

REVIEW ARTICLE OPEN ACCESS

Abalone Gut Microbiome Regulators: A Review Synthesizing Gut Physiology, Microorganisms, Diet and the Environment

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Received: 25 October 2025 | **Revised:** 15 June 2026 | **Accepted:** 15 July 2026

Keywords: abalone | diet | digestive system | environmental stress | gut microbiome | microbes | nutrition

ABSTRACT

Abalone are economically, ecologically and culturally significant marine molluscs, with both wild and farmed populations under pressure due to intrinsic and extrinsic stressors. Abalone performance and health are centred on a highly specialized digestive system supported by a diverse gut microbiome, which enables nutrient assimilation, polysaccharide digestion, immune regulation and disease resistance. This review consolidates our current understanding of the abalone gut microbiome regulation by examining the interactions among host digestive physiology, microbial diversity and function, dietary influences and environmental conditions. Based on a systematic evaluation of sequencing-based studies published between 2015 and 2025 and spanning 14 abalone species, a shared core gut microbiome was identified, primarily composed of genera including *Mycoplasm*, *Psychrilyobacter* and *Vibrio*. This review also evaluates microbiome-related symbiosis and dysbiosis, with emphasis on how diet and environmental stress reshape microbial functions linked to growth, immunity and disease susceptibility. Finally, current methodological limitations and major knowledge gaps are outlined, particularly the need for mechanistic and multi-omics approaches, standardized sampling and longitudinal surveys. As microbiome research progresses, these insights can be translated into practice, moving abalone aquaculture and fisheries beyond reactive management toward precision strategies that ultimately enhance animal health, productivity and long-term ecological sustainability.

1 | Introduction

Abalone (Haliotidae spp.) are highly valued marine molluscs in global aquaculture, recognized for their economic, nutritional and cultural importance (Negara et al. 2021; Cook 2025). Beyond consumption, they support valuable aquaculture and fisheries industries, while their shells are used in decorative industries, and abalone-derived bioactive compounds are gaining attention because of their potential pharmaceutical and biomedical applications (Chung et al. 2024; F. Zhao et al. 2025). Ecologically, abalone function as herbivorous grazers that regulate algal growth and contribute to the stability of marine ecosystems

(Zeeman et al. 2012). Despite their importance, both wild and cultured abalone populations are increasingly threatened by multiple stressors, including recruitment limitations, overfishing handling stress, environmental change, disease outbreaks and high stocking densities (Ragg and Watts 2015; Morash and Alter 2016; Lachambre et al. 2017; Hart et al. 2020).

The abalone digestive system is highly adapted to digest complex macroalgal polysaccharides and formulated feeds. This digestive capability is supported by symbiotic gut microbial communities that contribute key enzymatic functions, such as cellulase alginate, lyase and carbohydrate-active enzymes involved in

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polysaccharide degradation (Frederick et al. 2022). Increasing evidence suggests that these microbial communities are influenced by host development, dietary composition and environmental conditions, including temperature and water quality, all of which influence abalone growth and physiological performance (Mabuhay-Omar et al. 2019; X. Yu et al. 2025). In aquaculture systems, environmental variability, specifically seasonal temperature variation and associated changes in microbial load, has been linked to changes in gut microbial diversity and structure in Australian aquaculture abalone species (Danckert et al. 2021). Consequently, the gut microbiome is increasingly viewed not only as a contributor to host nutrition and digestion, but also as a sensitive indicator of environmental change.

Beyond nutrient metabolism, the abalone gut microbiome contributes to immune defence, and overall health and growth (Iehata et al. 2014; Gobet et al. 2018; Z. Wu, Yu, et al. 2022; Zou et al. 2022; Hur et al. 2023). Despite the rapid advancements in sequencing-based microbiome studies, important gaps remain in understanding how interactions among host physiology, microbial community structure and environmental drivers translate into functional outcomes for the host. Disruptions in host-microbe symbiosis have been linked to reduced digestive efficiency, impaired growth and increased disease susceptibility (Salloum et al. 2025). For example, withering syndrome has been linked to shifts in gut microbial composition occurring alongside infection by *Candidatus Xenohalotus californiensis*, suggesting broader microbial dysbiosis during disease progression (T. Zhang et al. 2022). Conversely, stable and functionally diverse microbiomes may strengthen host resilience by supporting digestive efficiency and immune functions (Apprill 2017; Z. Wu et al. 2024). As a result, microbiome-based assessments are increasingly being explored as tools for improving aquaculture management, animal health and water quality monitoring in rearing systems (Z. Zhang, Yang, et al. 2025).

In this review, the abalone gut microbiome is examined as a key biological interface linking host physiology, diet, environmental variability and disease susceptibility. We synthesize findings from sequencing-based studies spanning multiple abalone species, developmental stages, dietary treatments and environmental conditions, to identify recurring patterns in microbial community composition, functional potential and responsiveness to stressors. By addressing both symbiotic and dysbiotic states, we evaluate how environmental changes, dietary intervention and pathogen exposure reshape gut microbial communities and influence host performance. In addition, methodological limitations and conceptual gaps are discussed, including inconsistencies in anatomical sampling, limited functional validation and the need for longitudinal and multi-omics approaches. Collectively, this review aims to consolidate current knowledge into a framework that supports hypothesis-driven research and microbiome-informed strategies for improving abalone health, resilience and productivity.

2 | Symbiosis or Dysbiosis in Host–Microbiome Interactions

The microbiome describes a characteristic microbial community within a well-defined habitat, along with its associated genomes

and functions. This generally encompasses microorganisms, such as archaea, bacteria, fungi, protozoans and microbial eukaryotes (Berg et al. 2020). The gut microbiome's composition and function are shaped by intrinsic influences, including genetics, sex, age, developmental stage and physiological condition, as well as extrinsic factors such as diet, feeding behaviour, nutrient availability, probiotic use, seasonality, water quality, temperature, contaminants and pathogen exposure (C.-Z. Chen et al. 2022; Diwan et al. 2023). Interactions between a host and its microbiome play a central role in maintaining and responding to environmental challenges. These interactions can be broadly categorized as symbiosis, which supports host health or dysbiosis, which reflects an imbalance and potential dysfunction (Apprill 2017). Symbiosis is associated with a stable microbial community that supports normal physiological processes, often influenced by diet, environmental stability and host genetics (Carey and Duddleston 2014). On the other hand, dysbiosis refers to a disrupted microbial state characterized by shifts in community composition, structure or function and is often driven by factors such as pathogen exposure, environmental stress or nutritional imbalance (Egan and Gardiner 2016; Infante-Villamil et al. 2021). In a symbiotic state, the gut microbiome contributes to host immunity, growth, physiological development and digestion. In contrast, dysbiosis is commonly associated with disease, inflammation and compromised immune function (Danckert et al. 2021). While host–microbiome interactions typically exist along a dynamic continuum, stable conditions generally favour symbiosis, whereas environmental or physiological stress can disrupt this balance and promote dysbiosis (Carey and Duddleston 2014; Apprill 2017; C.-Z. Chen et al. 2022). Dysbiosis may also impair immune regulation and nutrient absorption, thereby influencing host health and growth performance (Z. Li, Ke, et al. 2025). In abalone, emerging studies have shown that shifts in gut microbial communities under stressors, such as temperature fluctuations, dietary changes or pathogen exposure can lead to dysbiotic states, associated with reduced growth and increased disease susceptibility. This distinction is particularly relevant in fisheries and aquaculture, where understanding microbiome dynamics can inform strategies to improve and monitor abalone health and support production outcomes.

Host physiological functions and adaptive responses to environmental or internal changes are influenced by a core gut microbial community (Z. Zhang, Yang, et al. 2025). A review by Salloum et al. (2025) highlights the importance of the molluscan microbiome in regulating the complex interplay between hosts and their associated microbial communities. Microorganisms contribute to key host physiological processes, including health, growth, feeding, digestion, nutrient absorption, pathogen resistance, intestine development and the stimulation of mucosal immunity as well as the establishment of stable microbial ecosystems (Villasante et al. 2020; X. Wang et al. 2020; Choi et al. 2021; X. Yu, Luo, et al. 2022).

Genetic factors can influence the microbiome, with some studies suggesting the potential for vertical transmission of microorganisms from parents to offspring (Lasa and Romalde, 2021), although this remains poorly resolved in abalone. By comparison, horizontal transmission occurs through environmental exposure, where microorganisms are acquired from surrounding environments, such as seawater, natural diets and sediment (Kijewska

et al., 2023). While molluscan microbiota are shaped by both vertical and horizontal transmission, environmental factors, including abiotic conditions (temperature, salinity, pH, dissolved oxygen level, etc.) and diet, are recognized as key drivers of microbiome composition and structure (Scanes et al. 2021; Unzueta-Martínez et al. 2022; Salloum et al. 2025). The abalone intestinal tract is generally dominated by bacteria, with community composition influenced by diet, age, aquaculture practices (e.g., cleaning and handling), and seasonal variation, contributing to the establishment of specific gut microbial communities (Danckert et al. 2021). Given that the microbiome is taxonomically and ecologically diverse and influenced by host species, environmental conditions and health status, it is essential to understand the baseline stability of these microbial communities before changes can be reliably quantified and interpreted (C.-Z. Chen et al. 2022).

Microbial communities colonize both internal and external host tissues based on selective pressures that influence their assembly. Internal communities, such as the gut, are primarily affected by diet, but also by host immune responses and digestive processes, while external communities are strongly influenced by environmental conditions (Ochoa-Sánchez et al. 2023). Distinct microbiota is associated with different host tissues, including the digestive glands, gills, haemolymph and shells, reflecting both host-driven selection and specialized microbial niches (Lorgen-Ritchie et al. 2023). For example, microbial communities on the shells surface have been linked to shell biomineralization processes (Dade-Robertson et al. 2015; Brugman et al. 2018), while gill-associated microbiota may contribute to respiration processes through carbon fixation (Mizutani et al. 2020; Chalifour and Li 2021). In addition, pathogenic microorganism may colonize both external and internal tissues, potentially leading to disease in the host (Moore 2023). In abalone, this includes the presence of foodborne pathogens, which may pose risks to both animal health and human consumers when abalone is consumed raw (M.-J. Lee et al. 2016).

Assessment of abalone health and condition requires an understanding of the composition, transmission pathways and functional roles of microbiota across different host tissues, together with interactions between host genetics, environmental conditions and microbial community dynamics that influence microbiome stability. Collectively, these factors highlight the microbiome as a dynamic and interconnected component of abalone biology, continuously shaped by host traits, environmental conditions and microbial transmission pathways. Establishing robust baselines for microbial diversity, composition and tissue specificity is therefore essential for distinguishing symbiotic from dysbiotic states and for interpreting microbiome responses to dietary, environmental and pathological drivers, which are examined in the subsequent sections.

3 | Assessing the Microbiome

Efficiently quantifying microbial richness, abundance and diversity in an animal host is key to exploring the underlying microbial functions and identifying the genes involved in host-microbe interactions (Djemiel et al. 2022). Microbial quantification methods can be broadly categorized as culture-dependent and culture-independent approaches. Culture-dependent methods rely on

the growth and isolation of microorganisms on selective media under laboratory conditions, followed by direct cell counts or biomass estimation (Fusco and Quero 2014). Although these methods allow the isolation of viable microorganisms and enable downstream functional studies via biochemical assays (Demko et al. 2021; W. Wang, Gao, et al. 2021), they are time-consuming and often fail to capture the full microbial community, particularly viable, but non-culturable organisms present in samples at the time of processing (Koerner et al. 2023). By comparison, culture-independent methods encompass a range of molecular approaches that allow the study of microbial communities without cultivation. These include quantitative polymerase chain reaction (PCR) and sequencing-based approaches, such as amplicon sequencing (16S/ITS) and shotgun metagenomic using next-generation sequencing platforms (e.g., Illumina, Ion Torrent) (Ditz et al. 2020).

Sequencing-based methods offer a broader and more comprehensive assessment of microbial diversity by detecting unculturable and low-abundance taxa that are often overlooked by culture-dependent methods (Su et al. 2012). In addition, these approaches support high-throughput processing of large sample sets, generating extensive datasets for comparative analyses (Satam et al. 2023). Although next-generation sequencing has become a standard tool in microbiome research, its use in abalone-related studies is still comparatively new and therefore merits a brief overview of the underlying workflows.

A general next-generation sequencing workflow for microbiome assessment comprises laboratory processing and bioinformatic analysis. Laboratory steps involve the extraction of genomic deoxyribonucleic acid (gDNA) from host tissues, followed by PCR amplifications of targeted microbial genes (e.g., 16S/18S ribosomal RNA), and preparation of amplicon libraries for sequencing (Athanasopoulou et al. 2023). Generated sequence data are then processed using established bioinformatic pipelines, which include quality filtering, removal of artefacts, such as chimeric sequences, and the identification of amplicon sequence variants (ASV) (B. Gao et al. 2021). These ASVs are subsequently taxonomically classified by alignment against curated reference databases (e.g., NCBI, Silva, GreenGene, RDP, KEGG pathways), facilitating characterization of microbial community structure as well as inferred functional potential (Infante-Villamil et al. 2021). Overall, the integration of rigorous wet-lab protocols and robust computational analyses is critical for producing reliable and interpretable microbiome datasets.

Microbial richness and diversity are fundamental metrics in microbiome research. Richness refers to the number of species present in a community, and can be estimated using various indices (e.g., Chao1) (Xia et al. 2018). Diversity incorporates both species richness and relative abundance, reflecting community evenness and structure (Vitorino and Bessa 2018; Wagner et al. 2018). Diversity is commonly described at three levels: Alpha-, beta- and gamma-diversity. Alpha-diversity represents within-sample diversity and is often expressed using indices, such as Shannon's and Simpson's (Fasolo et al. 2024). Beta-diversity describes differences in community composition between samples or environments, typically quantified using similarity or dissimilarity matrices (e.g., Bray-Curtis or UniFrac distances) (Walters and Martiny 2020). Gamma-diversity reflects overall

diversity across multiple habitats or sample groups, providing a broader ecological perspective. In this context, core microbiota is often defined as taxa consistently present across samples calculated to describe a set of microbial species, found in all habitats or sample groups (Marathe et al. 2021). Together, these metrics enable characterization and comparisons of microbiome structure to facilitate environmental or host-associated responses.

4 | Abalone Production, Physiology and Digestive Interactions

Abalone are classified as one of the most commercially valuable farmed marine molluscs due to their high nutritional quality and meat flavour, with prices of live abalone reaching up to \$100 per kilogram in Asian markets (Cook 2025). Beyond live trade, abalone is processed into several forms, including canned, dried or frozen products (Negara et al. 2021) and are consumed in a range of culinary preparations such as raw, boiled or cooked dishes (M.-J. Lee et al. 2016). In addition to their economic value, abalone play important ecological roles and support recreational fisheries as well as culturally significant practices, particularly within indigenous and small-scale coastal fisheries (Orchard et al. 2024). They are integral components in marine food webs, serving as prey for predators, including starfish, octopuses, whelks and lobsters (Hofmeister et al. 2018). Moreover, abalone-derived extracts and bioactive components, including amino acid peptides, polysaccharides, oils, lipids and proteins are increasingly utilized as nutraceutical and pharmaceutical applications (Suleria et al. 2017; F. Zhao et al. 2025), while shells are used for decorative purposes, jewellery and for reef restoration materials (Chung et al. 2024).

Abalone are cultivated and fished across many regions of the world, with aquaculture now representing the primary source of global production. China dominates the industry, contributing more than, 95% of worldwide abalone production (W. W. You 2023). In 2021, aquaculture production was estimated at approximately 243,506 metric tons globally, whereas wild-capture fisheries contributed only about 4510 metric tons (Cook 2025). Harvesting from wild populations is generally managed through quota-based systems, that regulate total allowable catch within specific regions to promote long-term stock sustainability (Neubauer 2022; Ryder et al. 2025). However, the status of wild populations varies geographically, with many regions experiencing declines due to overexploitation. For example, New Zealand, hosts one of the last remaining significant wild abalone fisheries (Gerrity and Schiel 2025). Ongoing pressures from both recreational and commercial harvesting have led to the collapse of abalone fisheries in several countries (Mundy et al. 2023). As a result, aquaculture, ocean ranching and stock enhancement strategies (e.g., “put and take” fisheries) have been adopted to sustain production and support the recovery of wild populations (Gerrity and Schiel 2025).

Abalone aquaculture comprises a seed production phase, a larval rearing phase and a grow-out phase in which juveniles are reared to market size (Mamat et al. 2025). Broodstock are also maintained in hatcheries as a source of gametes (Daume 2006). All production stages are influenced by environmental factors and diseases, which in turn can alter microbial communities in

both the surrounding environment and the host (T. Zhang et al. 2022). Microorganisms and parasites can pose significant challenges to abalone culture, particularly under intensive farming or environmental degradation (Mabuhay-Omar et al. 2019). Key environmental parameters, including seawater temperature, pH, salinity and nutrient availability, influence abalone populations (Z. Li, Ke, et al. 2025) and negatively impact abalone growth (Morash and Alter 2016). To cope with fluctuating conditions, abalone exhibit behavioural adjustments and physiological plasticity, alongside genetic variations within populations that may support adaptive capacity (F. Yu et al. 2023).

Abalone physiology comprises the biological and biochemical processes that support the survival, growth, reproduction, stress response and interactions with the environment (Morash and Alter 2016; Pratiwi et al. 2025). Abalone exhibit the classic molluscan body plan, consisting of a head-foot region and a visceral mass, which is enclosed within a univalve shell bearing a series of respiratory pores along the shell's left margin (Mamat et al. 2025). The head-foot region contains a muscular foot, supported by haemolymph-filled cavities that function as a hydrostatic skeleton and facilitate attachment and locomotion. The visceral mass houses the digestive, reproductive and circulatory organs, which are responsible for digestion and nutrient absorption, gamete production, oxygen and nutrient transport and excretion and detoxification functions (Venter et al. 2018). Abalone physiology incorporates multiple systems that enable responses to physical, chemical, biological and procedural stressors. For example, Khan (2025) describes how environmental, dietary and disease related stressors affect abalone physiology. Morash and Alter (2016) further outline physiological responses to farming conditions, while Nguyen et al. (2022) demonstrate that abalone respond to stress at genomic, transcriptomic, proteomic and metabolic levels. Together, these studies highlight the ability of abalone to implement coordinated physiological responses that support adaptation to changing environmental conditions.

Dietary interventions and adjustments are an effective way to mitigate the effects of stress in aquaculture practices (Ciji and Akhtar 2021). The incorporation of feed additives, including antimicrobial peptides, organic acids, plant-derived extracts, prebiotics, herbs and probiotics, has been tested in abalone diets (X. Li et al. 2024). These additives aim to enhance abalone growth performance, improve product quality and strengthen immune responses, thereby increasing resilience to environmental stressors (Bullon et al. 2023). Similarly, the inclusion of macroalgae as feed ingredients has been shown to improve feeding activity, health and marketability in abalone (Bansemer et al. 2016). Yet, inadequately formulated diets or poorly timed dietary transitions can negatively affect production outcomes (Hannon et al. 2013). Given their nocturnal and herbivorous grazing behaviour (Sales and Britz 2001), abalone feeding patterns should also be carefully considered in aquaculture systems to optimize feeding efficiency. Understanding feeding behaviour across different life stages therefore remains important for the effective application of dietary strategies to mitigate stress impacts.

Abalone have distinct feeding patterns across the various production phases, including consumption of microalgae and diatoms during larval phases, macroalgal diets as wild adults (Hur et al. 2023) and formulated feeds in aquaculture grow-out systems to

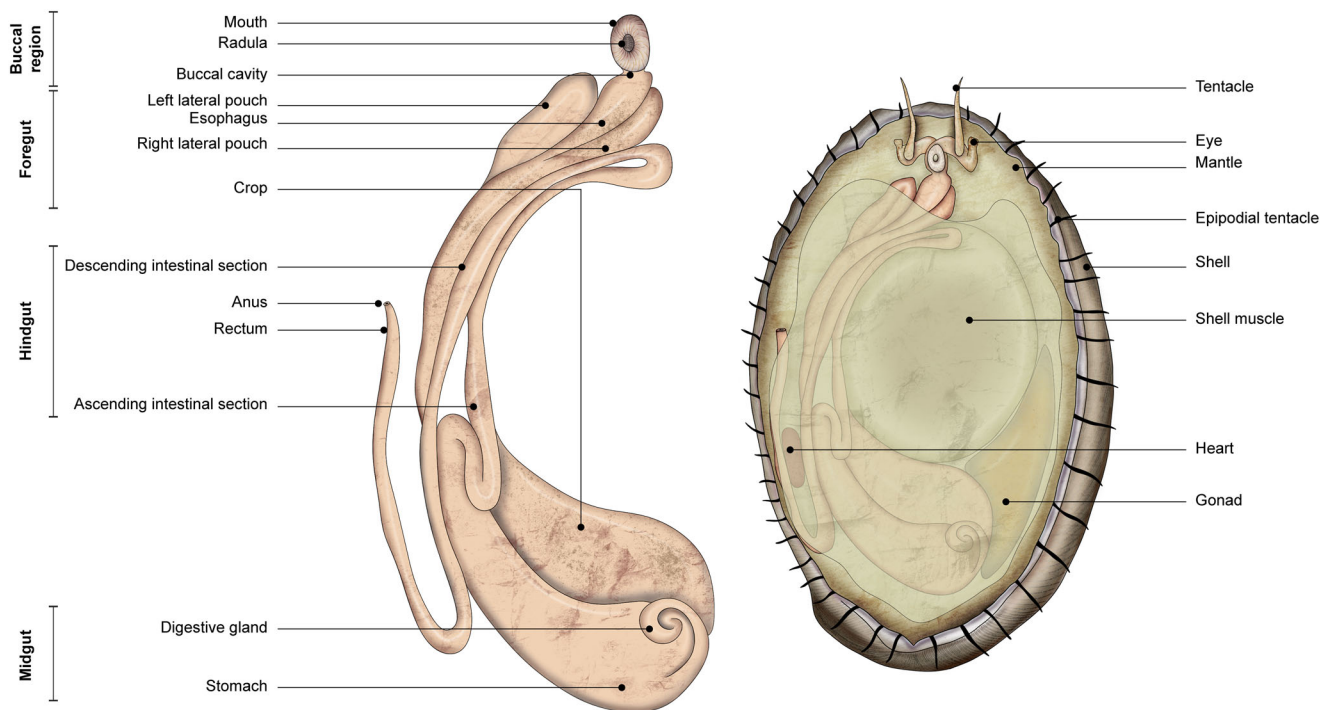


FIGURE 1 | Abalone digestive system highlighting the buccal region, foregut, midgut and hindgut areas. Illustration 2025, Anja Erasmus, Scientia illustratio.

promote growth (Bullon et al. 2023). Adult abalone possess a complete digestive system with specialized tissues that can be broadly categorized into four sections: Buccal region (month and buccal cavity), foregut (oesophagus and crop), midgut (stomach and digestive gland), and hindgut (intestine, rectum and anus) (J. O. Harris et al. 1998). Functions of the digestive system gradually shift from physical to biochemical processing (including enzymatic digestion via the digestive glands and microbial contributions in the gut) across these four regions (Figure 1 and Table 1). Food is ingested using the rhipidoglossan radula, which is flexible, with outer marginal teeth that sweep the substratum along a small number centre sturdy teeth (Kuehl and Donovan 2021). Food particles then pass to the buccal region and mix with large quantities of mucus (Dixon 1992). Mucus provides a barrier for host epithelial cells and serves a substrate for microbial growth and attachment (Danckert et al. 2021). Ingested food moves through the salivary gland ducts into the oesophagus, followed by the muscular crop, which houses digestive fluids (Dixon 1992). The crop contains numerous secretory and mucous cells with limited ciliated cells, and functions primarily as a storage organ (J. O. Harris et al. 1998). It then extends to the stomach, by forming a 180° loop at the posterior end before extending adjacent to the crop (Johnston et al. 2005). The stomach surface is rough, maximizing surface area for mechanical processing and facilitating biochemical interactions (Hur et al. 2023). The digestive gland overlays the crop and stomach via a series of ducts that extend to the intestine and rectum (Martin et al. 2011). The digestive gland consists of columnar epithelial cells, secretory (basophilic) cells and digestive cells (Hur et al. 2023) and preforms functions, such as secretion of digestive enzymes, absorption of nutrients, intracellular digestion, detoxification and storing of glycogen, lipids and calcium (Lobo-da-Cunha 2019). Enzymes of the digestive gland, such as carboxypeptidases,

aminopeptidases, chymotrypsin and trypsin, are involved in protein and polysaccharide degradation (Frederick et al. 2022). The gastrointestinal tract (including the stomach and intestine) harbours microorganisms with diverse functions (e.g., digestion and antimicrobial activities) and is characterized by an acidic pH of 5.3 to 6, offering a stable internal environment that is either anaerobic or microaerophilic (Gobet et al. 2018). Undigested feed passes through the hindgut comprising the intestine, rectum and is eliminated by the anus (Bullon et al. 2023).

The structural complexity and functional specialization of the abalone digestive tract often benefit from targeted dietary strategies to enhance nutrient absorption and digestion. For instance, fresh microalgae and mixed formulated diets (often enhanced with fatty acids) have been used in abalone broodstock to improve overall dietary nutritional value (Daume 2007). Similarly, encapsulated probiotics and nutrients have been successfully delivered to the intestine of *H. iris* to improve feed conversion efficiency (Dezfooli et al. 2023). Collectively these findings highlight the intestine as a key site for nutrient digestion and absorption. Given its central role in digestion, the abalone gut microbiome has been widely studied across species for its involvement in nutrient assimilation, metabolic regulation and immune modulation.

5 | Approach to the Review of Abalone Gut Microbiome Literature

Abalone gastrointestinal and digestive gland microbial research emerged in the 1990s, initially based on-culture-dependent characterization of cultivable bacteria (Y. Wang, Pyecroft, et al. 2021) and has since progressively evolved with advances in molecular and high-throughput sequencing approaches. This development

TABLE 1 | Regions of the abalone digestive system comprising the buccal region, foregut, midgut and hindgut with associated functions.

Classification	Region	Function	Description
Buccal region	Mouth	Collection of food	Radula brings food to the mouth and scraps the substrate into particles.
	Buccal cavity	Initial food processing	Mucus, houses microorganisms and supports the mixing of ingested food.
		Transportation	Mucus assists with the movement of food from the buccal cavity into the oesophagus.
Foregut	Oesophagus	Transportation	The oesophagus moves ingested food from the buccal cavity to the crop via salivary gland ducts.
Midgut	Crop	Temporary food storage	The crop temporarily stores ingested material.
	Stomach	Initial digestion	The digestive fluids assist with food breakdown, while secretory and mucous cells contribute enzymes and mucus to aid this process.
		Mechanical digestion	Crushing and grinding food particles.
		Preparation for enzymatic digestion	Physical breakdown of food enhances exposure to digestive enzymes from the digestive gland.
Hindgut	Digestive gland	Digestive enzyme secretion	Secretes enzymes to enable the efficient breakdown of diverse dietary components.
	Intestine	Digestion and nutrient absorption	Support intracellular digestion to ensure that nutrients are processed and assimilated at the cellular level for absorption and storage.
		Transit of undigested material	Undigested feed and residual digestive matter move through the intestine.
		Microbial fermentation and degradation	The intestine is heavily colonized by bacteria driving the breakdown of complex polysaccharides.
	Rectum and anus	Excretion of waste	Final outlet for faecal material and waste disposal.

has expanded into a detailed investigation of abalone-associated bacterial communities within aquaculture production systems (Danckert et al. 2021). This systematic review was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Page et al. 2021) to synthesize the current knowledge on abalone-microbiome interactions. A review protocol was not formally registered prior to study commencement; however, all methodological procedures were predefined and consistently applied in accordance with PRISMA 2020 recommendations. The study selection process is illustrated in Figure 2 and comprises four stages: Identification, screening, eligibility assessment and final inclusion. A systematic literature search was conducted across Scopus, Web of Science and PubMed databases, focusing on peer-reviewed articles published over the last decade (2015–2025). Searches were performed using the Boolean string: (*abalone* OR *Haliotis*) AND (*microbiome* OR *microbiota* OR “*microbial community*” OR “*bacterial community*” OR *microorganism**). This process yielded 190, from which 88 duplicates were removed prior to screening. Title and abstract screening led to the exclusion of 37 articles deemed irrelevant (e.g., studies not involving *Haliotis* species), leaving 65 full-text articles for eligibility assessment. Following full-text review, an additional 24 studies were excluded for not meeting the inclusion criteria, resulting in a final set of 41 studies included in the qualitative synthesis (Supporting Information). Studies were eligible for inclusion if they: (1) reported empirical research conducted on a *Haliotis* species; (2) employed sequencing-based approaches to characterize the microbiome, including methodological descriptions of library preparation and data-processing workflows; and (3) reported core bacterial taxa at phylum and/or genus level. Studies not meeting these criteria were excluded during the screening and eligibility phases.

The summarized research targets 14 abalone species including: *H. corrugata*, *H. discus*, *H. discus hannai*, *H. diversicolor*, *H. fulgens*, *H. gigantea*, *H. iris*, *H. laevigata*, *H. laevigata* × *H. rubra*, *H. midae*, *H. rufescens*, *H. sorenseni*, *H. tuberculata* and hybrid species *H. discus hannai* × *H. fulgens*. Concurring with global trends, 52.5% of these studies were conducted on *H. discus hannai*, with all remaining species documented once or twice, accounting for 2.5% or 5% of the studies, respectively (Figure 3a). These microbiome studies predominantly include research with nutritional themes, but also address environmental, health, growth and rearing, and organismal profiling questions. The main findings from the body of literature (41 summarized studies) focus on microbial dynamics in abalone in response to dietary interventions, environmental changes and infections and diseases. Moreover, this section highlights shortcomings, research gaps and key opportunities relating to microbiome studies in abalone.

5.1 | Characterization of Abalone Core Gut Microbiome

Among documented abalone microbiome communities, the microbial composition, diversity and intrinsic biochemical pathways of the digestive tract (extending from the buccal cavity to the anus, collectively referred to as the “gut”) have been predominantly studied in abalone for two main reasons. First, the gastropod digestive tract harbours taxonomically and functionally

diverse and complex microbial communities, as microorganisms are introduced directly into the gut through food ingestion and seawater (T. Zhang et al. 2022; Z. Li, Ke, et al. 2025; Salloum et al. 2025). Second, the gut microbiome plays a crucial role in food digestion and nutrient absorption (Zou et al. 2022), and contributes to immunity, epithelial renewal and overall growth and health of abalone (Z. Wu, Yu, et al. 2022).

Dominant bacterial taxa documented in the abalone digestive system have been reported across a broad range of anatomical terms, including samples described as: Intestine, gut, gastrointestinal tract, digestive gland, stomach, viscera, digestive gland merged with gonad, digestive tract, oesophagus, content of the gastrointestinal tract, gill, left kidney and soft tissue (Figure 3b; Supporting Information). From these reports 42% of the studies explicitly stated that intestinal samples were collected for microbiome analyses. This lack of anatomical specificity is problematic, as the abalone digestive system comprises morphological and functionally distinct regions, each with unique cell types, microbial niches and physiological roles, as previously outlined in this manuscript. Therefore, greater precision in anatomical terminology and methodological reporting is strongly encouraged in future abalone microbiome research.

The abalone studies analysed include research on a wide range of abalone species, sourced from both wild and aquaculture settings, spanning various sizes and life stages, and subjected to diverse experimental interventions or sampled from large natural populations, using a variety of analytical techniques (Supporting Table). Despite these differences, a consistent set of dominant bacterial phyla has been identified across studies, namely: Proteobacteria, Tenericutes, Firmicutes, Fusobacteria and Bacteroidota (Figure 3c). At the genus level, frequently reported taxa include *Mycoplasma*, *Psychrilyobacter* and *Vibrio* (Figure 3d). These taxa are recurrently detected across diverse host and environmental contexts, suggesting they form a stable microbial signature associated with the abalone digestive system (Figure 4).

Mycoplasma, is widely reported across abalone gut microbiome studies and has been proposed as a common member of the abalone-associated microbial community (Y. Wang, Pyecroft, et al. 2021). Members of this genus are facultative anaerobes capable of fermentative metabolism, including the production of lactate and acetoacetate (Z. Guo et al. 2024), and can utilize substrates, such as glucose and arginine (X. Wang et al. 2020). *Mycoplasmas* are members of the class Mollicutes, a group of Gram-positive bacteria derived from the Bacillus/Clostridium lineage within the Firmicutes phylum (X. Yu et al. 2025). They are adapted to the mucus-rich, low-oxygen environment of the abalone intestinal tract (Wei et al. 2025). Within this environment, *Mycoplasma* species have been associated with the catabolism of complex substrates, such as oligosaccharides, polysaccharides, glycans and proteins (Ma et al. 2021; Hur et al. 2023), and may contribute to the turnover of simple carbohydrates and amino sugars available to the host (Cicala et al. 2018). They have been suggested to be involved in digestive processes in abalone (Villasante et al. 2020; Danckert et al. 2021), although their exact functional role remains context dependent. *Mycoplasma* spp. have also been described as pathogens linked to infections (Z. Li, Ke, et al. 2025), with the potential to disrupt host digestive

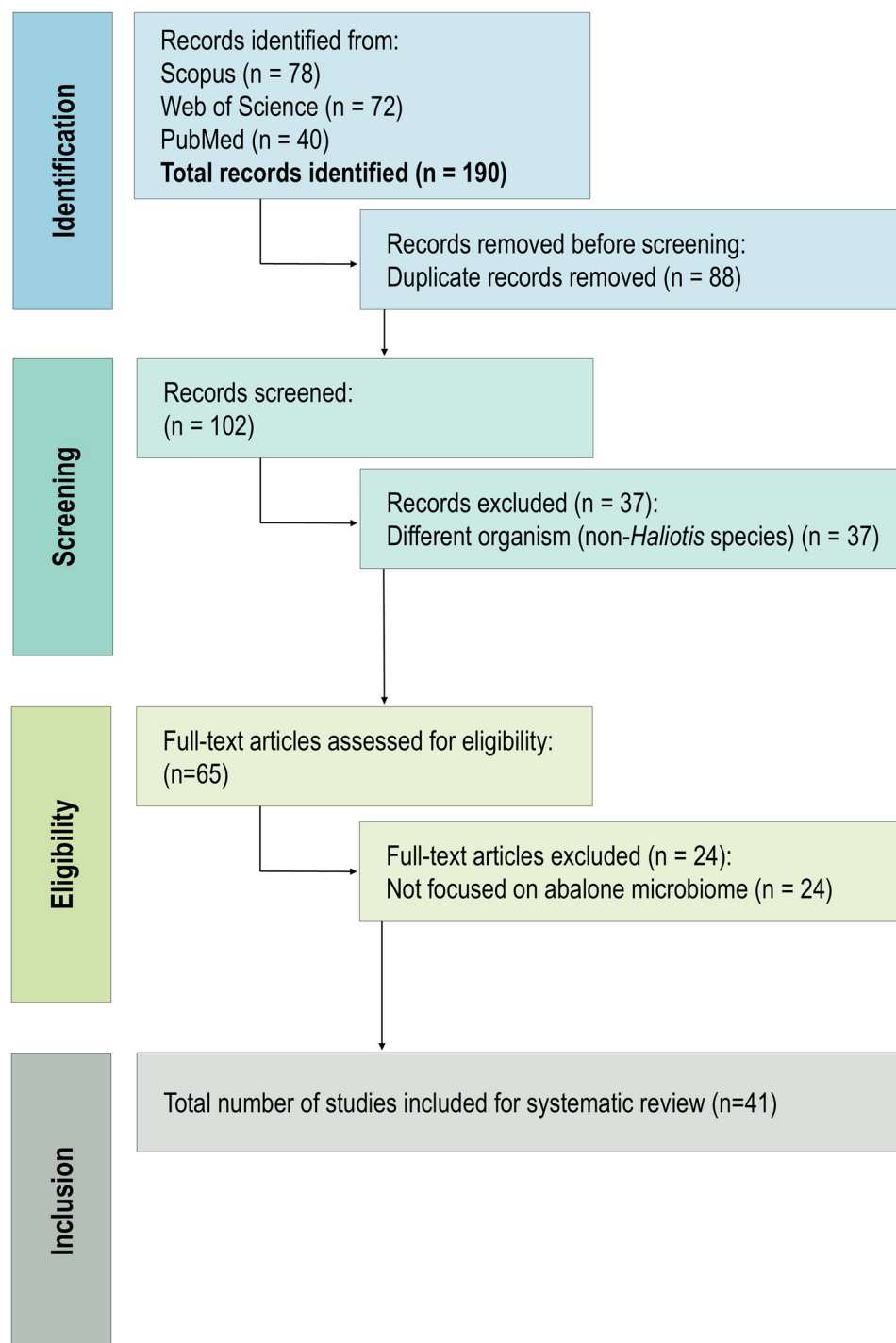


FIGURE 2 | PRISMA 2020 flow diagram of the literature search and study selection process. Database searches (Scopus, Web of Science and PubMed) yielded 190 records. Following duplicate removal ($n = 88$), 102 records underwent title and abstract screening, with 37 records excluded due to irrelevance (e.g., non-*Haliotis* species). Full-text assessment of 65 articles resulted in the exclusion of 24 studies that did not meet the inclusion criteria. Ultimately, 41 studies were included in the systematic review.

and absorptive capabilities (Z. Wu et al. 2023). Conversely, some studies suggest possible protective roles against microbial pathogens through mechanisms, such as degradation of sialic acid coatings and competitive exclusion of pathogen attachment sites (Cicala et al. 2018; Cicala et al. 2023). In the last 10 years, the genus *Mycoplasma* has been reported in multiple abalone species, including *Haliotis gigantea* (Mizutani et al. 2020; Wei et al. 2025), *H. fulgens* and *H. corrugata* (Cicala et al. 2018; Cicala et al. 2023),

H. laevigata (Danckert et al. 2021; Y. Wang, Pyecroft, et al. 2021), *H. laevigata* $\times$ *H. rubra* (Danckert et al. 2021), *H. tuberculata* (Gobet et al. 2018), *H. midae* (Nel et al. 2017), *H. rufescens* (Villasante et al. 2020), hybrid *H. discus hannai* $\times$ *H. fulgens* (X. Wang et al. 2020) and *H. discus hannai* (Nam et al. 2018; X. Wang et al. 2020; Choi et al. 2021; Ma et al. 2021; Z. Wu, Yu, et al. 2022; W. Yu, Lu, et al. 2022; X. Yu, Luo, et al. 2022; T. Zhang et al. 2022; Zou et al. 2022; P. Chen et al. 2023; Hur et al. 2023; Z. Wu et al. 2023; Cadangin

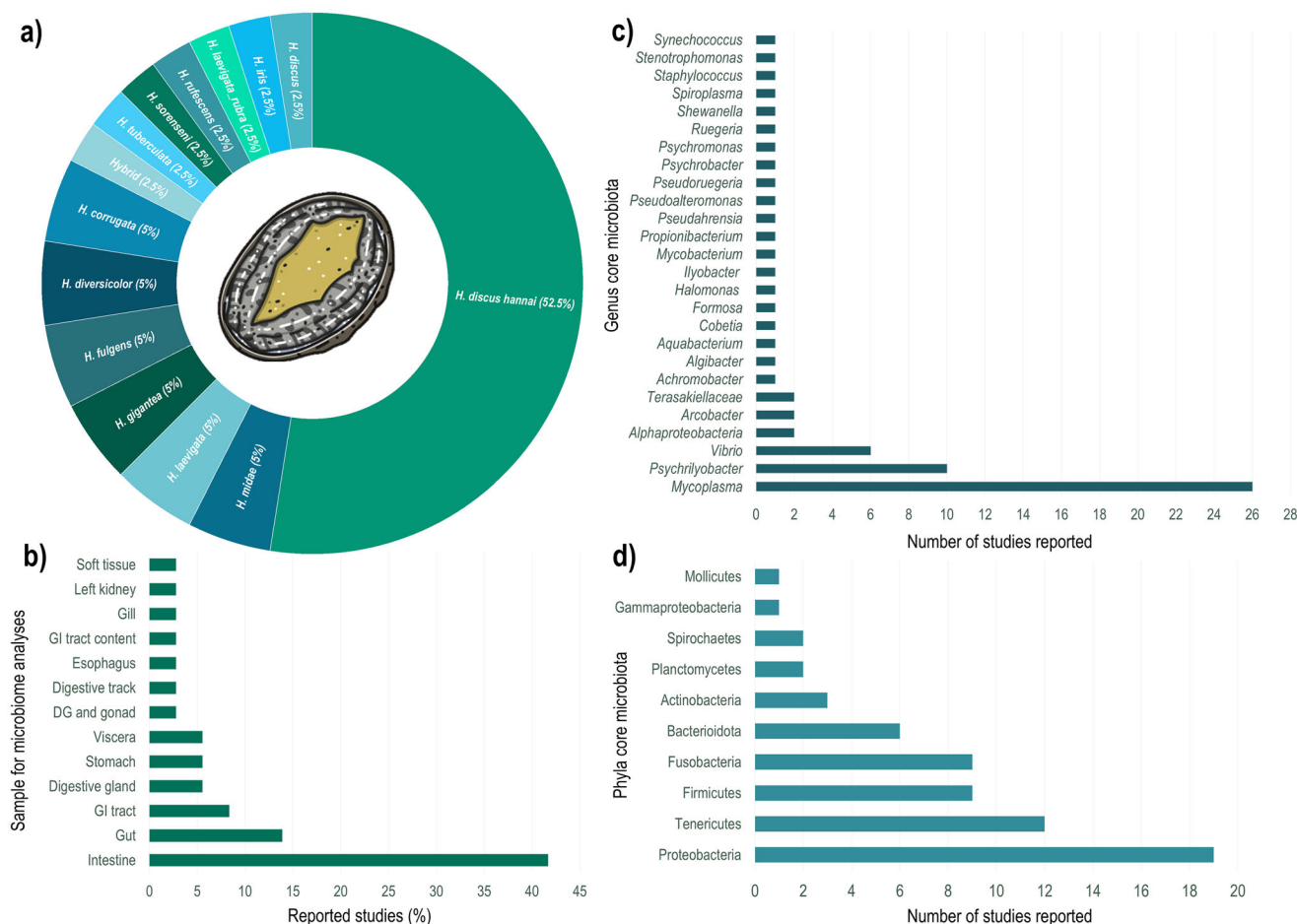


FIGURE 3 | Overview of 10-years (2015–2025) worth of abalone microbiome studies including (a) the percentage of studies per *Haliotis* species, (b) the tissue types reported for microbiome analyses, (c) the dominant bacterial genus and (d) phyla reported in abalone gut microbiome composition.

et al. 2024; Z. Guo et al. 2024; Z. Li, Ke, et al. 2025; Tabuariki et al. 2024; Z. Wu et al. 2024; X. Yu et al. 2025).

Psychrilyobacter is an obligate anaerobe within the phylum Fusobacteria, and has been associated with functions relevant to digestion, nutrient absorption, fermentative metabolism (Z. Guo et al. 2024) and protein degradation (Hur et al. 2023). They have been reported to favour marine sediment environments (Danckert et al. 2021). In abalone-associated microbiomes, *Psychrilyobacter* metabolizes carbon sources, such as sugars, organic compounds and amino acids, producing hydrogen and acetate that may contribute to host metabolic processes (X. Wang et al. 2020; Wei et al. 2025). It has further been linked to the production of fermentation-derived metabolites, including short-chain fatty acids and antimicrobial agents (Z. Li, Ke, et al. 2025), as well as acetyl-CoA formation associated with the breakdown of complex oligo-polysaccharides (Choi et al. 2021). Its metabolic activity may also include pyruvate fermentation leading to short-chain fatty acid production (Zou et al. 2022), which has been implicated in energy metabolism and immune homeostasis in the host (Danckert et al. 2021). Reports of *Psychrilyobacter* in abalone include *H. gigantea* (Wei et al., 2025), *H. laevigata* (Y. Wang, Pyecroft, et al. 2021), *H. tuberculata* (Gobet et al., 2018), *H. laevigata* and *H. laevigata* × *H. rubra* (Danckert et al. 2021), hybrid *H. discus hannai* × *H. fulgens* (X. Wang et al., 2020) and *H. discus hannai* (X. Wang et al. 2020; Choi et al. 2021; Zou

et al. 2022; P. Chen et al. 2023; Hur et al. 2023; Z. Li, Ke, et al. 2025).

Vibrio is widely reported in abalone gut microbiome studies and is frequently identified as a dominant member of the digestive tract-associated microbial community (Cadangin et al. 2024). Members of this genus belong to the phylum Proteobacteria and are facultative anaerobes (Danckert et al. 2021) capable of fermentative metabolism (Choi et al. 2021). *Vibrio* species have been associated with the degradation of complex polysaccharides via the production of exogenous digestive enzymes (Hur et al. 2023) and some strains (i.e., *Vibrio midae* SY9 [Huddy and Coyne 2014], *Vibrio halioticoli* [Sawabe et al. 2003]) have been investigated in an aquaculture context for their potential to utilize macroalgal substrates (Danckert et al. 2021). Their ability to degrade seaweed polysaccharides, such as alginic acid and laminarin has been linked to host digestive processes (Wei et al. 2025). However, *Vibrio* also includes pathogenic strains that have been associated with marine disease outbreaks (Z. Guo et al. 2024; Z. Li, Ke, et al. 2025). Pathogenic *Vibrio* can produce toxins that induce oxidative stress and inflammatory responses, thereby impacting host immune function (X. Yu et al. 2025). Overall, the role of *Vibrio* in abalone is highly strain-dependent and influenced by environmental conditions, with interactions ranging from potentially beneficial to pathogenic at sampling time (Danckert et al. 2021). Reports of *Vibrio* in abalone include

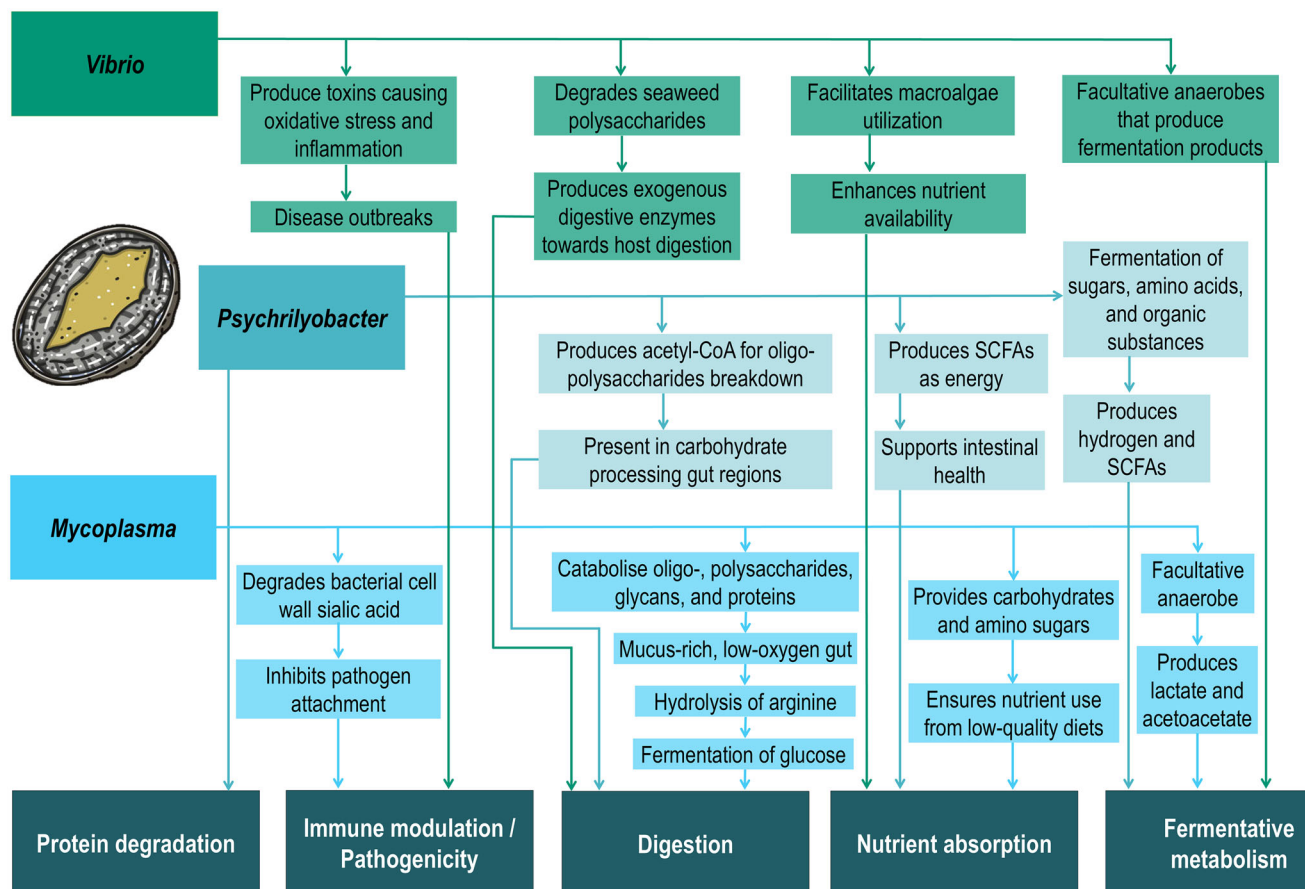


FIGURE 4 | Dominant genus-level taxa in abalone as *Mycoplasma*, *Psychrilyobacter* and *Vibrio* fulfilling functions linked to protein degradation, immune modulation and pathogenicity, digestion, nutrient absorption and fermentative metabolism.

H. gigantea (Mizutani et al. 2020; Wei et al. 2025), *H. fulgens* and *H. corrugata* (Cicala et al. 2018; Cicala et al. 2023), *H. laevigata* and *H. laevigata* × *H. rubra* (Dancert et al. 2021), *H. tuberculata* (Gobet et al. 2018) and *H. discus hannai* (Nam et al. 2018; Choi et al. 2021; T. Zhang et al. 2022; Hur et al. 2023; Cadangin et al. 2024; Z. Guo et al. 2024; Z. Li, Ke, et al. 2025; X. Yu et al. 2025).

5.2 | Abalone Microbiome Changes Associated With Dietary Interventions

Gut microbial communities both modulate and are influenced by the physical and biochemical environment of the digestive tract, as well as the food that passes through it (Vernocchi et al. 2020). Abalone primarily feed on seaweed, which are broadly classified as microalgae (e.g., diatoms) and macroalgae (including red, green and brown seaweed). The nutritional composition of these algae varies considerably (Bansemer et al. 2016; Peñalver et al. 2020; Salido et al. 2024), but generally includes lipids, polysaccharides and proteins (Xie et al. 2024). The nutrient composition of seaweed has been reported extensively. Moreover, bacteria belonging to the classes Bacilli, Actinomycetia, Gammaproteobacteria and Clostridia have been associated with the breakdown of these macronutrients (L. You et al. 2020; Yesiltas et al. 2021; Abomohra et al. 2022). Alongside natural diets, formulated feeds have been extensively used in the abalone aquaculture industry (K. W. Lee et al. 2017), where they have been

shown to influence gut microbiota composition and contribute to improved growth performance (Bullon et al. 2025). These artificial diets offer advantages, as their nutritional composition can be carefully designed and consistently controlled (Van der Poel et al. 2020). The inclusion of feed additives, such as probiotics (beneficial bacterial strains), has also been explored to enhance abalone performance (Dezfooli et al. 2023), with corresponding changes observed in gut microbial composition and diversity (J. Zhao et al. 2018). Feeding strategies may further influence the gut microbiome, for example, intermittent fasting (of 24 h) has been shown to alter intestinal bacterial communities in of Pacific abalone, indicating that feeding frequency can reshape gut microbial structure (Cai et al. 2025). Dietary composition is widely recognized as a key factor influencing the digestive tract microbiome (Beam et al. 2021). This is supported by studies published over the past decade (Table S1), which report shifts in abalone gut microbiota in response to dietary interventions, including variations in algae sources, lipids and protein content, probiotics, and other feed additives. The following section summarizes key studies investigating these dietary influences on the abalone gut microbiome.

5.2.1 | Algal Diets

Abalone aquaculture largely relies on cultured microalgae during early life stages, providing both a settlement cue for larvae and

a primary food source for post larvae and juveniles, until they transition to formulated feeds in the grow-out phase (Daume 2006). The use of macroalgae in aquaculture, both as broodstock feed or seasonal supplementation, and in wild abalone diets, is primarily based on carbohydrate-rich seaweeds (Bullon et al. 2023). Abalone can digest most carbohydrates in macroalgae due to gut-associated bacteria that hydrolyse structural and storage carbohydrates using a variety of carbohydrate-degrading enzymes, including laminarinase, α -amylase, maltase, agarase, alginate lyase, carrageenase, carboxymethylcellulase, sucrase and β -galactosidase, etc. (Bansemer et al. 2016). Microbiome studies are generally less focused on specific digestive enzymes but often report shifts in associated microbial communities linked to algal consumption. Macroalgae (as brown, red, or green seaweed) are commonly associated with distinct polysaccharide profiles. For example, alginate, laminarin and fucoidan are the primary polysaccharides in brown macroalgae (Phaeophyta), which are widely consumed by abalone (Hay 1990; Wernberg et al. 2003; Almanza and Buschmann 2013; Abe et al. 2020). Red seaweeds (Rhodophyta) contain agar and carrageenan, which are crucial ingredients in formulated aquaculture diets (Cotas et al. 2020). Abalone also consume green seaweeds (Chlorophyta), such as *Ulva* spp. which contain sulphated polysaccharides and are frequently used in hatcheries as settlement substrates to promote early abalone growth (Wikfors and Ohno 2001; Bansemer et al. 2016).

Bacterial strains capable of digesting brown, red and green seaweeds (e.g., *Sargassum horneri*, *Ecklonia maxima*, *Laminaria japonica*, *Gracilaria lemaneiformis*) are abundant in the gut microbiota of *H. discus hannai*, *H. midae*, *H. gigantea*, hybrid species and *H. tuberculata*, and are summarized below based on reported microbiota profiles. For instance, in a 12-week feeding trial in post-larval *H. discus hannai*, *Undaria pinnatifida* was replaced with varying levels of *S. horneri* (brown macroalgae). Herein *Psychrilyobacter* was highly abundant in the absence of *S. horneri*, but decreased when only *S. horneri* was consumed. Overall, *S. horneri* enhanced growth and supported gut microbial communities in this abalone species (Hur et al. 2023). In a second study, heating and fermentation of *S. horneri* did not improve the nutritive value of this seaweed for abalone (Hur et al. 2024). In *H. midae* fed brown kelp, (*E. maxima*) incorporated into formulated feeds, *Mycoplasma* was abundant in the gut and associated with a balanced microbial community, attributed to kelp-derived phytochemicals and dietary regulation effects (Nel et al. 2017). In a subsequent study, post-settled, *H. midae* weaned onto fresh *E. maxima*, showed dominance of anaerobic *Clostridium* species, likely due to high levels of fermentable polysaccharides in this macroalgae (Nel et al. 2018). In two-year-old *H. gigantea*, fed fresh brown kelp (*L. japonica*) for six months, dominant genera included *Stenotrophomonas* and *Vibrio*. When fed red macroalgae (*G. lemaneiformis*), higher relative abundance of *Psychrilyobacter* was observed (Wei et al. 2025). The hybrid *H. discus hannai* $\times$ *H. fulgens*, showed stable dominant bacterial communities, including unidentified Oxyphotobacteria regardless of the diet (*G. lemaneiformis*—red macroalgae, *L. japonica*—brown macroalgae or an artificial diet) (X. Wang et al. 2020). A six-month feeding trial with monospecific algal diets in juvenile *H. tuberculata* revealed a diet-specific core microbiota, including aerobic algal polysaccharide degraders. *Polaribacter* and *Pseudahrensia* were associated with *Palmaria palmata* (red algae), *Escherichia*—

Shigella with *Ulva lactuca* (green algae), *Roseibacillus* with *Laminaria digitata* (brown algae) and *Ulvibacter* with *Saccharina latissima* (brown algae). However, diet explained only a small proportion of microbiome variability suggesting that other factors, such as microbial gene transfer may play a larger role (Gobet et al. 2018). Finally, Z. Guo et al. (2024) reported that juvenile *H. discus hannai* fed a formulated diet (compared to starvation and fresh kelp), showed increased Proteobacteria abundance, alongside improved growth performance and digestive enzyme.

Overall, macroalgal diets shape distinct gut microbial profiles in abalone, with specific bacterial taxa responding to the structural complexity of algal carbohydrates. Future research should incorporate enzyme profiling to characterize carbohydrate-active enzymes (CAZymes) produced by marine microbial communities (Hehemann et al. 2010) to infer degradation capacity of dietary polysaccharides. This was demonstrated by Gobet et al. (2018), who explored the algal polysaccharide digestion potential of the core abalone digestive microbiota by means of a model bacterium for the bioconversion of algal polysaccharides. It is also important to note that diet alone does not fully explain microbiome variability, and that additional influences, such as host genetics, developmental stage and horizontal gene transfer should also be considered.

5.2.2 | Lipids

Gut microbiota contributes to host lipid metabolism by modifying dietary lipids through microbial lipase activity and by transforming lipid-derived compounds, thereby influencing the overall lipid pool available to the host (Yoon et al. 2024). Lipids in microalgae, such as diatoms and dinoflagellates, are generally more abundant than in macroalgae (Leyland et al. 2020). Microbial communities associated with lipid-rich diets have been shown to shift in composition, within enrichment of taxa involved in lipid metabolism, including *Acinetobacter*, *Lactobacilli*, *Bifidobacteria*, *Rhodococcus*, *Roseburia*, *Mycobacterium*, *Clostridium*, *Syntrophomonas*, *Chloroflexi*, and *Bacteroidetes* (Durazo-Beltrán et al. 2003; Guest et al. 2008; Pan et al. 2018). In Pacific abalone *H. discus hannai* diets with an optimized eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA)-ratios have been associated with increased relative abundances of *Clostridium*, *Mycobacterium*, *Bacilli* and *Bacteroides*, taxa linked to lipid metabolic activity and improved digestive performance (Tabuariki et al. 2024).

5.2.3 | Protein

Proteins are an important group of macronutrients essential for abalone growth, and their digestion involves both host enzymes and gut microbial contributions (Ringø et al. 2016). Research on dietary protein effects on abalone gut microbiota has mostly focused on farmed abalone species due to the controlled feed formulations and consistent macronutrient composition. Abalone utilize dietary proteins by breaking them down into amino acids and peptides, which support protein synthesis and growth (Tung and Alfaro 2012; Bullon et al. 2023). These protein-derived metabolites can also influence gut microbial community

composition. In addition, undigested dietary proteins may serve as substrates for microbial fermentation, thereby influencing gut microbial diversity (S. Wu, Bhat, et al. 2022). This is evident in *H. discus hannai* fed formulated diets with varying protein levels. The highest microbial diversity was observed at 275.9 g/kg dietary protein, with increased relative abundance of *Flavobacteriaceae*, a bacterial family previously reported to include iso-amylase producing members, such as α - and β -amylase-producing strains. *Acinetobacter* was more abundant at 230.3 g/kg protein inclusion and has been associated with digestive enzyme production in other aquatic systems, where it has been shown to produce proteases, amylases and lipases that may enhance nutrient utilization. Overall, both excessively high and low dietary protein levels were associated with reduced microbial diversity and digestive enzyme activity in *H. discus hannai* (Ma et al. 2021).

Aquafeed formulations often replace fishmeal with plant protein sources (e.g., soybean, corn gluten, rapeseed meals) and animal by-products (e.g., meat and bone, poultry meals) (Hua et al. 2019). Similarly, alternative protein sources have been widely explored in abalone feed development, including insect meal, grape marc, soybean-derived products, corn gluten meal, poultry by-product meal and ethanol fermentation protein products. Notably, the use of these alternative protein-based feeds has been associated with shifts in the gut microbiota of abalone. For instance, following a 165-day feeding trial, juvenile *H. iris* fed insect-meal and grape marc showed increased Firmicutes and Fusobacterium, taxa associated with polysaccharide degradation (Bullon et al. 2025). In *H. discus hannai*, corn gluten meal diets (administered in a 120-day trial) increased *Marinifilaceae* and *Bacteroides*, alongside reduced Proteobacteria. Microbe-enzyme association analysis indicated that these shifts were associated with reduced pectinase activity in the gut, an enzyme involved in the breakdown of plant-derived polysaccharides, which may consequently affect nutrient digestion and absorption in abalone (Ma et al. 2025). Moreover Ma et al. (2025) showed that diets containing dehulled soybean-meal, increased *Bacteroidetes*, which were reported to influence glycolysis and gluconeogenesis pathways through the microbiota-gut-digestive gland axis. In contrast, soy protein-concentrated diets enriched *Paraburkholderia*, *Ralstonia* and *Ahrensia*, which were associated with improved nutrient metabolism and microbial functional potential (Ma et al. 2025). Complete replacement of fishmeal with enzyme-treated soybean meal in a formulated diet for *H. discus hannai* resulted in increased *Mycoplasma* and *Terasakiellaceae* and reduced *Halomonas*, *Zobellella* and *Bacillus*, accompanied by decreased growth performance (X. Yu, Luo, et al. 2022). Partial replacement of soybean protein concentrate (25%) in a formulated diet for *H. discus hannai*, reduced potentially harmful bacteria, such as *Mycoplasma* and *Vibrio*, whereas full replacement (100%) altered microbiome structure and increased disease risk (X. Yu et al. 2025). Similarly, in the study by X. Yu et al. (2025), 50% soybean meal inclusion decreased *Dinoroseobacter* and increased microbial diversity, which was associated with improved growth performance and nutrient utilization. Higher inclusion levels of corn gluten meal ($\geq 10.8\%$) negatively affected the gut microbiome of *H. discus hannai*, increasing the relative abundance of taxa, such as *Mycoplasma*, *Terasakiellaceae*, *Alphaproteobacteria* and *Spiroplasma*, and coinciding with reduced nutrient digestion and absorption (Z. Wu, Yu, et al. 2022). The use of a poultry by-product meal increased *Pseudahrensia* abundance in the gut

samples of *H. discus hannai*, and was associated with altered host physiology and reduced growth (Z. Wu et al. 2023). The addition of *Clostridium autoethanogenum* protein (CAP), a by-product of ethanol fermentation, promoted probiotic bacterial genera such as *Ruegeria* and *Bacteroides* in *H. discus hannai*. The role of CAP in enhancing immunity, as indicated by the expression of inflammatory genes, is concluded in this study by Z. Wu et al. (2024).

5.2.4 | Probiotics and Compounds

Probiotics are beneficial live microorganisms (mostly bacteria) that aim to enhance the growth of the farmed abalone in aquaculture by optimizing digestive efficiency (Preece 2006; Silva-Aciaries et al. 2011; Hadi et al. 2014). Prominent bacterial genera, such as *Bacillus*, non-pathogenic strains of *Vibrio* (i.e., *Vibrio* JH1), *Enterococcus* and *Exiguobacterium*, have been cultured and isolated, and their contributions to abalone survival and growth have shown promising results (Hadi et al. 2014; Van Doan et al. 2020; Masoomi Dezfooli et al. 2021). Specifically, dietary supplementation using two exogenous probiotics (*Bacillus* sp. KRF-7 [KRF-7], *Bacillus* sp. PM8313 [PM8313]) and one prebiotic β -glucosaccharide (BGO) candidate in juvenile *H. discus hannai* showed diet-specific core microbiota following three months of rearing. These findings indicate that BGO, KRF-7 and PM8313 have potential application in abalone aquaculture as immune-enhancing and growth-promoting supplements, with particular emphasis on the roles of *Mycoplasma* and *Algibacter* species (Cadangin et al. 2024). A 180-day trial in *H. diversicolor* showed that diets supplemented with *Bacillus stratosphericus* A3440, *Phaeobacter daeponensis* AP1220, or both diets enhanced immune status and survival. *Bacillus* A3440 notably increased Enterobacteriaceae and Alcaligenaceae, while reducing Mycoplasmataceae (J. Zhao et al. 2018). An important goal of introducing probiotics to abalone diets is to modulate and diversify microbial communities within the digestive tract, thereby enhancing biochemical functions, such as macronutrient digestion and anti-microbial mechanisms. The use of probiotic bacterium, *Lactobacillus plantarum* to ferment abalone feed significantly enhanced *H. discus hannai* gut microbiota, increasing Firmicutes and *Mycoplasma*, while also promoting microbiota-metabolite interactions (Ke et al. 2025). Similarly, R. Wang et al. (2025) reported benefits of dietary probiotic treatments (*Bacillus*, photosynthetic bacteria and *Lactobacillus*) in terms of abalone weight gain and intestinal microbiome composition.

Other compounds with reported benefits in abalone feeding trials include bile acids and curcumin. Dietary bile acid supplementation in *H. discus hannai* resulted in decreased Actinobacteria and *Mycobacterium* and increased Firmicutes and *Mycoplasma* with rising bile acid concentrations. At appropriate inclusion levels, bile acids were reported to promote intestinal health of Pacific abalone following the 105-day feeding trial (P. Chen et al. 2023). Likewise, in a 100-day trial, *H. discus hannai* fed 0.1 g/kg curcumin showed increased Firmicutes, Fusobacteriota, along with a higher Firmicutes/Bacteroidetes ratio. Dominant genera included *Mycoplasma*, *Psychrilyobacter* and *Vibrio*. Curcumin resulted in shifts in enhanced bacterial proliferation that supports abalone growth and immunity (Zou et al. 2022).

In summary, diet strongly influences abalone gut microbiota, with direct implications for digestion, immunity and growth. Distinct bacterial groups are associated with different dietary components, including various macroalgal sources and formulated feeds, while additional factors, such as environment, microbial gene exchange and host species also contribute to shaping gut microbial communities. Formulated diets allow for precise nutrient control and enable the delivery and the incorporation of probiotics and functional compounds, which may further modulate the gut microbiome. Variations in lipid and protein sources, together with supplemental additives, such as probiotics, bile acids and curcumin, have been shown to significantly affect both microbial composition and host physiology. Understanding these diet-microbiome interactions remains important for optimizing feed formulations to support gut health and improve overall abalone performance.

5.3 | Abalone Microbiome Changes Associated With Environmental Changes

Apart from dietary macronutrients, environmental factors also influence abalone gut microbial composition and diversity (J. M. Harris 1993). Both farmed and wild abalone are exposed to changing coastal oceanographic conditions that shape their physiology (Morash and Alter 2016). Fluctuations in the environmental parameters (e.g., temperature, salinity, wave exposure, pH and sedimentation) can significantly impact abalone biology, resulting in impaired larval settlement (Naylor and McShane 2001; Onitsuka et al. 2008), inhibited shell formation (Auzoux-Bordenave et al. 2020), increased mortality (Samuel et al. 2019), reduced growth rates (Cummings et al. 2019), changes in gene expression (Boamah et al. 2024), altered metabolic rate (Fan et al. 2025) and modified enzyme activity (F. Gao et al. 2024). To cope with these environmental fluctuations, abalone need to adapt through both genetic mechanisms and physiological. The gut microbiome contributes to host resilience by modulating functional processes, including shifts in metabolic pathways, such as glycan biosynthesis and metabolism, which reflect microbial responses to changes in host physiology (Z. Zhang, Wang, et al. 2025). Accordingly, the abalone gut microbiome varies with season, sampling location, temperature and host species. These factors collectively shape the intestinal microecology of abalone through environmentally driven selection of functionally distinct microbial groups and changes in host-microbe metabolic interactions, as outlined below.

When investigating wild populations of *H. discus hannai* across different months, *Psychrobacter*, *Vibrio* and *Shewanella* were identified as the dominant genera. *Psychrobacter* was more abundant at lower temperatures, consistent with its psychrotolerant physiology and ability to function under cold conditions, including high catalase activity. In contrast, higher water temperatures showed increased microbial diversity and overall bacterial load, indicating temperature-driven shifts in microbial community structure (M.-J. Lee et al. 2016). Regional environmental conditions further shape gut microbiota composition through mechanistic links to nutrient cycling and host-microbiome metabolism. Z. Li, Ke, et al. (2025) reported in a study on the gut microbiome of *H. discus hannai* that in nutrient-variable marine environments, distinct microbial signatures were observed across

sampling sites. For example, *Pelagibacterium* was enriched at one site and associated with *amoA* gene (encoding ammonia monooxygenase), a marker of nitrogen cycling functions, potentially indicating adaptation to nutrient-limited conditions. Also, *Psychrilyobacter* was positively correlated with host nutrient assimilation and salinity, potentially through the production of short-chain fatty acids that enhance host energy acquisition. At the second site, *Mycoplasma* and *Vibrionimonas*, taxa often linked to pathogenicity, were more abundant, indicating increased host vulnerability under environmental stress. A third site showed enrichment of *Chitinophaga*, associated with chitin degradation and nutrient recycling. Collectively, these findings demonstrate that environmental factors, such as pH and nutrient availability, influence microbial community structure through shifts in metabolic functions, including nitrogen cycling, short-chain fatty acid production and organic matter degradation. Disruptions in these processes, particularly under nutrient-rich and low pH conditions, were further linked to alterations in lipid and sulphur metabolism in *H. discus hannai*, emphasizing the sensitivity of host-microbe interactions to environmental change (Z. Li, Ke, et al. 2025).

In farmed *H. laevis*, *Fusobacteria* contributed to seasonal variation in gut microbiota, while genera, such as *Pseudoruegeria*, *Arcobacter*, *Shewanella* and *Pseudoalteromonas* displayed temporal shifts likely influenced by site-specific environmental conditions and host-related factors, including life stage and tissue type (Y. Wang, Pyecroft, et al. 2021). However, mechanistic explanations for these seasonal patterns remain limited, highlighting a broader gap in current abalone microbiome research. (Y. Wang, Pyecroft, et al. 2021). Seasonal variability has also been reported in the digestive gland of *H. tuberculata*, where microbial community composition shifted over time despite consistent dominance of *Psychrilyobacter*, *Mycoplasma* and *Vibrio*. These changes were linked to temperature-driven alterations in the water column, influencing taxa, such as *Vibrio*, *Psychromonas*, an unclassified *Rhodobacteraceae*, *Polaribacter* and *Pseudahrensia*. Altogether, seasonal environmental variations, rather than specific algal diets, significantly shaped the composition and diversity of *H. tuberculata* gut microbiota (Gobet et al. 2018). Similar trends were observed in farmed tiger (*H. laevis* × *H. rubra*) and greenlip (*H. laevis*) abalone, where microbial composition varied significantly with sampling date, corresponding to seasonal shifts and host age. *Psychrilyobacter*, *Vibrio* and *Mycoplasma* were the dominant genera in both abalone species over a yearly average, yet the relative abundance of these changed with season (Danckert et al., 2021). Temperature specifically alters microbial function rather than completely restructuring dominant taxa. X. Wang et al. (2020) reported in *H. discus hannai*, that the gut microbiome was more temperature-sensitive than in hybrid species (*H. discus hannai* × *H. fulgens*), with *Mycoplasma* and *Psychrilyobacter*, remaining dominant across different temperature conditions. Mechanistically, these taxa possess metabolic flexibility, including anaerobic fermentation and utilization of diverse substrates, such as sugars, organic acids and amino acids. At 20°C, microbial communities showed enrichment of carbohydrate metabolism pathways, including functions linked to glucan biosynthesis and sugar utilization. By contrast, elevated temperatures (28°C) disrupted metabolic processes, including reduced expression of transport systems for sugars, such as trehalose and maltose, indicating impaired microbial energy metabolism.

These findings suggest that temperature shifts primarily affect microbial functional capacity rather than taxonomic composition (X. Wang et al. 2020). Environmental pollutants further influence microbiome structure and function. Yao et al. (2024) showed that in *H. diversicolor*, cadmium exposure altered both microbial diversity and the abundance of antibiotic resistance genes (ARGs), including *tet* (tetracycline resistance), *sul* (sulfonamide resistance) and *aadA* (aminoglycoside adenylyltransferase-mediated resistance). In terms of underlying mechanisms, co-selection of metal resistance genes and ARGs on mobile genetic elements may promote the proliferation of resistant and potentially pathogenic bacteria. Increased association between ARGs and genera such as *Cellvibrio* and *Delftia* under cadmium exposure suggest that pollution can reshape gut microbial networks and enhance the risk of resistance transfer, with implications for both host health and environmental safety (Yao et al. 2024).

Taken together, these studies reveal the influence of environmental variability on the structure and function of the abalone gut microbiome. Microbial genera, such as *Mycoplasma*, *Psychrilyobacter* and *Vibrio* occur consistently across species and regions, although their relative abundances and functional roles shift in response to environmental conditions. These changes are likely driven by alterations in microbial metabolic activity, including pathways related to carbohydrate metabolism, nitrogen cycling (e.g., *amoA*-associated nitrification) and short-chain fatty acid production, with implications for host nutrient assimilation and stress responses. Temperature influences microbial metabolic potential without necessarily replacing dominant taxa. Shifts in carbohydrate metabolism and transport processes under different thermal conditions suggest that environmental stress primarily affects microbial function rather than taxonomic composition. In addition, factors such as pH, nutrient availability and pollutant exposure can disrupt host–microbiome interactions by altering key metabolic pathways and promoting the co-selection of antibiotic resistance genes. Gobet et al. (2018) further reported that the abalone gut microbiota is largely established within the first year of life, after which environmental influences may play a more limited role in shaping overall community structure. This stability may reflect early-life colonization and host-driven selection, although further work is needed to assess microbiome resilience across species and environments.

5.4 | Abalone Infections and Diseases and Microbial Findings

The growth of abalone aquaculture has led to an increasing incidence of abalone disease outbreaks, which negatively affect animal health and result in significant economic losses (X. Gao et al. 2023). Abalone are affected by a range of microbial pathogens, including viruses, bacteria and protozoan parasites. These include abalone viral ganglioneuritis (AVG), caused by *Haliotid herpesvirus-1* (HaHV-1), bacterial pathogens, such as *Vibrio* spp. and *Pseudoalteromonas shioyasakiensis* and protozoan parasites, such as *Perkinsus* spp. and *Candidatus Xenohalotis californiensis*, reported in *H. rufescens*, *H. discus hannai*, *H. diversicolor supertexta*, *H. iris* and *H. rubra* (Nicolas et al. 2002; Cruz-Flores et al. 2015; M. Li et al. 2021; Zou et al. 2022; Muznebin et al. 2023; Y. Li, Chen, et al. 2025; Bai et al. 2019). In contrast, metazoan parasites in abalone include nematodes, polychaetes

and snail-associated parasites (Du et al. 2025), which affect host tissues through physical damage and resource competition rather than microbial colonization.

A balanced gut microbiota is important for reducing microbial infections and diseases in abalone, as aquatic diseases are frequently associated with shifts in the gut microbiome (Ghosh et al. 2025). Gastropods intestinal microbial communities can produce antimicrobial compounds against marine pathogens, contributing to host immune regulation (Offret et al. 2019; Z. Li, Ke, et al. 2025). In addition, abalone gut microbiota can modulate immune responses by regulating the expression of host immune-related genes, thereby influencing immune cells activation and proliferation (Cicala et al. 2018; Nam et al. 2018). Overall, the gut environment functions as a key interface between immune and microbial components, maintaining equilibrium against microbial invasions (Okumura and Takeda 2017).

Therapeutic interventions, such as antibiotics, are also used to mitigate microbial infections and diseases in abalone stocks; however, these treatments may significantly alter gut microbiota composition. For instance, white abalone (*H. sorenseni*) treated with oxytetracycline showed effective antimicrobial activities against *Candidatus Xenohalotis californiensis*, the agent of withering syndrome, but also exhibited loss of core bacterial taxa, such as *Fusobacteria* (Parker-Graham et al. 2020). Similarly, W. Yu, Lu, et al. (2022) reported reduced microbial diversity in abalone fed antibiotic-formulated diets, which was also associated with decreased feed efficiency. These findings indicate that while antibiotics can be effective against specific pathogens, they may also disrupt beneficial microbial communities, highlighting the complexity of microbiome–disease interactions. Further experimental studies are required to optimize antibiotic use for targeted and sustainable disease control in abalone aquaculture.

6 | Future Research Directions and Conclusions

Microbiome research in the digestive tracts of wild and farmed abalone, particularly within the intestine, remains relatively underdeveloped compared to that of fish and humans. Characterizing microbial composition, including richness and diversity, is a critical first step toward understanding microbiome function, genetics and host–microbe interactions. A core microbiome has been identified across abalone species, commonly dominated by taxa, such as *Mycoplasma*, *Psychrilyobacter* and *Vibrio*. China currently leads global abalone microbiome research, focusing on *H. discus hannai* and its hybrid variants. Investigations on other abalone species, which may have distinct dietary requirements and face different environmental challenges, remain limited. Hybridization of abalone species has proven useful to enhance key traits, such as stress resilience, growth rates and food conversion (W. You et al. 2019). These improvements are closely tied to the microbiome, which may exhibit greater metabolic activity and suppression of pathogenic taxa in hybrid animals. Insights from microbiome studies in hybrid fish species (Cui et al. 2022) highlight the potential to translate these findings to abalone, providing a promising avenue to explore how host–microbe interactions contribute to performance gains.

A further limitation in microbiome research is the small sample sizes commonly used, which may limit statistical power and the robustness of conclusions regarding microbial community structure (C.-Z. Chen et al. 2022). To accurately characterize microbiomes and generate ecologically and biologically meaningful conclusions, adequately powered studies with larger, well-replicated sample sets are essential, especially in systems with complex host–environment interactions, such as aquaculture species. In addition to sufficient samples sizes, future studies should incorporate environmental sampling, including surrounding water, seaweed and sediment to better contextualize microbial sources and transmission pathways. As an illustration, a microbiome study on *H. iris* showed that habitat characteristics and the nutritional composition of consumed seaweeds were associated with direct microbial transfer to the abalone digestive microbiome (J. Guo et al., 2026). Furthermore, early life microbiomes can have long-term effects on host health, highlighting the importance of longitudinal studies that track microbial dynamics across developmental stages to identify functional biomarkers linked to health, stress resilience and growth performance. For example, research on crabs has demonstrated stage-specific microbiome shifts, where probiotic supplementation improved growth performance during early life stages and supported effective larval culture (Fu et al. 2024). Given that larval settlement remains a major bottleneck in abalone aquaculture (Hannon et al. 2013), microbiome-based approaches may provide valuable insights into improving larval development and survival.

Studying the effects of dietary nutrition on the abalone gut microbiome under controlled laboratory conditions can help clarify the role of bacteria in digestion and growth (Danckert et al. 2021). Experimental findings can further inform diet formulation by linking microbial shifts to measurable physiological outcomes, such as growth rate, meat quality, nutritional composition, gut microbial diversity and disease prevalence. Interestingly, in fish, bacterial DNA present in feed has been shown to contribute to feed-associated microbiome carry-over effect, with gut microbial profiles in the distal intestine differing from those in the diet itself (Karlsen et al. 2022). This phenomenon represents a promising area for investigation in abalone, particularly given the reliance of abalone aquaculture on formulated feeds (X. Li et al. 2024).

Considering changing oceanographic and environmental conditions, shifts in gut microbial communities of wild abalone stocks should be monitored and tracked over time (Sawant et al. 2025). Increasingly, the microbiome is being recognized as a sensitive bioindicator of host health in aquaculture systems and may provide useful diagnostic insight for management practices (Makwarela et al. 2025). However, monitoring alone is insufficient. Greater emphasis is needed on resolving the functional roles of associated microbes in order to differentiate taxa that contribute positively to host health from those with pathogenic potential (Danckert et al. 2021). Addressing this challenge requires the use of complementary methodological approaches, as 16S rRNA gene sequencing alone cannot reliably distinguish functional differences at strain level or clearly separate beneficial from harmful variants. Integrating multi-omics approaches, such as metabolomics, offers a more direct way to link microbial activity with host physiological responses to environmental and nutritional stressors (Alfaro and Young 2018). Metabolite profiles associated with microbial activity can

further be used to infer functional potential, helping to place microbial community shifts into a physiological context (C.-Z. Chen et al. 2022). In parallel, bioinformatic techniques, such as co-occurrence network analysis and functional annotation can be used to explore ecological interactions and infer microbial contributions to host physiology (Codello et al. 2023). Collectively, multi-omics-driven insights can support evidence-based management strategies aimed at improving abalone health and promoting sustainable aquaculture practices.

In conclusion, abalone are benthic, herbivorous marine invertebrates of significant ecological, economic and culture value worldwide, making the protection of both wild and farmed stocks a shared global concern. This review highlights the gut microbiome as central regulator of abalone health, underpinning key functions including digestion, nutrient assimilation, immune regulation and pathogen defence. Although advances in high-throughput sequencing have greatly expanded our understanding of microbial richness and diversity across 14 abalone species; a major challenge remains in translating descriptive profiles into mechanistic and functional insights. Here, we emphasize that integrating microbiome data with host physiology, diet and environmental context is essential for resolving the roles of symbiotic and dysbiotic states in shaping abalone performance. The broader adoption of multi-omics approaches, combined with standardized sampling protocols, functional validation and longitudinal study designs, offers a practical pathway toward moving beyond taxonomic descriptions and developing more predictive and actionable understanding. As microbiome science continues to advance, its integration into abalone research and management holds strong promises to support resilient aquaculture, informed fisheries management and long-term growth of abalone populations under rapidly changing environmental conditions.

Author Contributions

Jinchen Guo: investigation, writing – original draft, Writing – review and editing, software, formal analysis, data curation, conceptualization, visualization. **Leonie Venter:** investigation, writing – original draft, visualization, writing – review and editing, formal analysis, data curation. **Donnabella C. Lacap-Bugler:** writing – review and editing, supervision. **Andrea C. Alfaro:** conceptualization, funding acquisition, writing – review and editing, supervision, resources.

Acknowledgements

This work was supported by The Pāua Industry Council (New Zealand) and the Vice-Chancellor's Doctoral Scholarship provided by Auckland University of Technology. We thank Anja Erasmus (Scientia Illustratio, South Africa) for creating the scientific illustration of the abalone digestive system.

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this study are provided as supplementary material.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supplementary materials: aff270298-sup-0001-SuppMat.xlsx