) a vertebra from an old *Salmo salar* specimen studied in Turrero *et al.* (2012); and (c) a longitudinal cut of a *Salmo salar* vertebra (each white arrow head points a circulus; this specimen spent 1 year in freshwater and 3 years in the sea). Picture (c) is reproduced with permission from Turrero *et al.* (2012).

ized by relatively low air temperatures, while the two other periods (and particularly the Azilian/Asturian) were warmer and closer to temperatures encountered today (see Hofreiter & Stewart 2009). They inferred four life history traits: number of years in the river, number of years in the sea (which corresponds to the age at maturity), the season of migration to the sea and the season of migration to the river. Overall, they found no differences in the freshwater phase between periods; most specimens (irrespective of the species) spent only 1 year in freshwater. On the contrary, differences were found regarding the marine phase between contemporary and ancient specimens. Although most specimens spent a total of 1 year in the sea, there was a significant increase in specimens spending only 1 year in the sea. These specimens (called 'grisles') were absent in the older and colder period (the Solutrean), began to appear in warmer periods (Magdalenian) and particularly Azilian/Asturian and were frequent among contemporary specimens.

This shift in life history over time provides support for an effect of climate on *Salmo* species and has several implications. First, by reducing their time spent in the sea, *Salmo* spp. reduce their age at maturity and hence the overall generation time. Turrero *et al.* estimated that generation time was reduced by nearly 15% over the last 20 000 years (from approximately 3.06 years in the Solutrean to approximately 2.60 years in contemporary populations). As observed for birds (*Parus major*; Husby *et al.* 2011), a reduced generation time should accelerate evolutionary rates, which may be adaptive in rapidly changing environments. Second, by reaching spawning areas sooner, the *Salmo* spp. females also reproduce smaller, which may have implications for population dynamics. Indeed, in salmonids, the reproductive success of females is negatively correlated with their body size and age (Thériault *et al.* 2007); as such, younger reproduction may negatively affect population dynamics. Turrero *et al.* provide evidence for such a negative correlation between age at maturity and population growth rate: they used mitochondrial DNA sequences from contemporary specimens to estimate demographic trends over the last 20 000 years. Overall, they found an acute decrease in population growth rate for both fish species in relatively recent periods (<2000 years BP) of intense warming. Although Turrero *et al.* lack specimens from these periods, it is likely that this decrease in population growth is related to the reported decrease in age at maturity.

Conclusion and future avenues

Turrero *et al.* provide the first evidence of long-term changes in key life history traits in a vertebrate species that may be attributable to climatic changes. By combining palaeoecological data with molecular data, they provide further evidence for a link between intraspecific trait variation and population growth rate over long time periods (see also Pelletier *et al.* 2007). This demonstrates the strength of interdisciplinary research and parallels recent calls (Willis

et al. 2007; Hofreiter & Stewart 2009) for connecting genetic, palaeoecological and long-term ecological analyses to provide new insights into the responses of species and populations to climate and environmental changes.

These results are not without caveats and should definitely be taken with care. As acknowledged by Turrero *et al.*, more palaeoecological data are needed to confirm some results, notably regarding the decrease in generation time. Similarly, the identification of species from vertebrae should be as thorough as possible, possibly including analyses of ancient DNA. In addition, these analyses remain correlative, and pointing a finger to a single causative factor (climate) is probably over-simplistic. Regardless of these potential limitations, patterns highlighted by Turrero *et al.* intriguingly match recent findings from a long-term survey in birds that global warming increases evolutionary potential while decreasing population growth rate (Husby *et al.* 2011). These two studies hence posit interesting questions about the adaptive value of changes observed in wild populations: Can an increased evolutionary rate help organisms cope with climate change? Is there a trade-off between evolutionary rate and population growth rate in populations facing rapid environmental changes? If yes, will this trade-off be sufficiently well balanced to allow species to survive contemporary global changes? Experimental and modelling approaches, as well as integrative analyses of additional palaeoecological and molecular data, will undoubtedly contribute to the further clarification of such central and challenging questions.

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