

Ecological Trade-Off in Marine Bioremediation: A Comparative Analysis Between *Alcanivorax borkumensis* and *Pseudomonas spp.*

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ABSTRACT

This literature review examines the ecological trade-off between *Alcanivorax borkumensis*, a specialist hydrocarbon-degrading bacterium, and *Pseudomonas spp.*, which exhibit broader metabolic versatility. *A. borkumensis* possesses specialised alkane-degradation pathways that can support rapid hydrocarbon degradation in oil-contaminated marine environments.

In contrast, *Pseudomonas spp.* exhibit broader metabolic versatility, with reported degradation of hydrocarbons, aromatic compounds, and selected synthetic polymers. However, its generalist nature can reduce degradation efficiency for individual substrates, while the specialist nature of *A. borkumensis* limits adaptability when faced with a variety of plastics and oil waste. Environmental conditions including pH, temperature, salinity, nutrient availability, and pollutant composition can further influence the performance of both microorganisms.

This review evaluates whether co-culturing *A. borkumensis* with the adaptive *Pseudomonas spp.* could complement these contrasting characteristics in heterogeneous marine pollution. The metabolic characteristics of *A. borkumensis* and *Pseudomonas* species provide a reason for testing this specialist-generalist consortium, but whether these complementary characteristics provide measurable cooperation remains to be experimentally validated.

LITERATURE SEARCH/METHODOLOGY

Literature relevant to marine microbial bioremediation was identified through searches of Google Scholar and PubMed databases using combinations of terms including “*Alcanivorax borkumensis*,” “*Pseudomonas*,” “marine bioremediation,” “hydrocarbon degradation,” “plastic degradation,” “microbial consortium,” “biosurfactants,” “and “biofilms.” Searches focused primarily on literature published between 2015 and 2026, although older studies were included when they provided important information not found within the preferred date range. Only peer-reviewed studies published in English were considered. Studies were selected if they addressed hydrocarbon or plastic degradation, metabolic

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pathways, environmental adaptability, biosurfactant or biofilm production, or microbial co-culturing relevant to *A. borkumensis* or *Pseudomonas* species. Studies that were not peer reviewed, were not published in English, or lacked direct relevance to microbial degradation and bioremediation were excluded. Reference lists of relevant articles were also examined to identify additional studies that met the inclusion criteria.

INTRODUCTION

Marine ecosystems are increasingly exposed to heterogeneous mixtures of pollutants, including crude oil and plastics. Approximately 11 million metric tons of plastic and up to 1.3 million metric tons of crude oil enter marine environments annually (40). Since these pollutants have significant differences in chemical structure, how long they remain in the environment, and have interactions with each other (41), no single microorganism is likely to efficiently degrade all components of a mixed pollutant system. This heterogeneity raises a challenge for microbial bioremediation, which is how a single microorganism can simultaneously achieve high degradation efficiency while maintaining sufficient metabolic flexibility across chemically diverse pollutants. Instead of focusing on individual strands, the review asks whether two microorganisms, such as *Alcanivorax borkumensis* and *Pseudomonas spp.*, could be combined in a way that they play to each other's strengths to degrade plastic and oil found in marine habitats sustainably.

Traditional Remediation Methods

Conventional marine remediation approaches, including mechanical cleanup, chemical dispersants, recycling, and dredging, can reduce pollution but have important limitations when applied to heterogeneous marine waste. While these methods can provide positive short-term effects, such as the physical removal of marine debris from affected areas (42), temporarily removing plastic and other waste from waters, more will continue to enter the oceans. Chemical dispersants can reduce the surface accumulation of oil, but their effectiveness and ecological consequences vary depending on environmental conditions (53). Current recycling methods include reusing and degrading, which turn certain plastics and their polymers into new products, and chemically dissolving polymers, respectively. Dredging, which removes unwanted particle matter from the ocean, can damage benthic ecosystems, as can mechanical cleanup (54). Additionally, recycling most plastic that ends up in the ocean is unproductive, as the plastics are not sorted because of their varied polymer compositions (55).

Marine Microorganisms as a Promising Sustainable Method

Microbial bioremediation offers an alternative approach because microorganisms can transform or metabolize certain pollutants rather than physically removing them from the environment. However, microorganisms differ greatly in substrate specificity, degradation kinetics, and environmental tolerance. To compare these characteristics, Table 1 categorizes representative microorganisms according to

ecological strategy, main substrates, classification, environmental adaptability, and their potential for mixed pollutants.

Table 1. Representative Marine Microorganisms Used in Recent Bioremediation Studies

Bacteria	Ecological strategy	Main Substrates	Classification	Environmental adaptability	Mixed-pollutant potential
Alcanivorax borkumensis (1)	Specialist	Alkanes	High	Low	Limited
Ideonella sakaiensis (36)	Specialist	PETase and MHETase to degrade PET plastic	High	High only with PETase	Limited
Dokdonella kunshanensis (37)	Specialist	Carbohydrates, nitrogen-containing compounds	High	Low	Suitable
Fibrobacter succinogenes (38)	Specialist	Cellulose, beta-glucans, cellodextrins	High	Moderate	Limited
Zoogloea (39)	Specialist	WSC, organic acids, sugars, aromatic hydrocarbons	High	Moderate	Suitable
Pseudomonas spp. (16)	Generalist	Hydrocarbons	Moderate	High	Suitable
Bacillus subtilis (31)	Generalist	Keratin, petroleum hydrocarbons	Moderate	High	Highly suitable
Acinetobacter (45)	Generalist	Phenols, aromatics, nitrogen compounds, petroleum,	Moderate	High	Highly suitable

		plastics			
Phanerochaete chrysosporium (46)	Generalist	Aromatic compounds, pesticides	Slow	High	Highly suitable

The classifications of degradation performance (high, moderate, and slow) are qualitative comparisons based on the relative degradation performance reported in the cited studies. Since the studies examined different substrates, organisms, experiential conditions, exposure periods, and outcome measures, these categories should not be interpreted as standardized quantitative thresholds or used for direct cross-study comparison.

Degradation performance in Table 1 was classified qualitatively based on the relative performance reported within the cited studies. Direct numerical thresholds were not applied because degradation measurements varied substantially in substrate type, experimental conditions, duration, and measurement methodology. For example, the high environmental adaptability determined for *Ideonella sakaiensis* (36) was based on the experiment's use of high-crystallinity PET from commercial soft-drink bottles, also adjusting the environment (pH, 72 h exposure, 30°C, etc.) is different from the experiment defining *Acinetobacter*'s highly suitable mixed-pollutant potential (47), isolating the bacteria with oil sludge that contains saturated hydrocarbons, PAHs, and even inorganic pollutants like Zinc and Cadmium. Thus, due to the variety of experiments, these classifications are intended only to provide a broad comparative overview of the microorganisms discussed in this review.

THE SPECIALIST MICROORGANISM: *Alcanivorax borkumensis*

Among marine bioremediating bacteria, *Alcanivorax borkumensis* is a highly specialized hydrocarbonoclastic organism that can rapidly populate in oil-contaminated environments because of its specialized alkane-degradation pathways (1, 4). Its specialization allows it to efficiently utilize hydrocarbons as carbon and energy sources, making it particularly well suited to oil-contaminated marine environments (2, 3). After an oil spill occurs, the hydrocarbons that it consists of are distributed into the waters, which can favor *A. borkumensis* over microorganisms that are less capable of exploiting these substrates, allowing it to form population blooms in contaminated areas (5, 8).

The efficiency of *A. borkumensis* is largely attributed to its specialized alkane-oxidation pathways. *A. borkumensis* uses a stepwise oxidation process and the additional diversity that has been discovered within the enzymes that the bacteria can use, enforcing its adaptability while remaining specific to certain needs, such as the use of "alkane monooxygenase" (6) as the first step. In the overall stepwise oxidation process, alkane monooxygenase (often known as AlkB-type) converts the alkane to an alcohol, going

through other complicated chemical reactions to reach the end product, Acetyl-CoA. However, a new finding in this paper by researchers off the North Atlantic coast has discovered that there are alternating alkane-activating enzymes that *A. borkumensis* utilizes in its process to remediate oil-concentrated areas in Earth's waters (6). This specialization allows *A. borkumensis* to efficiently channel hydrocarbons through defined metabolic pathways. However, the same metabolic specialization that increases efficiency towards alkanes can constrain the organism's ability to use other chemical pollutants as energy sources. Thus, specialization represents the main strength but also the principal limiting factor of *A. borkumensis* in heterogeneous marine pollution.

Cross-Feeding in Alcanivorax borkumensis

Cross-feeding refers to the consumption of metabolites released by one microorganism by another member of a microbial community (7). Although cross-feeding is well established in microbial communities, direct evidence demonstrating this interaction specifically between *A. borkumensis* and *Pseudomonas spp.* remains limited. Therefore, the potential for metabolite exchange between these organisms should be a proposed mechanism rather than a concrete and documented interaction. Biosurfactant production may provide another mechanism through which *A. borkumensis* modifies pollutant accessibility. By reducing interfacial tension between membrane phospholipids and increasing their oil-water interface, biosurfactants can improve access to hydrophobic hydrocarbons for microbial degradation (8). This production is not unique to *A. borkumensis*, since *Pseudomonas* strains such as *P. putida* also produce biosurfactants (13). Therefore, one potential advantage of a consortium would not be from biosurfactant production of one organism alone, but from whether these extracellular products improve pollutant accessibility for the microbial community as a whole. *A. borkumensis* forms a glycine-glucolipid biosurfactant, and blooms are the result of reactions to the sudden increase in concentration of oil that could enter the waters at any given time. Biosurfactants play an important role in substrate accessibility by breaking down the oils, which enhances the microbial degradation activity. The result of biosurfactant production is extremely useful to *A. borkumensis* and *Pseudomonas spp.*, as it reshapes the inaccessible pollutants into biologically available resources for further remediation.

Biofilm and Biosurfactant Cooperation in Alcanivorax borkumensis

In addition to the formation of biosurfactants, a similar phenomenon that occurs is the creation of a biofilm, which is a layer of bacteria that forms around crude oil droplets or surfaces of plastics that the microorganisms can detect (9). Biosurfactant production and biofilm formation may act as complementary systems by improving microbial attachment to the waste surface and expanding pollutant accessibility. *A. borkumensis* will secrete biosurfactants to alter the hydrophobicity of its own cell membranes, but also of the plastic surface, which increases the strength of attraction from the bacteria to the waste particle (13). Then, these microbes will multiply until they form an expansive structure called the biofilm, trapping enzymes closer to the waste surface for efficient degradation. The microbes continuously secrete enzymes to break the polymer chains of the waste element while producing

biosurfactants to soften the plastic (13), making it easier for the enzymes to break down. There are different combinations of enzymes integrated into the system of biosurfactants and biofilms, such as the enzymes of alkane hydroxylases like AlkB1 and AlkB2, in combination with biosurfactants like glycine-glucolipids to work simultaneously (2). The biosurfactant phenomenon serves as an important factor for the efficient, specific degradation of *A. borkumensis*.

Environmental Limitations of A. borkumensis

While *A. borkumensis* performs well in localized, high-concentration oil environments, the process is energetically costly and environmentally dependent, which narrows its scalability (29). This limitation of draining resources relatively fast is a concern since the oceans' behaviors are unpredictable. Factors such as varying temperatures, nutrient distributions, and changing salinity levels can all influence *A. borkumensis* degradation efficiency simultaneously.

In particular, however, salinity plays a huge role in regulating this microorganism's enzyme function. For instance, take the research findings found by Pereira et al., which demonstrated a decreasing trend in protein production as the molarity of NaCl increased from 0.3 M to 0.6 M and 1.2 M. The observed decline in protein production across increasing NaCl concentrations suggests that salinity can constrain the physiological performance of *A. borkumensis* under some experimental conditions (10). Moreover, enzyme activity in *A. borkumensis* is closely related to the function of environmental stability, such as the AlkB-type enzymes requiring detailed structural conditions to function (11).

Along with changes in salinity, pH fluctuations and changing pollutants will destabilize enzymes in their normal environment. These salinity changes negatively affect transportation of nutrients and enzymes across the membrane, protein folding, and substrate availability. As a result, even though *A. borkumensis* is well-adapted to its familiar plastic polymers and biofilm production, these findings suggest that the performance of *A. borkumensis* may vary substantially across marine environments with different conditions.

Although *A. borkumensis* is highly efficient as defined by the various microorganism skills seen in Table 1, its narrow substrate range, limited adaptability, and ecological dependence continue to drive research away from using single specialist organisms for future bioremediation. This progression can be seen as scientists consider the complementary metabolic pathways, also taking into consideration the environmental context, which concludes that more than one microorganism is required to keep the coexistence system going (43). Thus, while *A. borkumensis* demonstrates strong hydrocarbon degradation, its limitations provide an incentive for investigating whether the versatility of *Pseudomonas spp.* could complement its weaknesses in mixed-pollutant marine environments.

THE GENERALIST MICROORGANISM: *Pseudomonas spp.*

In contrast to the substrate specialization of *Alcanivorax borkumensis*, *Pseudomonas spp.* exhibit broad metabolic versatility that allows individual strains to utilize chemically diverse substrates. *Pseudomonas spp.* are capable of degrading hydrocarbons, aromatic compounds (12, 13, 14), pesticides, and certain synthetic plastics, which makes them one of the most adaptable organisms currently used in bioremediation investigations and applications. This class of compounds is often found in the remains of burned organic materials, which commonly end up near landfill soil as polycyclic aromatic hydrocarbons (PAHs) (13). The PAHs can be found in recycled plastics and rubber, both of which are in abundance in landfills and in water bodies (14).

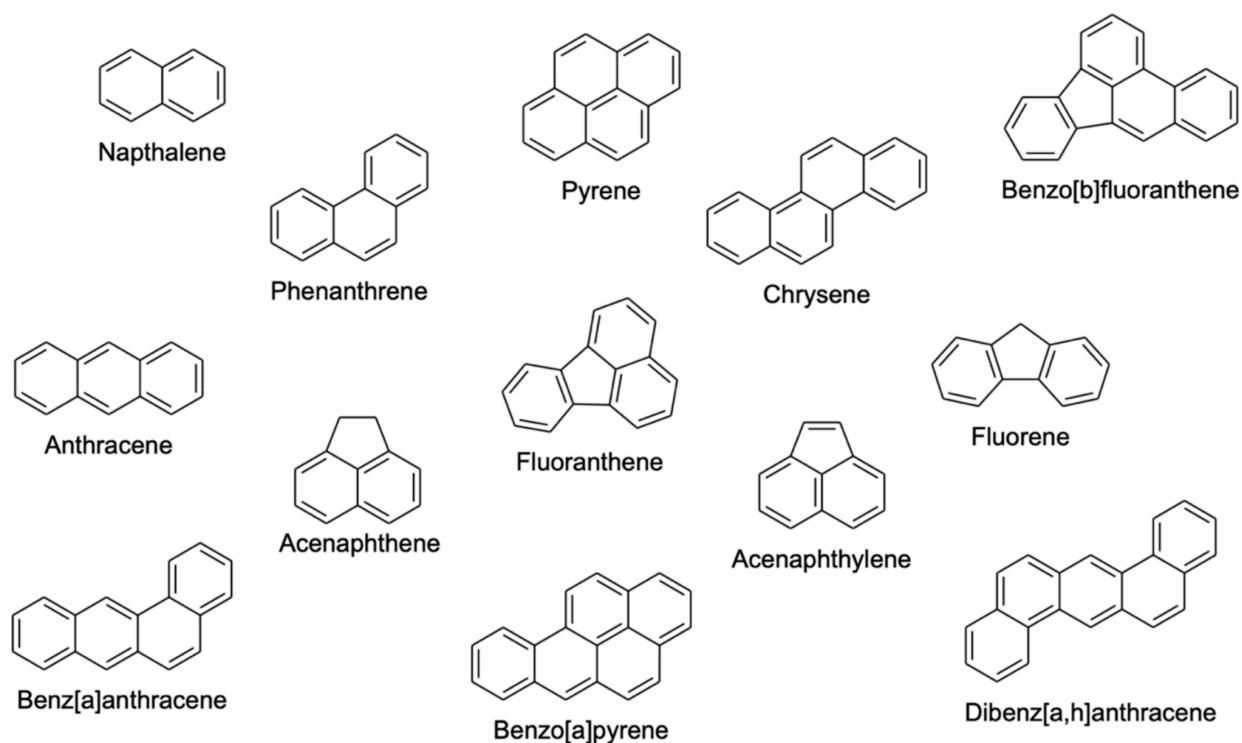


Figure 1. Structures of Representative Polycyclic Aromatic Hydrocarbons (PAHs) (35). *Pseudomonas spp.* can degrade Naphthalene, Phenanthrene, Anthracene, Pyrene, and Fluorene. This variety of PAHs demonstrates the generalist's capability to metabolize a variety of structurally diverse chemicals.

The structural diversity of PAHs illustrates the breadth of substrates that *Pseudomonas* can encounter and metabolize. Low-molecular-weight (LMW) PAHs generally contain fewer fused aromatic rings and are more readily degraded, whereas high-molecular-weight (HMW) PAHs are more chemically stable and therefore more difficult to break down. With the execution of these microorganisms' oxygenase-mediated pathways, however, *Pseudomonas* can metabolize compounds from both groups and lead the degradation

products into main carbon metabolism systems (44). Certain *P. aeruginosa* strains have been shown to degrade fluorene, phenanthrene, and pyrene with degradation efficiencies up to 98% (44), doing this by using the beta-ketoadipate pathways introduced in Figure 2 below.

Elements of *P. aeruginosa*, one of *Pseudomonas spp.*'s strains, can degrade polyethylene (PE), polyurethane (PU), and polystyrene (PS) polymers, among others (15), while using a variety of energy sources such as carbohydrates. Unlike highly specialized degraders, *Pseudomonas spp.* have been reported to metabolize numerous synthetic polymers that differ substantially in chemical composition, abundance, and environmental persistence. Table 2 illustrates the chemical and environmental diversity of plastic substrates reported to be degraded by *Pseudomonas spp.*

Table 2. Common Plastics Degraded by *Pseudomonas spp.*

Type of Common Plastics Able to Be Degraded by <i>Pseudomonas spp.</i> :	What it's found in:	Estimated share of global plastic production (%)	Reported marine occurrence (%)	Hydrocarbon composition:	Aromatics composition:
Polyethylene (15)	Rigid containers, packaging, household and consumer goods, plumbing pipes	26 - 30%	40-80%	Pure Hydrocarbon	None
PET (15)	Beverage and condiment bottles, textiles and fabrics, film materials	8%	10-20%	No hydrocarbon; contains oxygen	Yes, semi-aromatic
PUR (41)	Flexible foams, liquid coatings, synthetic fibers (eg. spandex)	7%	5-10%	No hydrocarbon, classified as a polymer with urethane linkages	Yes
PS (47)	Grocery item containers, insulation, toys and novelties	5%	2-5%	Pure Hydrocarbon	Yes

PCL (48)	Biomedical implants, biodegradable packaging, 3D printing filaments	Less than 1%	Negligible	No Hydrocarbons	None
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The range of polymers shown in Table 2 demonstrates the broader substrate depth of *Pseudomonas spp.* compared with the alkane specialization of *Alcanivorax borkumensis*. However, the presence of a reported degradation pathway does not necessarily indicate rapid or complete degradation under marine conditions. In contrast to their generalist functions, there are different pathways that *Pseudomonas spp.* will exhibit for different plastic polymers, such as the one demonstrated with Polyethylene terephthalate (PET).

Pseudomonas spp. performs well in its degradation of plastic particles, but plastics are evolutionarily difficult to remove. Plastics are synthetic, and microbe strains such as *P. aeruginosa* did not evolve to specifically access the internal polymers to degrade. The versatility of catabolic pathways in this microbe is often incomplete or inefficient (17, 18). The degradation process consists of three main steps: biofilm formation, enzyme hydrolysis, and the synthesis of monomers. *Pseudomonas spp.* take over hydrophobic (water-hating) plastic surfaces by forming biofilms, which then break down enzymes and cellular structures that make up PET. Since the biofilm tends to spread over the entire surface (17), it maximizes the localized concentration and increases rates of degradation (19).

There are similar steps that *Pseudomonas spp.* takes to ensure efficient degradation of other plastic polymers, like styrene (PS), polyurethane (PUR), or polycaprolactone (PCL). The multiple aromatic catabolic pathways of the generalist bacteria's popular strains, *P. aeruginosa* can be explored in fourteen different ways (20), occurring through several interconnected biochemical routes. Another example that is greatly abundant is PE. For the degradation mechanism of this plastic polymer, *P. aeruginosa* relies on enzymatic oxidation to introduce hydroxyl groups into long chains of polyethylene and paraffin polymers to shorten them (20). After the PE chains are shortened, the resulting alkanes are metabolised through the beta-oxidation pathway and become simple organic materials that can be re-absorbed into the earth. While these pathways are diverse and are essential for adaptive flexibility, generalists such as *Pseudomonas* sacrifice the chemical optimization of specific substrates like *A. borkumensis*, making for an important trade-off.

The interconnection of these routes in their diverse enzymatic systems have their unique factor with specific substrates for initial depolymerization, but the resulting metabolic elements often converge on some common central pathways. The beta-ketoadipate pathway is adopted in *Pseudomonas* immediately after the depolymerization of PET into its basic aromatic monomers, which can be seen in benzoate, further being broken down into Acetyl-CoA and other harmless byproducts. As shown in Figure 2, Acetyl-CoA is produced. Rather than relying on a narrow range of substrates, these bacteria possess

detailed catabolic pathways that allow responses to multiple pollutant types simultaneously (16). These pathways vary according to polymer or hydrocarbon substrate, but many ultimately converge on central metabolic intermediates like Acetyl-CoA, suggesting possible complementary uptake of the intermediate between both bacteria (37). However, shared use of a metabolite does not by itself demonstrate cross-feeding between the organisms. This common use of end products in metabolic pathways as a result of combining a specialist and generalist bacterium shows the potential in co-culturing to degrade mixed marine pollution more efficiently.

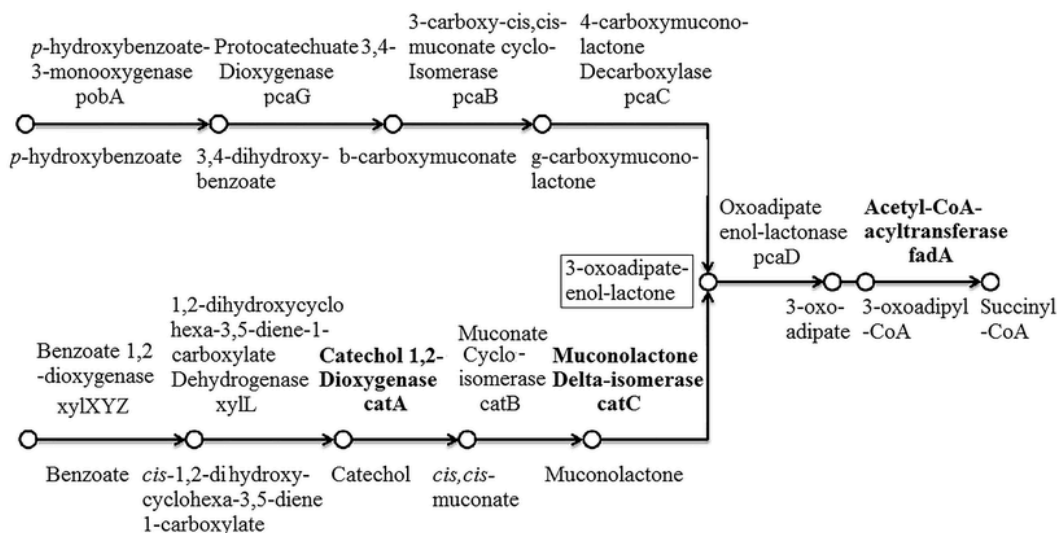


Figure 2. Beta-Ketoadipate Pathway Used By *Pseudomonas spp.* Adapted from Ref. (37)

Additional metabolic routes, including the homogeneous state pathway shown in Figure 3, demonstrate how specific substrates can enter broader central metabolic networks in *Pseudomonas spp.* and their specific strains, like *P. aeruginosa*. This strain is commonly studied for upcycling plastic (15), as they secrete extracellular enzymes (esterases, lipases, etc.) that can depolymerize plastics such as PCL, as shown in the diagram.

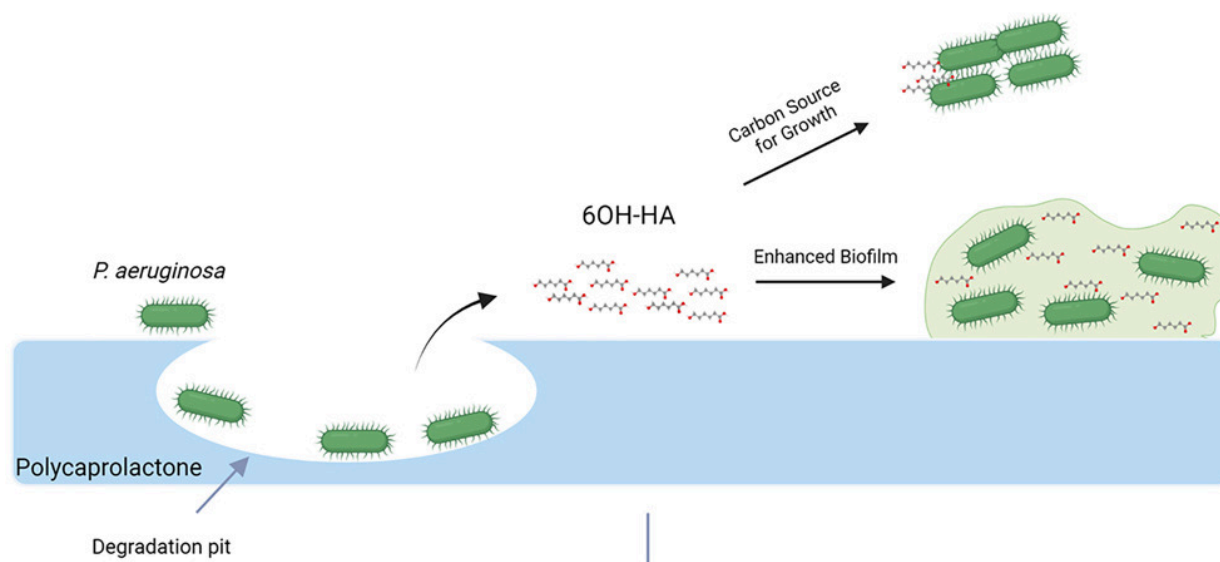


Figure 3. Homogentisate Pathway Used By *Pseudomonas* spp. Adapted from Ref. (17)

By implementing the combination of specific substrates in the first few stages of the pathway with central pathways near the ending stages, it provides *Pseudomonas* with greater environmental responsiveness, ultimately being useful in a wider sort of heterogeneous solution with different quantities of crude oil, plastic materials, and other waste that can be bioremediated.

In the real world, scientists are working with *Pseudomonas* isolates such as *P. aeruginosa*, *P. putida*, and *P. mendocina*, which generally perform better than isolates of other marine microorganisms, such as *Bacillus* and *Actinomyces* (12). The different strains of *Pseudomonas* spp., specifically *P. aeruginosa*, have the function of producing biosurfactants that emulsify plastics and form biofilms that concentrate enzymes on the surface to enhance degradation (15). Additionally, *P. aeruginosa* exhibits strong biofilm-forming capabilities that improve environmental resilience by excreting exopolysaccharides (EPS), enhancing its bacterial invasion capabilities (21). These biofilms allow bacterial communities to attach to oil droplets and plastic surfaces while increasing resistance to environmental stressors such as extreme pH, salinity fluctuations, temperature drops, nutrient limitation, and changes in the quantity of oxygen.

To resist extreme pH and crude oil, marine *Pseudomonas* strains such as *P. aeruginosa* will secrete dense EPS structures to shield the bacterial community (21). Recalling the mention of PAHs and *Pseudomonas*'s generalist aspect in utilizing a variety of degradation pathways, the combinations allow them to use toxic PAHs and even certain plastics as carbon sources, which is another stress resistance mechanism (21). Apart from the stress of extreme pH levels, this microorganism demonstrates high adaptability to changes in salinity fluctuation (22), as the cells accumulate compatible solutes to balance external and internal solute concentrations to prevent water loss from osmosis. Under decreasing temperatures, *P. aeruginosa*

and *P. putida* can alter membrane lipid composition to maintain membrane fluidity (23). Under nutrient limitation, in some scenarios, such as when the carbohydrates and sugars that the two strains need for energy become scarce (24). The cells will shrink in size, ultimately reducing their surface area, decreasing the rate at which they need to process and remediate plastics. The variety in responses measured in *Pseudomonas spp.* demonstrate its versatility, but the weaknesses it demonstrates through the scarcity of nutrients show that *Alcanivorax borkumensis* can be combined through the co-culturing mechanism to target more specific enzymes and resources that *Pseudomonas* cannot use. These characteristics provide a rationale for testing whether *Pseudomonas* could complement the environmental limitations of *A. borkumensis* in co-culture.

***Pseudomonas* Limitations**

However, metabolic versatility doesn't function consistently well. For example, *P. aeruginosa*. invests cellular energy across multiple degradation pathways, meaning that its efficiency toward individual substrates is often lower than that of highly specialized organisms such as *Alcanivorax borkumensis* (25). One limitation is the automatic repression of catabolites (26), which strictly regulates its carbon intake. This phenomenon is called Carbon Catabolite Repression (CCR). Even though easily digestible sugars (which are the preferred carbon sources of *Pseudomonas*) may be present, the operon that usually expresses the gene to degrade complex pollutants is repressed. Toxic PAHs and their use for metabolic defense to form biofilms have proven to be useful as well, but the intermediates that they generate are highly toxic as well (27). Often, secondary pathways used to remediate toxic intermediates are inhibited, and when this occurs, these intermediates can poison the cell. This dilemma shows that, for *Pseudomonas* and its role in degrading plastic by forming biofilms, if the secondary pathways are inhibited, they can more efficiently break down the polymers but are at risk of system failure due to poisoning. Another unique limitation of *P. aeruginosa* and its degradation process is that many pathways are plasmid-encoded (17). Some catabolic traits are plasmid-encoded, which may introduce additional concerns regarding genetic stability under changing environmental conditions. These limitations demonstrate that the generalist aspect of *Pseudomonas spp.* does not eliminate metabolic constraints, but shifts the trade-off from substrate specialization toward a wider range of adaptability.

TRADE-OFF BETWEEN SPECIALISTS AND GENERALISTS

The contrasting characteristics of *A. borkumensis* and *Pseudomonas spp.* illustrate a specialist-generalist trade-off between degradation efficiency and ecological flexibility. This review analyzes and compares the specialist *Alcanivorax borkumensis* as a specialist hydrocarbon degrader and *Pseudomonas spp.* as generalists. Comparing their respective strengths and limitations provides a structure to evaluate whether their characteristics could complement and support a defined co-culture for mixed plastic and oil pollution. Specialist organisms perform a few functions with extremely high quality, as their metabolic

burden is lower, also in marine habitats providing abiotic gradients where there are many niches that can be exploited (45).

A. borkumensis is a specialist organism that utilizes specific alkane degradation pathways as its main energy source for bioremediation of crude oil, having detailed catabolic pathways but not having a wide range of adaptability to changing situations in bodies of water. Conversely, generalists perform many functions at a low-quality rate, indicating their versatility. *Pseudomonas spp.* are generalist organisms with a variety of productive and isolated strains, as documented by scientists and their existing research (46).

The *Pseudomonas* tab is more involved in the degradation of plastic, which is an aspect of remediation that *A. borkumensis* does not focus on as extensively. Comparing both organisms shows that in bodies of water with heterogeneous mixtures of plastics, crude oils, and other waste, more than one bacterium may contribute to improved ecosystems in oceans and seas. Evolutionary optimization creates biological constraints such as trade-offs, which mean that specialists gain efficiency through narrow adaptation but lose resilience. In contrast, generalists gain resilience but sacrifice the productivity of metabolic pathways. Thus, integrated microbial systems may outperform isolated strains.

Specialist Advantages Under Favorable Conditions

A. borkumensis serves as an example of a specialist hydrocarbon-degrading organism since it achieves fast and targeted degradation through highly specialized metabolic pathways (such as the beta-oxidation pathway discussed and its enhanced rates when biofilm is produced as well (9, 37)). Their narrow substrate specificity allows for efficient hydrocarbon metabolism, especially in the moments right after oil spills that are relatively smaller in volume in comparison to the response of the generalist organism, *Pseudomonas spp.* In addition to their specialized hydrocarbon metabolism, their capability to form biofilms in conjunction with biosurfactants, as well as nutrient scavenging abilities, gives *A. borkumensis* a competitive advantage in stable conditions where temperatures are relatively unchanging, pH is not extreme, and other conditions do not require the microorganism to adapt constantly. Environmental stability may facilitate sustained biofilm formation and nutrient acquisition, whereas strong currents or changing chemical conditions could disrupt these processes. High waves and currents can physically strip the biofilm structure away from the oil droplet, making it less accessible. When crude oil batches (containing carbon) are introduced into the ocean from runoff, the natural ratio of carbon to nitrogen is skewed, which limits bacterial growth (28). However, *A. borkumensis* has efficient gene systems that can locate dissolved nitrogen and phosphorus, along with simple sugars from the surrounding seawater (28). Stable conditions matter for nutrient scavenging, as it allows the bacteria to continuously hunt for dissolved elements without harsh currents and other conditions that can whisk the nutrients away. It can also help them to bloom and outcompete indigenous marine microbes that are more likely to have evolved to a specific environment that dissolves a common oil compound present.

Why Generalists Outperform in Variable Conditions

Generalist organisms such as *Pseudomonas spp.*, in contrast to specialist organisms, possess broader metabolic activity and adaptability to constantly changing conditions in marine habitats, which allows a greater percentage of survival in chemically diverse waters. The strains *P. aeruginosa* and *P. putida* demonstrate versatility and secrete EPS (20), acting as a physical barrier against sudden changes in oceans such as salinity or osmotic pressure. This resilience broadens the range of degradable pollutants, even though it degrades the effectiveness of individual substrates.

Ultimately, the strains of *Pseudomonas* can handle toxic element stress, which matters because in variable conditions (usually the case in waterways, on marine coastlines, rivers, and near wastewater treatment plants), there are mixed-waste streams, and their tolerance protects the plastic-degrading process from chemical toxicity. Additionally, the realistic nature of generalists outperforming in variable conditions is suitable in comparison to stable conditions, which are becoming more distant in the world due to the intensifying impact of climate change on waters and their behaviors. *P. aeruginosa* can also enter dormancy in nutrient-poor waters, and they can live off minimal energy (30) where other bacterial species could die off. This is another reason why the generalists can outperform, because when the other weaker species die off, the competition to search for resources can be diminished.

CO-CULTURING AS A POTENTIAL STRATEGY TO ADDRESS THE SPECIALIST-GENERALIST TRADE-OFF

The limitations of individual specialist and generalist organisms provide a rationale for investigating microbial consortia. Rather than requiring one organism to perform every stage of pollutant degradation, a consortium could distribute complementary metabolic functions across multiple species. Three potential mechanisms are particularly relevant: metabolic labor, metabolite exchange, and environmental modification through biofilms/biosurfactants. However, these mechanisms should be differentiated between those experimentally demonstrated in specific consortia and those reported based on the known information of the organisms. Unlike monocultures that rely on the complete metabolic capacity of a single organism, co-culturing allows microorganisms to divide their biological responsibilities while collectively degrading heterogeneous mixtures of crude oil and plastic pollutants. In the division of metabolic labor, one study found that *A. borkumensis* could degrade liquid polypropylene (PP) but could not use PP as its sole carbon and energy source. Degradation only occurred when an additional carbon source, like pyruvate, was supplied (49). This dependence illustrates how a consortium could potentially distribute complementary metabolic functions across organisms rather than requiring one species to independently sustain all processes (50).

Building off of metabolic labor, the exchange between these intermediates can be seen through metabolic pathways making downstream products like extracellular PHA (51). This illustrates how metabolites

generated by one organism can become resources within a microbial community, suggesting potential cross-feeding behavior.

Environmental modification may provide another mechanism through which microbial consortia can overcome the constraints of individual specialists, which is the effectiveness of bacteria dependent on environmental conditions. In one study, indigenous isolates from Omani polluted sediments near a body of water tolerated salinities of 2-7‰ (52), while the effectiveness of an introduced bacterial consortium varied between sediments. These findings demonstrate that microbial degradation cannot be considered independently of the surrounding environment. Within a consortium, therefore, microorganisms that alter their local environment through biosurfactant production could potentially improve pollutant accessibility to create more favorable conditions. However, evidence that metabolically complementary consortia can improve hydrocarbon degradation does not establish that the same effect would occur specifically in an *A. borkumensis*-*Pseudomonas* consortium.

A fundamental advantage of microbial consortia is the division of metabolic labor, in which different bacterial species specialize in distinct stages of pollutant degradation instead of repeating the same biochemical reactions. Within these systems, *A. borkumensis* could serve as the primary hydrocarbon initiator by rapidly colonizing oil droplets and performing the initial oxidation of long-chain alkanes immediately following contamination of waste (3). Rather than investing all of its metabolic resources into degrading a broad spectrum of pollutants, *A. borkumensis* concentrates on the efficient activation of petroleum hydrocarbons while producing biofilms and biosurfactants that facilitate oil colonization. Conversely, *Pseudomonas spp.* could occupy a complementary role by utilizing a wider diversity of carbon sources, including PAHs, plastic-derived monomers, and metabolic intermediates that remain inaccessible to the specialist bacterium alone. Consequently, the two organisms could occupy complementary ecological niches instead of directly competing for identical substrates, reducing metabolic redundancy while expanding the consortium's overall degradation capacity. A study of microbial consortia between *Bacillus subtilis* and *Pseudomonas aeruginosa* provides evidence that combining metabolically complementary microorganisms can improve oil degradation compared with monocultures (31). When 2 mL of *Bacillus subtilis* and *P. aeruginosa* were mixed on the same spread plate, the presence of oil dramatically increased *B. subtilis* cell density while *P. aeruginosa* density remained similar. Biosurfactant production also increased within the co-culture compared to individual strands. *A. borkumensis* has also proven to be adaptable, as seen in its adaptation to toxic organic compounds and uncommon alkanes experimented by J Naether et al. (32). It demonstrates bacteria growth with alkanes ranging from C10 to C20, indicating versatility. This finding further indicates that if a co-culture between one *Pseudomonas spp.* strain and *B. subtilis* shows improved signs of oil degradation, it is likely to have the same results as with *A. borkumensis*. However, whether these findings extend specifically to an *A. borkumensis* and *Pseudomonas* consortium remains uncertain.

The efficiency of this co-culturing partnership between the two microorganisms is further strengthened through cross-feeding, a process in which metabolites generated by one microorganism become substrates

for another member of the consortium. During alkane degradation, *A. borkumensis* uses specialized hydroxylases such as AlkB1 and AlkB2 to initiate hydrocarbon oxidation (33). The resulting intermediates, such as pyruvate and short-chain fatty acids (34), from the oxidation process could potentially serve as substrates for other organisms like the metabolically versatile *Pseudomonas spp.* However, whether these specific metabolites are transferred from *A. borkumensis* to *Pseudomonas spp.* under co-culture conditions has not been established. So, cross-feeding represents a plausible mechanism for consortium-level cooperation rather than concrete evidence of interaction demonstrated between these two organisms. In this potential system, *Pseudomonas spp.* have common networks capable of processing aromatic hydrocarbons and plastic-derived compounds. This improves carbon recovery (12) while minimizing the accumulation of partially degraded products that may inhibit microbial activity or damage the environment further.

This metabolic cooperation creates a smoothly operating degradation network in which the specialist bacterium performs rapid hydrocarbon activation while the generalist bacterium extends degradation into additional substrate classes, allowing pollutant removal to proceed more efficiently than either organism could accomplish independently.

Microbial synergy extends beyond metabolic exchange through biosurfactant cooperation, in which one organism modifies the surrounding environment to improve degradation efficiency for the entire consortium. Biosurfactants, secreted by *A. borkumensis*, emulsify hydrophobic oil droplets by reducing interfacial and surface tension, which increases the oil-water surface for enzymatic reactions.

Biosurfactant production by *A. borkumensis* may provide an additional mechanism in which the specialist could modify pollutant accessibility for neighboring microorganisms. However, biosurfactant production is not unique to *A. borkumensis* since several *Pseudomonas* strains, as seen in Table 3, have been shown to produce biosurfactants. Enhanced pollutant solubilization allows the generalist bacterium to access substrates that would otherwise remain physically inaccessible because of the low water solubility of petroleum hydrocarbons. In addition, biofilm formation stabilizes bacterial attachment to contaminated surfaces, which allows them to maintain proximity between species and facilitate efficient metabolite exchange during cross-feeding. Studies investigating other defined microbial consortia have reported enhanced degradation when *Pseudomonas spp.* is co-cultured with other microorganisms. For example, Kang et al. (31) investigated a co-culture of *P. aeruginosa* and *Bacillus subtilis* and reported improved oil-related performance compared with the individual organisms. However, this evidence does not demonstrate that similar enhancement would occur in an *A. borkumensis* - *Pseudomonas* consortium. Separately, the documented adaptability of *A. borkumensis* to different alkanes and toxic organic compounds (32) provides a rationale for experimentally testing such a consortium. These findings and inferences suggest that biosurfactants function as individual physiological adaptations, but more extensively as shared ecological resources that enhance the collective performance of the microbial community.

Limitations of *A. borkumensis* and *Pseudomonas* Co-Culture

Current constraints of the co-culture solution between *A. borkumensis* and *Pseudomonas spp.* include competition for resources, metabolic interference, environmental compatibility, and the scale at which this co-culture can be executed. Both *Alcanivorax borkumensis* and *Pseudomonas* are aerobic microorganisms, which means they require O₂ to perform metabolic functions. In co-cultures, nitrogen is an essential element for both bacteria (1), as high C/N ratios in fermentation can reduce biomass but increase biosurfactant yield in *A. borkumensis*, suggesting that N limitation can shift metabolic priorities away from its maximum efficiency to degrade hydrocarbons (56). *Pseudomonas* strains such as *P. putida* may preferentially consume readily available carbon sources such as acetate or pyruvate, potentially altering resource availability within the consortium (56). Resource competition can potentially inhibit the activity of another. *A. borkumensis* growth triggers the local depletion of alkanes, but it doesn't significantly inhibit aromatic degradation in *P. putida* (57).

Environmental capacity limitations arise when alkane-rich areas saturate with biomass of *A. borkumensis* (28), while *Pseudomonas* thrives in aromatic-rich environments and is less affected by hydrophobic constraints. When forming biofilms around oil droplets, it can enhance metabolite exchange (58) but potentially limits diffusion of oxygen and other nutrients as well. The possibility of co-culture between *A. borkumensis* and *Pseudomonas* is promising, as seen in indirect lab evidence; however, it would be difficult to execute this system at a larger scale, such as in oceans or seas.

CONCLUSION

Overall, the comparison reveals a specialist-generalist trade-off in which *A. borkumensis* provides efficient hydrocarbon degradation while *Pseudomonas spp.* contribute broader metabolic versatility. Their complementary capabilities provide a theoretical system of co-culturing, through potential division of metabolic labor, metabolite exchange, and environmental modification. However, direct evidence of these interactions within an *A. borkumensis* - *Pseudomonas* consortium remains limited, and resource competition, population instability, environmental compatibility, and scalability may constrain its effectiveness. Therefore, co-culturing represents a promising but unvalidated strategy for addressing mixed marine pollution, given that experimental studies determine whether these proposed interactions produce measurable improvements in pollutant degradation under realistic marine conditions.

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Amy Ma: Conceptualization, literature search and review, investigation, writing – original draft preparation, and manuscript revision.

Veronika Mantziou: Conceptualization, supervision and mentorship – review, editing, and contributions to manuscript preparation/revision. Both authors reviewed and approved the final manuscript.

ABBREVIATIONS

PETase - Polyethylene terephthalate hydrolase (enzyme)
MHETase - Mono(2-hydroxyethyl) terephthalate hydrolase (enzyme)
WSC - water-soluble carbon
PET - Polyethylene terephthalate
AlkB1/2 - Two variants of Alkane Hydroxylase
Acetyl CoA - Acetyl Coenzyme A
PAH - Polycyclic Aromatic Hydrocarbons
LMW PAHs - Low Molecular Weight Polycyclic Aromatic Hydrocarbons
HMW PAHs - High Molecular Weight Polycyclic Aromatic Hydrocarbons
PCL - Polycaprolactone
PE - Polyethylene
PU, PUR - Polyurethane
PS - Polystyrene
CCR - Carbon Catabolite Repression
PHA - Polyhydroxyalkanoate

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