MICROBE PROFILE
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Microbe Profile: *Alteromonas macleodii* – a widespread, fast-responding, 'interactive' marine bacterium

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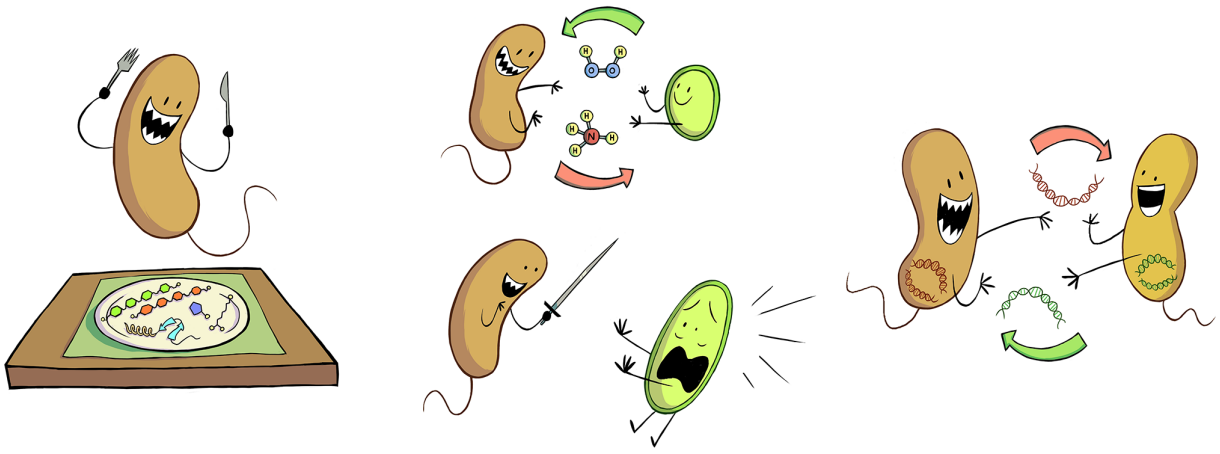

Graphical abstract

Alteromonas macleodii can degrade diverse carbon sources (left), positively and negatively interacts with other microbes (middle), and engages in extensive horizontal gene transfer (right). Illustration by Yarden Ben-Tabou de-Leon.

Abstract

Alteromonas macleodii is a marine heterotrophic bacterium with widespread distribution – from temperate to tropical oceans, and from surface to deep waters. Strains of *A. macleodii* exhibit considerable genomic and metabolic variability, and can grow rapidly on diverse organic compounds. *A. macleodii* is a model organism for the study of population genomics, physiological adaptations and microbial interactions, with individual genomes encoding diverse phenotypic traits influenced by recombination and horizontal gene transfer.

TAXONOMY

Alteromonas macleodii is affiliated with the bacterial genus *Alteromonas* (*Gammaproteobacteria*: *Alteromonadales*: *Alteromonadaceae*), which includes 35 validly described species as of November 2022. The type strain is *Alteromonas macleodii* ATCC 27126^T, isolated from Hawaiian surface seawater in the 1970s.

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Keywords: intraspecific diversity; metabolic versatility; microbial interactions; ocean; pangenome evolution; *r* strategist.
Abbreviation: FAIR, Findable, Accessible, Interoperable, Reusable.
A supplementary table is available with the online version of this article.

PROPERTIES

A. macleodii is a Gram-negative, aerobic marine bacterium found throughout temperate and tropical oceans – from coastal to pelagic waters, and from the photic zone to the deep sea. Cells are rod-shaped, on average are 1–2 µm long, and motile via a single flagellum. This heterotrophic *r* strategist can be free-living or surface-attached, including associations with other organisms. Genomic diversity and metabolic versatility allow growth on diverse substrates, facilitating cultivability and utility as a model organism. Some strains can tolerate adverse conditions (e.g. heavy metals, high salinity, low oxygen).

GENOME

A total of 52 *A. macleodii* genomes, of which 23 originate from pure cultures and the others being metagenome-assembled genomes, are publicly available as of November 2022 (Table S1, available in the online version of this article). Fourteen complete genomes have provided fundamental insights into *A. macleodii* (pan)genome organization and evolution. *A. macleodii* genomes are relatively large (on average 4.5 megabases), with ~3000 core genes plus a sizable assemblage of accessory and unique genes [1]. Approximately half of the flexible genome is located in operon-like gene clusters, appearing as small synteny breaks. The other half is encoded in flexible genomic islands >10 kilobases, designated as either *replacement* (encoding different genes with similar functions across strains, e.g. membrane receptors) or *additive* (encoding a wide variety of genes that can be strain-specific). Genomic islands can shape the phenotype of individual strains or phylogenetic subgroups, for example encoding carbohydrate-active enzymes, secondary metabolites (polyketides, siderophores, homoserine lactones) or membrane lipopolysaccharides. Some strains harbour plasmids (size range 30–800 kilobases), many encoding metal resistance cassettes with varying gene order and content [1].

PHYLOGENY

A. macleodii strains share >99.5% rRNA gene sequence similarity and 90–98% average nucleotide identity, illustrating close interspecific relatedness even if isolated from opposite global locations or contrasting habitats. Some strains have almost identical genomes, with <10 genomic polymorphisms [2]. Initial genomic studies distinguished *A. macleodii* strains into *surface* and *deep* ecotypes, the latter with suggested preference for larger particles. Subsequently, the sequencing of additional strains has provided a more accurate picture, reclassifying deep-ecotype strains as *Alteromonas mediterranea*.

KEY FEATURES AND DISCOVERIES

A. macleodii and close relatives are important for organic matter cycling, both in the deep sea [3] and in coastal surface waters, where they can degrade the entire pool of labile substrates [4]. Pangenome analyses have linked this metabolic versatility to multiple genomic islands, mediating eco-evolutionary adaptations at overall genomic synteny [1]. Thus, even strains with >97% average nucleotide identity can encode distinct arrays of degradative enzymes and transporters. Physiological studies have confirmed that genomic traits translate to functional phenotypes, encompassing siderophore production, algal polysaccharide degradation and cellular communication [2]. *A. macleodii* strains can have both stimulatory and adverse effects on co-occurring microbes [5, 6]. For example, *A. macleodii* facilitates growth of the globally abundant cyanobacterium *Prochlorococcus*, both under 'standard' conditions and in response to temperature, nutrient and light stress [6]. This *A. macleodii* 'helper' phenotype contributes to the ability to counteract oxidative stress, with important ecological implications [7].

OPEN QUESTIONS

We propose four major open questions regarding *A. macleodii* ecology and evolution. A common theme is the role of diversity and versatility for marine microbial life, and how these aspects correspond to the 'paradox of the plankton' (i.e. how limited resources support a wide range of taxa) at the population level.

1. Highly versatile and fast growing – so why is *A. macleodii* often rare?

A. macleodii is readily cultivated and often numerically dominates incubation experiments, including the controls. Yet, culture-independent approaches commonly detect only minor proportions *in situ*. Hence, *A. macleodii* might form short-lived 'blooms' of active cells that are missed using traditional single-point sampling [8]. Viral activity and rapid grazing might be controlling factors [4], but the specific drivers of population dynamics remain unknown. Has *A. macleodii* 'prioritized' metabolic versatility at the expense of lower resistance against phages and grazers – and how would this influence 'boom-and-bust' dynamics, as well as carbon and nutrient fluxes?

2. How does metabolic versatility determine niche specialization?

A. macleodii strains encode different combinations of metabolic traits, enabling them to degrade various nutrients, access iron sources, and resist heavy metals. These abilities probably enhance fitness, yet the matching of specific traits and niches remains enigmatic. Furthermore, while some strains can outcompete others when co-cultured [2], habitat specialization (e.g. spatially segregated microniches) may support the co-occurrence of multiple *A. macleodii* strains. Finally, why does this versatility not extend to the polar oceans, which harbour *Pseudoalteromonas* rather than *Alteromonas*?

3. How stable is the genomic structure of *A. macleodii* populations?

Intraspecific variability and horizontal gene transfer are prevalent in *A. macleodii*. Do the currently known strains represent stable genotypes or merely snapshots in evolutionary time, randomly captured from a continuum of strains that appear and vanish? Is the natural assemblage a mixture of strains, whose individual abundances scale with environmental factors? Recent methodological advances – such as full-length 16S rRNA gene sequencing and long-read metagenomics – will facilitate linking strain-specific and population dynamics. This is fostered by public biodiversity collections and 'FAIR' ocean observation practices.

4. What are the ecosystem effects of *A. macleodii* interactions?

Many mechanisms underlying *A. macleodii*–phytoplankton interactions remain unclear. What are the molecular 'messages' transferred between partners? How important are metabolic cross-feeding, specific signalling molecules, detoxification of reactive oxygen species, antibiotics, and toxins? Do interactions require direct cell–cell contact, or are they mediated by dissolved molecules or vesicles? How do these interactions relate to the genomic and metabolic versatility, and how do secreted 'common goods' such as siderophores and hydrolytic enzymes [9, 10] influence these dynamics? Finally, it remains unclear to what extent laboratory observations translate to *in situ* processes, despite tantalizing preliminary evidence [7].

BIOGRAPHY

Matthias Wietz studies marine microbiome dynamics over time and space, genomic diversity, and ecophysiological adaptations. In *Alteromonas macleodii*, his main research interests are polysaccharide degradation and intraspecific diversity.

Mario López-Pérez studies the ecological and evolutionary implications of genomic diversity through comparative genomics, transcriptomics, and metagenomics. Using *Alteromonas* as a model organism, this provided a new model of evolution in closely related bacterial populations.

Daniel Sher and his lab study interactions between marine bacteria, including *Alteromonas*, and other organisms. Their work combines lab experiments, fieldwork (primarily in the Eastern Mediterranean) and mathematical modelling.

Steven Biller studies how marine microbial interactions affect cell physiology and community functions. His work has examined how *Alteromonas* and marine picocyanobacteria impact one another, including the role of extracellular vesicles in mediating intercellular exchanges.

Francisco Rodriguez-Valera has conducted pioneering genomic and metagenomic research – describing the first metagenomes from the Mediterranean Sea, the Amazon River, the Caspian Sea and Lake Baikal, including the first clear evidence for CRISPRs. In *Alteromonas* he studies population ecology, pangenomics, and evolution.

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Conflicts of interest
The authors declare no conflict of interest.

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