

Viral Hijacking and Metabolic Reprogramming in *Candidatus Pelagibacter ubique*: Ecological Consequences of Phage-Driven “Zombification” in the Global Ocean

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Abstract

Candidatus Pelagibacter ubique, a dominant member of the SAR11 clade, is among the most abundant heterotrophic organisms in the global ocean and plays a central role in marine carbon cycling. Despite possessing one of the smallest genomes of any free-living organism, SAR11 thrives in oligotrophic marine environments through extensive genome streamlining, efficient nutrient acquisition systems, and specialized metabolic adaptations. However, SAR11 populations are subject to persistent viral predation by pelagiphages, a diverse group of bacteriophages that influence microbial mortality, evolution, and nutrient turnover throughout the oceans. This review examines current understanding of SAR11 physiology, pelagiphage infection dynamics, and the ecological consequences of infection-induced metabolic reprogramming. Particular emphasis is placed on viral manipulation of host metabolism, auxiliary metabolic genes, host resource allocation, and the role of phage-mediated lysis in the marine viral shunt. The term “zombification” is used here as a conceptual analogy describing a transient physiological state in which infected cells may remain metabolically active while cellular functions become increasingly redirected toward viral replication. While aspects of this phenomenon have been observed in marine phage-host systems, several proposed mechanisms remain incompletely resolved in SAR11-pelagiphage interactions and require further experimental investigation. We further examine how viral turnover of SAR11 biomass contributes to dissolved organic matter recycling, nutrient redistribution, and the regulation of oceanic carbon sequestration. Finally, emerging genomic, transcriptomic, and imaging technologies are discussed as

tools for resolving outstanding questions concerning host-virus interactions in marine ecosystems. Understanding how pelagiphages alter the physiology and ecological function of SAR11 populations provides important insight into one of the most widespread biological interactions in the global ocean and its potential consequences under changing climatic conditions.

Keywords

Candidatus Pelagibacter ubique, SAR11, Pelagiphages, Marine Viral Ecology, Metabolic Reprogramming, Auxiliary Metabolic Genes, Viral Shunt, Carbon Cycling, Ocean Biogeochemistry, Marine Microbiology, Host-Phage Interactions, Climate Change

1. Introduction

Marine microbial communities are fundamental drivers of global biogeochemical cycles, mediating the transformation and movement of carbon, nitrogen, sulfur, and other essential elements throughout the oceans. Among these communities, the SAR11 clade of Alphaproteobacteria represents one of the most successful and abundant groups of microorganisms on Earth. Members of the SAR11 lineage, particularly *Candidatus Pelagibacter ubique*, are estimated to comprise approximately 25% - 50% of microbial cells in surface ocean waters and play a major role in the cycling of dissolved organic carbon within marine ecosystems [1] [2].

The ecological success of SAR11 is largely attributed to extensive genome streamlining, a process through which nonessential genes and energetically costly metabolic functions have been eliminated over evolutionary time. This adaptation allows SAR11 to thrive in oligotrophic environments characterized by extremely low nutrient availability while maintaining efficient nutrient acquisition and energy conservation strategies [1] [3]. As a consequence, SAR11 populations have become a dominant component of marine microbial food webs and exert considerable influence on global carbon flux.

Despite their remarkable abundance and ecological importance, SAR11 populations experience substantial mortality from viral predation. Marine viruses are estimated to infect and lyse a significant fraction of oceanic microbial biomass each day, thereby influencing microbial diversity, nutrient availability, and ecosystem productivity [4]-[6]. Among these viruses, pelagiphages specifically infect SAR11 and are now recognized as some of the most abundant bacteriophages in marine environments [7]. Recent genomic, transcriptomic, and cultivation-based studies suggest that pelagiphage infection can alter host physiology in ways that extend beyond simple cell death, affecting resource allocation, gene expression, and metabolic activity during the infection cycle [7] [8].

In this review, the term “zombification” is used as a conceptual analogy to describe a transient physiological state in which infected cells may remain metabolically active while host cellular functions become increasingly redirected toward

viral replication. This terminology does not imply that a distinct zombie-like biological state has been definitively demonstrated in SAR11. Rather, it serves as a framework for discussing infection-induced metabolic reprogramming observed across bacteriophage-host systems and its potential relevance to pelagiphage-infected SAR11 cells. Although several aspects of viral takeover have been experimentally characterized in marine phage systems, other proposed mechanisms remain incompletely resolved and continue to be active areas of investigation.

This review synthesizes current knowledge regarding SAR11 physiology, pelagiphage infection dynamics, host metabolic reprogramming, and the broader ecological consequences of viral infection. Particular emphasis is placed on the influence of phage-mediated processes on nutrient cycling, dissolved organic matter recycling, and carbon sequestration within marine ecosystems. Understanding these interactions is increasingly important as climate-driven changes in ocean temperature, stratification, and nutrient availability continue to alter marine microbial communities and the processes they regulate.

2. The SAR11 Clade: Evolutionary Success through Genome Streamlining

Members of the SAR11 clade are among the most abundant and successful microorganisms in marine ecosystems. Their widespread distribution throughout oligotrophic oceans is largely attributed to evolutionary adaptations that maximize metabolic efficiency while minimizing energetic costs. Genome streamlining, specialized nutrient acquisition systems, and photometabolic energy generation have enabled SAR11 populations to thrive under conditions that limit the growth of many competing microorganisms. These characteristics provide the physiological foundation for understanding both the ecological success of SAR11 and its interactions with pelagiphages.

2.1. Genome Streamlining and Nutrient Acquisition

The SAR11 clade is widely recognized as one of the most evolutionarily successful groups of marine microorganisms. Among its members, *Candidatus Pelagibacter ubique* possesses a highly streamlined genome of approximately 1.3 Mb, making it one of the smallest genomes known among free-living organisms [1]. This extreme reduction in genome size reflects a long evolutionary process in which non-essential genes, redundant metabolic pathways, and energetically costly regulatory systems were eliminated, allowing SAR11 to maximize efficiency in nutrient-poor marine environments [3].

Genome streamlining enables SAR11 to conserve cellular resources while maintaining the metabolic functions necessary for survival in oligotrophic oceans. Rather than investing energy in extensive regulatory networks, SAR11 relies on highly efficient nutrient acquisition systems and constitutive expression of transport proteins capable of scavenging dissolved organic compounds at extremely low concentrations. This strategy minimizes energetic costs while maximizing nutrient

uptake efficiency, providing a substantial competitive advantage in environments where nutrients are chronically limited [9].

Morphologically, SAR11 cells are exceptionally small, typically measuring between 0.1 and 0.3 μm in diameter. Their small cell size increases the surface-area-to-volume ratio, facilitating rapid nutrient acquisition from dilute seawater and reducing the energetic demands associated with cellular maintenance [7]. These adaptations contribute significantly to the ecological dominance of SAR11 populations throughout the world's oceans.

Unlike many marine bacteria, SAR11 lacks extensive metabolic redundancy and instead depends on highly specialized transport systems. ATP-binding cassette (ABC) transporters and tripartite ATP-independent periplasmic (TRAP) transporters allow the uptake of amino acids, carboxylic acids, sulfur-containing compounds, and dissolved organic carbon at nanomolar concentrations. These transport systems represent some of the most efficient nutrient acquisition mechanisms currently known among oligotrophic microorganisms and are central to the ecological success of the SAR11 lineage [1] [9].

The remarkable efficiency of SAR11 metabolism highlights how evolutionary specialization can promote ecological dominance despite severe nutrient limitations. However, the same streamlined physiology that enables success in oligotrophic environments may also influence susceptibility to viral infection, making SAR11 an ideal host for studying the ecological consequences of bacteriophage-mediated metabolic reprogramming (see Figure 1).

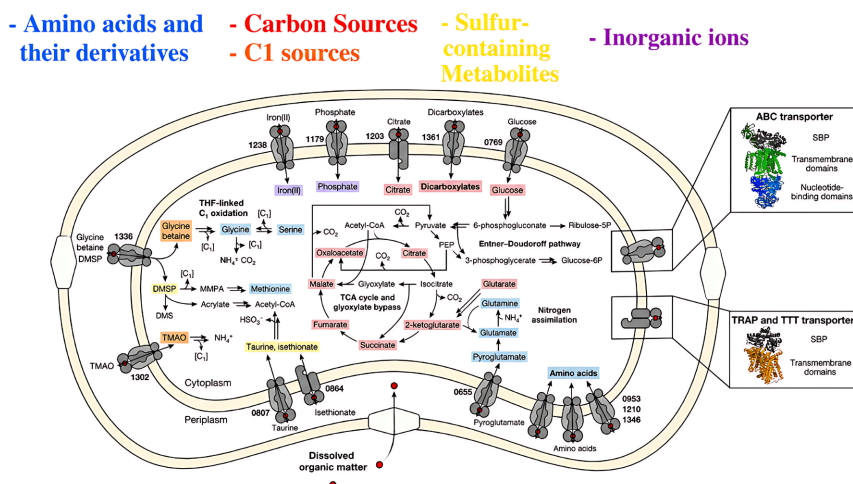


Figure 1. Nutrient acquisition systems and major metabolic pathways of *Candidatus Pelagibacter ubique*.

2.2. Proteorhodopsin and Adaptation to Oligotrophic Environments

A further adaptation contributing to the ecological success of SAR11 is the presence of proteorhodopsin, a light-driven proton pump that supplements cellular energy production under nutrient-limited conditions. Unlike photosynthetic or-

ganisms that capture light energy through chlorophyll-based systems, SAR11 utilizes proteorhodopsin to generate proton gradients across the cell membrane, thereby supporting ATP synthesis and improving energy efficiency in oligotrophic environments [1].

Proteorhodopsin is particularly advantageous in the sunlit surface ocean, where dissolved organic carbon and other essential nutrients may be scarce. By harnessing solar energy, SAR11 can reduce its dependence on organic substrates for energy generation and improve survival during periods of resource limitation. This photometabolic strategy is considered one of the key adaptations contributing to the widespread distribution and ecological dominance of SAR11 populations throughout marine ecosystems [2].

The presence of proteorhodopsin has also generated interest regarding its potential role during viral infection. Because pelagiphage replication requires substantial energetic investment, it has been hypothesized that light-driven ATP generation could indirectly support viral replication by helping maintain cellular energy production during infection. However, direct experimental evidence linking proteorhodopsin activity to pelagiphage infection dynamics remains limited. Consequently, any contribution of proteorhodopsin to sustaining infected cells should currently be regarded as a plausible hypothesis rather than a demonstrated mechanism.

Together, genome streamlining, highly efficient nutrient acquisition systems, and proteorhodopsin-mediated energy supplementation enable SAR11 to thrive in some of the most nutrient-depleted environments on Earth. These adaptations help explain the remarkable ecological success of the SAR11 lineage while also providing the physiological foundation upon which pelagiphages exert their influence through infection and metabolic reprogramming.

3. Pelagiphage Diversity and Infection Mechanisms

The ecological dominance of SAR11 populations has supported the evolution of a diverse assemblage of bacteriophages collectively known as pelagiphages. These viruses are now recognized as major regulators of microbial abundance, nutrient cycling, and evolutionary processes throughout marine ecosystems. Through infection, metabolic manipulation, and host-cell lysis, pelagiphages influence both the physiology of individual SAR11 cells and broader ecosystem-level processes. Understanding the diversity of pelagiphages and the mechanisms by which they infect and reprogram host cells is therefore essential for evaluating their ecological significance within the global ocean.

3.1. Pelagiphages and Viral Infection Dynamics

The extraordinary abundance of SAR11 populations supports equally abundant populations of bacteriophages collectively known as pelagiphages. Since their initial isolation and characterization, pelagiphages have been recognized as some of the most abundant viral groups in marine ecosystems and are now considered

major regulators of SAR11 population dynamics [7]. Through continuous infection and lysis of SAR11 cells, pelagiphages influence microbial mortality, genetic diversity, nutrient cycling, and the structure of marine microbial communities.

Pelagiphages exhibit substantial genetic and ecological diversity and include representatives of several major viral lineages, including members related to the Podoviridae, Myoviridae, and Siphoviridae groups. These viruses have evolved specialized mechanisms for recognizing and infecting SAR11 hosts, allowing them to persist in environments where SAR11 populations dominate microbial biomass [7] [10].

The infection cycle typically begins with adsorption to receptors located on the outer membrane of SAR11 cells. Following attachment, viral genetic material is introduced into the host cytoplasm, initiating a sequence of molecular interactions that progressively redirect cellular resources toward viral replication. Successful infection requires precise coordination between viral gene expression and host metabolic processes, enabling efficient production of new virions prior to host lysis.

Although infection frequencies vary across environmental conditions, pelagiphage infection is now recognized as a widespread ecological process in marine ecosystems. Because SAR11 populations often represent a substantial proportion of total microbial abundance in surface oceans, even modest infection rates can have significant consequences for nutrient turnover and carbon cycling at regional and global scales [2] [7]. Recent cultivation-independent studies further suggest that pelagiphage-host interactions occur across diverse marine habitats, highlighting their importance as a persistent force shaping ocean microbial ecology.

3.2. Viral Takeover of Host Cellular Processes

Once infection is established, pelagiphages progressively redirect host cellular resources toward viral replication. Successful production of new virions requires substantial quantities of nucleotides, amino acids, ATP, and membrane components, creating a strong selective advantage for viruses capable of manipulating host metabolism. As a result, infected cells often undergo extensive physiological changes that alter patterns of gene expression, energy utilization, and resource allocation [7] [8].

Studies of bacteriophage-host systems have demonstrated that viruses can modify host transcriptional activity, alter translational priorities, and redirect metabolic pathways toward viral biosynthesis. However, the degree to which individual mechanisms operate in SAR11-pelagiphage interactions remains incompletely resolved. While genomic and transcriptomic analyses provide evidence that pelagiphages substantially influence host physiology, several mechanistic details have been inferred from broader bacteriophage literature rather than directly demonstrated in SAR11 systems [8].

Recent investigations have revealed that pelagiphage infection can generate ri-

bosome-deprived cellular states within SAR11 populations, indicating that infection may significantly alter translational capacity and protein synthesis dynamics. These findings support the concept that viral infection involves more than simple host destruction and instead represents an active process of physiological reorganization during which host resources are redirected toward viral production [8].

In addition to influencing transcription and translation, viral infection may affect carbon metabolism, sulfur utilization, nucleotide biosynthesis, and other pathways necessary for efficient virion assembly. The extent to which these changes result from direct viral regulation, host stress responses, or interactions between both processes remains an important area of ongoing research. Nevertheless, available evidence indicates that pelagiphages are capable of exerting substantial control over host cellular function during infection.

Rather than functioning as passive agents of mortality, pelagiphages act as active participants in microbial ecosystem dynamics by modifying host physiology before lysis occurs. These infection-induced changes form the mechanistic foundation for the broader metabolic reprogramming discussed in the following section.

4. Metabolic Reprogramming and the “Zombie” State

One of the most intriguing consequences of pelagiphage infection is the extensive physiological transformation that occurs within infected SAR11 cells. Rather than functioning solely as agents of cell destruction, pelagiphages can alter patterns of gene expression, resource allocation, and energy utilization prior to host lysis. These infection-induced changes provide the foundation for what is described in this review as a “zombie-like” state, in which infected cells may remain metabolically active while progressively losing control over their cellular functions. Understanding this process is critical for evaluating how viral infection influences both microbial physiology and larger-scale ecological processes.

4.1. Defining the Zombie State

The concept of microbial “zombification” serves as a conceptual framework for understanding infection-induced physiological transformation in SAR11. In this context, the term does not describe a formally recognized biological state but rather a metaphorical condition in which infected cells remain metabolically active while host cellular functions become increasingly redirected toward viral replication. Although similar forms of metabolic reprogramming have been documented in numerous bacteriophage-host systems, the precise mechanisms governing this process in SAR11-pelagiphage interactions remain an active area of investigation.

During infection, SAR11 cells may continue acquiring nutrients, generating ATP, and maintaining basic metabolic activity. However, these processes increasingly support viral reproduction rather than host growth or survival. Viral gene expression progressively alters the intracellular environment, shifting cellular pri-

orities toward the production of viral genomes, structural proteins, and assembly components required for virion formation [8].

Recent transcriptomic and cellular studies suggest that pelagiphage infection can significantly alter translational capacity and resource allocation within SAR11 populations. Observations of ribosome-deprived cellular states provide evidence that infection involves substantial physiological reorganization rather than simple cellular decline. Nevertheless, the extent to which these changes represent direct viral manipulation, host stress responses, or a combination of both remains incompletely understood [8].

As infection progresses, host autonomy becomes increasingly compromised while metabolic activity may persist. This distinction between metabolic activity and physiological control forms the basis for the “zombie-like” analogy used throughout this review and highlights the complex nature of host-virus interactions in marine microbial ecosystems.

4.2. Auxiliary Metabolic Genes and Metabolic Reprogramming

A central mechanism through which viruses influence host physiology is the expression of auxiliary metabolic genes (AMGs). These genes, which are thought to have been acquired from cellular hosts during evolutionary history, enable viruses to manipulate key metabolic pathways and maintain cellular functions that support viral replication. In marine ecosystems, AMGs have been identified in numerous bacteriophage groups and are increasingly recognized as important drivers of virus-mediated metabolic reprogramming [11].

Although the diversity and functional roles of pelagiphage AMGs remain incompletely characterized, available genomic evidence suggests that these viruses may influence several pathways associated with energy production, carbon metabolism, sulfur utilization, and nucleotide biosynthesis. Such metabolic modifications allow infected cells to continue producing the resources required for efficient virion assembly while minimizing the physiological constraints imposed by nutrient limitation [7] [10].

Carbon metabolism is particularly important because SAR11 plays a major role in processing dissolved organic carbon within marine environments. Viral infection may redirect carbon flux toward the synthesis of nucleic acids, proteins, and structural components required for virion production. Similarly, alterations in nucleotide biosynthesis pathways can ensure an adequate supply of precursors for viral genome replication. These processes enable pelagiphages to maximize reproductive output while exploiting the highly efficient metabolic machinery of their hosts.

Sulfur metabolism may also be affected during infection. SAR11 populations are important participants in the cycling of sulfur-containing compounds such as dimethylsulfoniopropionate (DMSP), a molecule that contributes to marine sulfur flux and atmospheric processes. Although the extent of pelagiphage influence on sulfur metabolism remains uncertain, viral modification of these pathways

could have implications extending beyond individual cells and into broader ecosystem-level nutrient cycling.

The ability of viruses to alter host metabolism demonstrates that viral infection is not merely a process of cellular destruction but also a form of biological reprogramming. Through the manipulation of metabolic pathways and resource allocation, pelagiphages transform SAR11 cells into highly efficient viral production systems, setting the stage for the ecological consequences associated with host lysis and nutrient release.

5. Ecological Consequences: The Marine Viral Shunt

The effects of pelagiphage infection extend far beyond individual host cells. Because SAR11 populations dominate microbial communities throughout large regions of the global ocean, viral infection and lysis can influence ecosystem processes operating across vast spatial scales. Through the release of cellular contents, redistribution of nutrients, and alteration of microbial food-web dynamics, pelagiphages contribute to the marine viral shunt, a process that plays a critical role in global biogeochemical cycling.

5.1. Carbon Cycling and Dissolved Organic Matter Recycling

One of the most significant ecological consequences of viral infection is the release of dissolved organic matter (DOM) following host-cell lysis. During pelagiphage infection, cellular biomass that would otherwise be transferred to higher trophic levels is instead converted into dissolved organic compounds that become available to surrounding microorganisms. This process, known as the viral shunt, redirects carbon flow away from traditional food-web pathways and promotes microbial recycling within the water column [4]–[6].

Because SAR11 populations account for a substantial fraction of microbial biomass in oligotrophic oceans, pelagiphage-mediated lysis may represent an important source of dissolved organic carbon. The release of amino acids, nucleotides, carbohydrates, and other cellular components provides resources that can be rapidly utilized by neighboring microbial populations, thereby stimulating microbial activity and influencing community composition.

The viral shunt has important implications for carbon sequestration. By retaining carbon within microbial loops rather than transferring it to larger organisms, viral lysis can alter the efficiency of biological carbon export to deeper ocean waters. Consequently, virus-host interactions may influence the amount of carbon ultimately stored in the ocean interior, affecting processes that contribute to long-term climate regulation [5].

The ecological impact of pelagiphage infection therefore extends beyond host mortality alone. Through repeated cycles of infection and lysis, pelagiphages contribute to the continual transformation and redistribution of carbon throughout marine ecosystems.

5.2. Nutrient Redistribution and Ecosystem Effects

In addition to influencing carbon cycling, pelagiphage-mediated lysis contributes to the redistribution of essential nutrients including nitrogen, phosphorus, and sulfur. The release of intracellular compounds following host-cell destruction increases nutrient availability within the surrounding environment, where these resources can be rapidly assimilated by other microorganisms. This recycling process enhances nutrient turnover and supports continued microbial productivity in nutrient-limited marine ecosystems [4] [5].

Nutrient redistribution resulting from viral infection may also influence microbial community structure. By selectively targeting dominant bacterial populations such as SAR11, pelagiphages can reduce competitive advantages held by abundant taxa and create ecological opportunities for less dominant microbial groups. This mechanism, often referred to as “kill-the-winner” dynamics, contributes to the maintenance of microbial diversity and helps prevent competitive exclusion within marine ecosystems [12].

Beyond local ecological effects, the cumulative impact of viral infection has implications for ocean-scale biogeochemical processes. Continuous recycling of nutrients through viral lysis influences productivity, nutrient availability, and ecosystem stability across marine environments. As a result, pelagiphages should be viewed not only as agents of microbial mortality but also as important regulators of nutrient cycling and ecosystem function.

Together, the viral shunt and associated nutrient redistribution processes demonstrate how microscopic host-virus interactions can generate large-scale ecological consequences, linking the physiology of individual cells to global biogeochemical cycles.

6. Climate Change and Future Ocean Dynamics

Marine ecosystems are increasingly being affected by climate-driven changes including rising sea surface temperatures, increased ocean stratification, altered nutrient availability, ocean acidification, and shifts in primary productivity. Because SAR11 populations dominate many oligotrophic marine environments, changes in ocean conditions are expected to influence both host physiology and pelagiphage-host interactions [2] [6]. Understanding how these environmental pressures affect viral infection dynamics is therefore essential for predicting future changes in marine biogeochemical cycles.

Warming ocean temperatures can directly influence microbial growth rates, metabolic activity, and viral replication. Increased temperatures may accelerate infection cycles, alter host susceptibility, and modify the balance between viral production and host population growth [6] [13]. At the same time, environmental stress may affect the physiological condition of SAR11 cells, potentially influencing infection efficiency and the outcome of host-virus interactions. However, the magnitude and direction of these effects remain uncertain and may vary among different ocean regions and environmental conditions.

Ocean stratification represents another important consequence of climate change. As surface waters warm, vertical mixing is reduced, limiting the transport of nutrients from deeper waters into the photic zone. Because SAR11 populations are highly adapted to nutrient-poor conditions, they may maintain a competitive advantage under increasingly oligotrophic conditions [1] [2]. Consequently, changes in SAR11 abundance could indirectly influence pelagiphage populations and alter the frequency and ecological significance of viral infection.

Climate-driven changes in viral activity may also affect the marine viral shunt. Variations in infection frequency, host mortality, and nutrient recycling have the potential to influence carbon sequestration and dissolved organic matter dynamics [4]-[6]. Because SAR11 contributes substantially to global carbon cycling, even modest changes in pelagiphage-host interactions could have broader implications for ecosystem productivity and long-term carbon storage.

Although growing evidence suggests that climate change will influence marine virus-host relationships, significant uncertainties remain. Future research integrating laboratory experiments, long-term environmental monitoring, metagenomics, transcriptomics, and ecosystem modeling will be necessary to determine how changing ocean conditions affect pelagiphage ecology and the biogeochemical processes they regulate [11]. Understanding these interactions will be critical for predicting the future role of microbial communities in the global carbon cycle.

7. Emerging Technologies and Unresolved Questions

Despite significant advances in understanding SAR11 ecology and pelagiphage biology, many aspects of host-virus interactions remain poorly understood. Recent technological developments have greatly expanded the ability of researchers to investigate microbial communities directly within natural environments, providing new opportunities to examine infection dynamics, metabolic reprogramming, and ecological impacts at unprecedented resolution. These emerging approaches are helping to address longstanding questions while simultaneously revealing new complexities in marine viral ecology.

7.1. Advances in Marine Viral Ecology Research

The study of pelagiphage-host interactions has benefited substantially from advances in metagenomics, metatranscriptomics, single-cell genomics, and high-throughput sequencing technologies. These approaches allow researchers to investigate microbial and viral communities without relying exclusively on laboratory cultivation, an important advantage given the difficulty of culturing many environmentally relevant marine micro-organisms [2] [11].

Metagenomic analyses have revealed extensive pelagiphage diversity throughout the global ocean and have enabled the identification of previously unknown viral lineages. Similarly, metatranscriptomic approaches provide insight into patterns of gene expression during infection, allowing researchers to examine how

viral replication influences host physiology under natural environmental conditions [10].

Single-cell genomic techniques have further improved understanding of host-virus interactions by enabling direct examination of infected cells. These approaches can identify infection events, characterize viral genetic content, and reveal physiological responses occurring at the level of individual microorganisms. Recent studies utilizing single-cell methods have provided evidence for complex infection dynamics that may not be detectable using population-level measurements alone [8].

In addition to genomic technologies, advances in cryo-electron microscopy and high-resolution imaging are improving understanding of viral structure, attachment mechanisms, and host-cell interactions. Together, these technologies are transforming marine viral ecology from a largely descriptive field into one capable of directly examining mechanistic processes governing infection and metabolic reprogramming.

7.2. Outstanding Questions in Pelagiphage Ecology

Despite considerable progress, important questions regarding SAR11-pelagiphage interactions remain unresolved. One major area of uncertainty concerns the molecular mechanisms responsible for infection-induced metabolic reprogramming. Although genomic and transcriptomic studies suggest substantial alteration of host physiology during infection, the specific pathways affected and the regulatory processes involved remain incompletely characterized.

Additional uncertainty surrounds the ecological consequences of infection at larger spatial and temporal scales. While pelagiphage-mediated lysis clearly contributes to nutrient recycling and carbon turnover, accurately quantifying the cumulative impact of these processes across entire ocean basins remains challenging. Variability in environmental conditions, host abundance, viral diversity, and infection frequency complicates efforts to scale cellular observations to ecosystem-level predictions [5].

The role of climate change in shaping future host-virus interactions also remains poorly understood. Changes in ocean temperature, nutrient availability, and stratification may alter both SAR11 physiology and pelagiphage infection dynamics, potentially affecting the strength of the viral shunt and associated biogeochemical processes. Long-term monitoring programs and integrative ecosystem models will be essential for addressing these questions.

Continued advances in experimental, computational, and observational methodologies are expected to provide important insights into these unresolved issues. As understanding of pelagiphage ecology expands, researchers will be better positioned to evaluate the role of viral infection in regulating marine microbial communities and global biogeochemical cycles.

8. Limitations and Future Directions

While significant progress has been made in understanding SAR11 ecology and

pelagiphage biology, several important limitations continue to constrain current knowledge. A major challenge is the scarcity of direct infection time-course studies capable of tracking physiological and metabolic changes throughout the complete infection cycle. Consequently, many proposed mechanisms of host metabolic reprogramming remain inferred from genomic data, transcriptomic observations, or comparisons with other bacteriophage-host systems rather than direct experimental validation in SAR11-pelagiphage interactions [3].

Another limitation arises from cultivation bias. Although advances in microbial cultivation have enabled the isolation of several SAR11 strains and their associated pelagiphages, many environmentally relevant host and viral populations remain difficult to culture under laboratory conditions [2]. As a result, current understanding may not fully represent the diversity of infection strategies occurring in natural marine environments. Reliance on laboratory model systems can also limit the ability to capture environmental variability that influences host-virus interactions in the ocean.

Scaling cellular-level observations to ecosystem-level processes presents an additional challenge. While evidence strongly supports the role of viral lysis in nutrient recycling and dissolved organic matter production, accurately quantifying the contribution of pelagiphage infection to regional and global carbon flux remains difficult. Variability in environmental conditions, host abundance, infection frequency, and viral diversity introduces substantial uncertainty into efforts to estimate large-scale ecological impacts [5] [6].

Future research should integrate laboratory experimentation, single-cell analyses, metagenomics, metatranscriptomics, and ecosystem modeling to better resolve the mechanisms and consequences of pelagiphage infection. Long-term environmental monitoring programs may also provide valuable insight into how climate-driven changes affect host-virus interactions and associated biogeochemical processes. Addressing these limitations will be essential for developing a more comprehensive understanding of the role of pelagiphages in marine ecosystems.

9. Conclusions

The SAR11 clade, particularly *Candidatus Pelagibacter ubique*, represents one of the most abundant and ecologically significant groups of microorganisms in the global ocean. Through extensive genome streamlining, highly efficient nutrient acquisition systems, and specialized metabolic adaptations, SAR11 populations have achieved remarkable success in oligotrophic marine environments. However, their ecological influence extends beyond their own metabolic activities and is profoundly shaped by interactions with pelagiphages, which serve as major regulators of microbial mortality, nutrient cycling, and ecosystem function.

This review has examined current understanding of pelagiphage infection dynamics and the mechanisms through which viral infection alters host physiology. The concept of “zombification” was presented as a conceptual framework describing the progressive loss of host autonomy that may occur while infected cells re-

main metabolically active and increasingly dedicated to viral replication. Although growing evidence supports the occurrence of infection-induced metabolic reprogramming, many of the molecular mechanisms involved remain incompletely characterized and warrant further investigation.

Pelagiphage-mediated lysis contributes significantly to the marine viral shunt, facilitating the recycling of dissolved organic matter and the redistribution of carbon, nitrogen, phosphorus, and sulfur throughout marine ecosystems. Because SAR11 populations dominate microbial communities across vast regions of the ocean, these interactions have implications that extend from individual cells to global biogeochemical cycles. Consequently, pelagiphages should be viewed not only as agents of microbial mortality but also as important participants in regulating ecosystem productivity and nutrient dynamics.

As climate change continues to alter ocean temperature, stratification, and nutrient availability, understanding the relationship between SAR11 and pelagiphages will become increasingly important. Future advances in metagenomics, single-cell biology, transcriptomics, imaging technologies, and ecosystem modeling are expected to provide deeper insight into the mechanisms and ecological consequences of viral infection. Continued investigation of these host-virus interactions will improve understanding of marine microbial ecology and help clarify the role of viruses in shaping the future of Earth's oceans.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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