

Forum

Coastal *Vibrio* as a source of antimicrobial resistance?

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Coastal *Vibrio* harbor a high diversity of underexplored antimicrobial resistance genes (ARGs). Their selective maintenance in the absence of antibiotic selection is puzzling. While their mobilization is rare, it may just be a question of time when the ecological context turns the coastal environment into a source for ARG spillover.

Understudied dimensions of antimicrobial resistance in coastal ecosystems

Humans heavily utilize coastal ecosystems, causing high levels of microbial and chemical pollution, and watersheds transport and concentrate contaminants to the sea. Exposure in densely populated human areas increases the risk of disease emergence and transmission. Particularly, water- and foodborne diseases in humans and animals caused by *Vibrio*, which thrive in coastal environments, have increased in recent years in the wake of rising water temperatures [1,2]. In combination with the general lack of knowledge of **antimicrobial resistance (AMR)** (see [Glossary](#)) in the marine environment [3], this has led to a rise in worldwide studies investigating AMR in *Vibrio* to gauge effective treatment options with antibiotics. Due to the direct connection with human health, the majority of these studies concentrated on known human pathogens and aquaculture settings with high socioeconomic value [2,4]. This introduces a substantial

bias and underestimates the diversity of AMR within the genus *Vibrio*. Over the past years, metagenomics and culturomics studies have partly closed this gap and shown that AMR against several antibiotic families (e.g., aminoglycosides, β -lactams, diaminopyrimidines, fluoroquinolones, fosfomycin, polymyxins, phenicols, sulfonamides, and tetracyclines) as well as multidrug efflux systems is widespread in *Vibrio* from diverse aquatic environments, even in more pristine locations where selective pressures from anthropogenic antibiotics are presumably absent. However, the evolutionary origin and ecological fate of AMR in environmental *Vibrio* remain unclear. Here, AMR could act as a mediator of microbial competition, cross-species communication, or other poorly understood functions. As the underlying **antimicrobial resistance genes (ARGs)** can be transferred from environmental reservoirs and potentially return as pathogens to humans via food and occupational or recreational activities ([Figure 1](#)), the isolated view on a small set of *Vibrio* limits our understanding of the role of coastal environments as a potential source, reservoir, or sink of AMR and calls for a systematic investigation of selective and ecological factors favoring AMR in environmental *Vibrio*.

Underexplored diversity, ecological role, and evolution of ARGs in *Vibrio*

Genomic analyses using the large number of publicly available *Vibrio* genomes showed that *Vibrio* contains a high diversity of novel and known ARGs across many gene families [5–7]. For instance, a remarkable diversity of novel variants of the *mcr/epiA* genes, conferring resistance to last-resort polymyxins, and class A β -lactamase genes, conferring resistance to β -lactams, has been identified [6,7]. The wealth of genomic data from various environments enables us to reconstruct the evolutionary history of ARG acquisition, which can help to identify shared ecological factors that drive AMR selection. The data suggest that two main eco-evolutionary

Glossary

Antimicrobial resistance (AMR): the ability of a microorganism to survive and grow in the presence of antimicrobial compounds called antibiotics when used in human and animal health. AMR can be acquired by mutation or horizontal gene transfer.

Antimicrobial resistance gene (ARG): a gene that enables a microorganism to grow in the presence of an antimicrobial compound, typically by encoding mechanisms that inactivate the drug, alter its target or reduce its intracellular concentration.

Heavy metal resistance (HMR): the ability of a microorganism to grow in the presence of heavy metals (e.g., copper and zinc). HMR is often conferred by efflux pumps that reduce the intracellular concentration of metals.

Horizontal gene transfer (HGT): the transfer of genetic material between organisms, without reproduction. It allows genes such as ARGs to spread across bacterial species and strains.

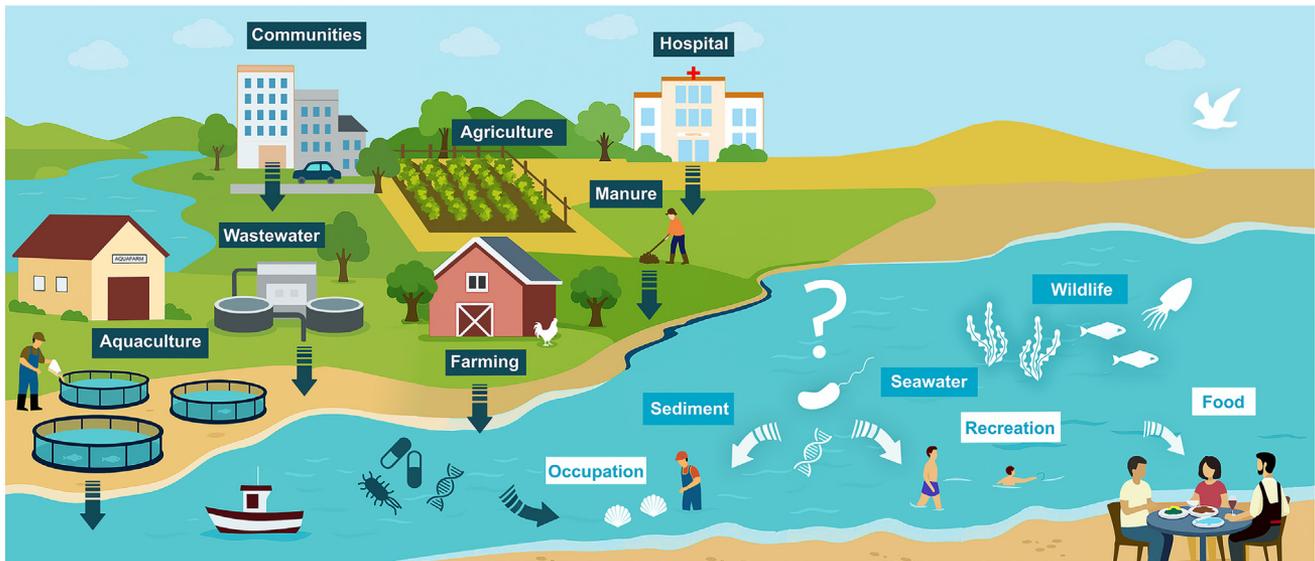
Mobile genetic element (MGE): a segment of DNA capable of moving between genomes facilitating the transfer of genes such as ARGs between microorganisms (e.g., plasmids, transposons, integrons, and insertion sequences).

Two-component regulatory system (TCS): a signal transduction system in bacteria that consists of a sensor kinase and response regulator. Together they detect environmental signals and adjust gene expression accordingly. They often regulate bacterial processes such as AMR and virulence.

pathways of ARG acquisition coexist in *Vibrio*: The first, and probably more prominent, involves the rapid, highly efficient propagation of **mobile genetic elements (MGEs)** carrying ARGs, directly responding to contemporary selective pressures from clinical and aquaculture sources in the antibiotic era. For example, in *Vibrio cholerae*, most ARGs are linked with integrative conjugative elements, prophages, conjugative plasmids, and transposons [5]. Similarly, highly modular conjugative pAQU-type plasmids conferring resistance to various antibiotics emerged in aquaculture settings, where they can rapidly spread to a broad range of *Vibrio* following antibiotic use in oyster hatcheries [8]. The second, and partly overlooked, pathway involves ARGs inherited after ancient acquisitions. Indeed, some ARG families are widely distributed in *Vibrio*, suggesting that they contribute

Known anthropogenic sources

Underexplored natural sources



Trends in Microbiology

Figure 1. Entry pathways and transmission routes of antimicrobial resistance genes (ARGs) in coastal ecosystems. In addition to the well-known anthropogenic sources (dark blue boxes and arrows), a large diversity of underexplored ARGs, which have been selectively maintained in *Vibrio* in the absence of antibiotic use, might emerge from natural sources (light blue boxes) and further contribute to exposure contacts of human users (white arrows and boxes).

significantly to intrinsic antibiotic resistance in these bacteria. These genes and their genomic contexts have evolved alongside the diversification of *Vibrio* species, with only few recent **horizontal gene transfer (HGT)** events [6,7]. These so-called intrinsic resistances are widespread and represent a large part of ARG diversity. Consequently, we need to ask ourselves why ARGs conferring intrinsic resistance are so widespread in the coastal *Vibrio*, and what environmental selection pressures maintain them across many *Vibrio* species.

What role do ARGs play in the biology and ecology of *Vibrio*?

For some ARG families, selective maintenance aside from antibiotic use seems straight forward: *mcr/eptA* genes, for example, confer resistance to colistin and other cationic antimicrobial peptides, which are immune system effector molecules conserved from unicellular to multicellular organisms. This function may

offer an advantage for *Vibrio* colonizing eukaryotic hosts and can be selected for as a mechanism of microbial colonization and resilience [9]. Other ARGs, such as β -lactamases, are abundant in *Vibrio* although β -lactam antibiotics are often below detection levels in the coastal environment. Hence, alternative biological roles of these genes are needed to explain their frequent occurrence. These may include pleiotropic effects beyond antibiotic resistance like the cell wall maintenance [10]. Furthermore, **heavy metal resistance (HMR)** genes occurring in the genomic neighborhood of ARGs could facilitate coselection by heavy metals from the environment despite of the buffering capacity of seawater potentially limiting metal bioavailability. Several studies simultaneously investigated antibiotic resistance and heavy metal resistance on the phenotypic level, but the functional connection between HMR and AMR via coselection is often lacking. This calls for systematic genome mining of ARGs and

heavy-metal resistance genes and their linkage to MGEs across environmental gradients of contaminant exposures, from naturally metal-rich sites (e.g., mines) to anthropogenically impacted watersheds, wastewater, and agricultural runoff. Additionally, **two-component regulatory systems (TCSs)** control expression of ARGs in the *Vibrio* Harveyi clade [6]. This might suggest a role in adaptation to more variable, fluctuating environments, which would fit well to the recent expansion of species from this clade (e.g., *V. alginolyticus* and *V. parahaemolyticus*) with climate change and rising temperatures [1]. Persistence over evolutionary times of these chromosomal ARGs with low maintenance costs contrasts sharply with the rapid spread of plasmid-mediated resistances. These parasitic conjugative plasmids are controlled by *Vibrio* defense systems and are ultimately lost in the natural environment despite their persistence in

laboratory cultures without antibiotic selection [8,11].

Are we looking at it the right way?

Standardized AMR protocols used in medical and veterinary studies (The Clinical & Laboratory Standards Institute/ The European Committee on Antimicrobial Susceptibility Testing) facilitate cross-study comparisons but employ culture media poorly suited for *Vibrio*, especially marine strains [12]. While adaptations such as salt supplementation and revised Epidemiological Cutoff values exist [13], medium composition profoundly alters resistance expression, particularly in seawater-mimicking conditions [6]. This supports genomic evidence that AMR is regulated by TCS and other regulatory systems highly responsive to diverse and incompletely defined environmental cues [6,9]. Overall, protocols for studying AMR in *Vibrio* should better reflect its ecology. These bacteria rarely exist as isolated strains but thrive in communities where cooperative interactions shape community structure and influence antibiotic production and resistance within *Vibrio* populations that share a common habitat [14]. For instance, widespread β -lactamase production in *Vibrio* may protect neighboring cells and amplify resistance at the community level. Moreover, *Vibrio* frequently adopt a biofilm lifestyle on particles, sediments, plastics, and biotic surfaces. This restricts antibiotic diffusion and facilitates HGT, making biofilms potential hotspots for AMR persistence and exchange. Therefore, resistance should be investigated not only in planktonic cultures but also within community and biofilm contexts.

Can *Vibrio* from aquatic environments be a source of novel ARGs?

Several compartments of the aquatic environments (sediment, biofilms, and cultured and wild fauna) can function as reservoirs for abundant and diverse

ARGs, some of which are clinically relevant [15]. The chromosomal ARGs of *Vibrio* may represent an important source of uncharacterized environmental ARGs, which are capable of conferring intrinsic AMR [6]. Unbiased mining approaches have already uncovered a novel diversity of ARGs, where low amino acid conservation (<40%) can still yield highly active resistance phenotypes [6]. The small number of families that have been studied so far suggests that only a small fraction of the existing diversity has been discovered, making coastal systems an emerging source of ARGs. Effective identification of novel ARGs in 'environmental samples' needs to employ relaxed conservation thresholds relative to those conventionally applied to clinical ARGs, while simultaneously enabling the detection of co-occurring selection markers and MGEs. These computational approaches must be integrated with culture-based phenotyping to functionally characterize the AMR profiles of environmental isolates.

Can these ARGs be transferred from aquatic ecosystems to humans?

Plasmid-mediated resistance remains the main entry pathway into human populations. The pAQU-type multidrug resistance (MDR) plasmids, which are recently emerging in aquaculture, could readily be transferred with high conjugation efficiency from *Vibrio* to enterobacteria [8], and environmental capture from the aquatic environment has already led to the global spread of the mobile colistin resistance gene *mcr-1*. However, the high diversity of chromosomal ARGs needs to be considered as another potential source. Although most of these ARGs have not yet been detected in clinical settings, the biofilm lifestyle of *Vibrio* together with evidence of HGT to potentially pathogenic strains [6] underscores the need to explore chromosomal ARGs beyond known clinical sequences. It is high time to extend the monitoring of clinical isolates

in wastewater and aquaculture with studies investigating the ecological dimension of AMR to better capture the full diversity of *Vibrio* ARGs and understand the ecological and evolutionary roles they play in coastal ecosystems. Better knowledge of the temporal and spatial dynamics of antibiotic-resistant *Vibrio* could identify conditions that promote ARG spillover and help to prevent future infections in coastal environments with high human exposure rates.

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Declaration of interests

The authors declare no competing interests.

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