

BACTERIAL EVOLUTION

Adapt to warming and catch your breath

An experimental evolution study shows that selection of a marine bacterium by warming favours adaptations that facilitate growth at low oxygen concentrations, linking evolutionary responses to these two key components of climate change in the ocean.

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More than a century ago, the American naturalist John Muir observed that: “When we try to pick out anything by itself, we find it hitched to everything else in the Universe.”¹ Biologists who study the responses of marine microorganisms to global change would do well to keep this lesson in mind. Currently, the bacterial and protistan assemblages that support nearly all ocean food webs and biogeochemical cycles are under ever-increasing selective pressure from a complex, shifting mosaic of anthropogenic change factors (Fig. 1). These diverse climate-related drivers include sea surface warming, accelerating deoxygenation, ocean acidification, changes in ocean circulation, altered nutrient supplies, changing light environments, and biological variables such as novel competitors and predators². In keeping with Muir’s observation, this set of rapidly shifting environmental factors is also intimately interconnected. Little-understood feedbacks and interactive effects between multiple drivers are often at least as consequential for the marine microbiota as changes in the individual factors themselves (Fig. 1)³.

In this issue of *Nature Microbiology*, Kent et al.⁴ offer a unique perspective on how the adaptive responses of a marine bacterium to warming are linked to the rest of this web of environmental change variables. They applied classic laboratory experimental evolution methods pioneered by Lenski and colleagues⁵, using a common marine alphaproteobacterium isolated from the Chesapeake Bay, USA, as a model organism. Published experiments on thermal adaptation in marine microorganisms are rare, although a number of global-change-focused studies have examined selection under high-carbon-dioxide, low-pH environments^{2,5,6}. The Kent et al.⁴ experiments break new ground, by showing that selection of aerobic bacteria by stressful warm temperatures can unexpectedly confer lifestyle changes that mitigate fitness losses due to another major environmental stressor: low oxygen concentrations.

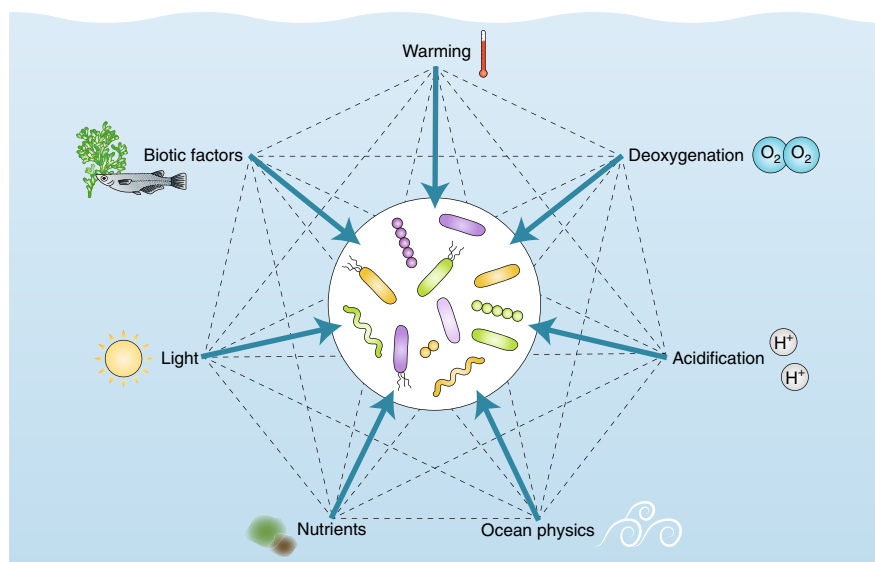


Fig. 1 | Marine microorganisms are presently under selection by a dynamic network of global change factors. Each driver individually influences microbial evolutionary responses (arrows), but it is the complex set of biological, chemical and physical interactions between this entire web of shifting variables (dashed lines) that will largely determine how the marine microbiota will adapt to a rapidly changing ocean environment.

This observation is striking as the two global change variables, temperature and oxygen, are tightly linked in the ocean. Gaseous oxygen is becoming progressively less soluble in seawater as the ocean warms, according to the basic chemical principles of Henry’s Law. The ocean’s naturally occurring suboxic zones, such as the major region of low- O_2 water in the eastern tropical Pacific Ocean, are also quickly expanding as a consequence of climate change. Finally, oxygen levels are declining dramatically in many parts of the coastal ocean due to human nutrient enrichment and consequent bacterial respiration of the excess primary production this produces, resulting in growing ‘dead zones’ in areas such as the Gulf of Mexico. It is evident that in general, the future ocean will be not only substantially warmer, but also much lower in dissolved oxygen than is the case today^{2,7,8}.

This trajectory of simultaneous ocean warming and deoxygenation means that the results of Kent et al.⁴ could have major implications for our understanding of how marine bacteria may respond to a changing climate. They found that after 500 generations of experimental selection, many high-temperature-selected (33 °C) cell lines of their model *Roseovarius* sp. marine bacterium had acquired one of two phenotypes that were rarely found in the ancestral and low-temperature-selected (25 °C) lineages. One of these, the ‘wrinkly’ colony morphotype, provides a greater surface area for bacterial colony gas exchange when oxygen levels are low⁴.

The other high-temperature phenotype that the authors often observed in their experiments is even more closely related to oxygen availability. In many lineages, thermal stress selected for mutations that

allowed the cells to grow as a surficial biofilm at the air–water interface, where they have the advantage of access to diffusive oxygen fluxes from the atmosphere. Both of these two different lifestyle adaptations allowed high-temperature-selected cell lines to grow faster under low-oxygen conditions than either the ancestor or the low-temperature-selected replicates⁴.

Genome sequencing showed that various cell lines exhibited several distinct types of mutation acquired during adaptation to elevated temperatures. These included mutations in genes involved directly in the secretion of exopolymers that promote biofilm assembly, or in one of two different gene regulatory systems that indirectly influence biofilm formation⁴. Notably, some of the most commonly observed mutations were in quorum-sensing regulatory pathways. Quorum-sensing-mediated crosstalk between cells is certainly an essential component of building a biofilm, but it is also integral to the coordination of many other population-level functions, ranging from exotoxin production to iron acquisition⁹. The Kent et al.⁴ results raise the intriguing question of how expression of these other types of quorum-sensing-regulated traits might also be altered by

adaptation to high temperatures in marine bacteria.

Subsets of the high-temperature-selected *Roseovarius* cell lines followed several divergent genomic ‘adaptive walks’ that independently led to the low-O₂-tolerant, biofilm-forming phenotype. In addition, the various mutations observed in this alphaproteobacterium had very little in common with those seen in previous thermal selection experiments using the distantly related gammaproteobacterium *Escherichia coli*⁴. The genomic pathways potentially conferring resistance to thermal stress in bacteria appear to be highly diverse across a broad range of phylogenetic levels, from major bacterial classes down to individual cell lines derived from the same isolate. This extreme genomic flexibility suggests that bacteria in general, including taxonomically diverse assemblages of marine bacteria, may have numerous different evolutionary strategies that will allow them to cope with future climate warming.

Muir, that canny old observer of the natural world, would perhaps not have been at all surprised to learn that evolutionary responses to warming and deoxygenation are tightly ‘hitched together’. A major challenge for marine microbiologists will be

deciding how to also incorporate the many other interlocking components of ocean environmental change into this picture (Fig. 1). Only then will we truly understand the net effects of this constellation of interacting anthropogenic change factors on the microorganisms that underpin the biological productivity of the largest ecosystem on the planet. □

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