



Bacterial degradation of perfluoroalkyl acids

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Advances in biological degradation of per- and polyfluoroalkyl substances (PFAS) have shown that bioremediation is a promising method of PFAS mineralization; however, most of these studies focus on remediation of more reactive polyfluorinated compounds. This review focuses on the defluorination of the more recalcitrant perfluorinated alkyl acids (PFAAs) by bacteria. We highlight key studies that report PFAA degradation products, specific bacteria, and relevant genes. Among these studies, we discuss trends in anaerobic versus aerobic conditions with specific bacterial species or consortia. This holistic review seeks to elucidate the state of PFAA biodegradation research and discuss the need for future research for environmental application.

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Introduction

Growing concern over PFAS (per- and polyfluoroalkyl substances) ubiquity and toxicity has galvanized PFAS fate and transport and remediation research. Physical removal may concentrate PFAS without degrading them, and chemical treatment technologies may produce toxic byproducts [1,2]. While significant progress has been made with the chemical reduction of PFAS [3–6], biological reduction is still in its infancy. Bioremediation of PFAS, if feasible, would potentially be a more cost-effective and environmentally friendly alternative for the mineralization of difficult-to-degrade PFAS, such as perfluoroalkyl acids (PFAAs), either by itself or combined with physical and/or chemical techniques [2,7,8].

PFAAs are a subcategory of PFAS that only contain C-C and C-F bonds in the carbon chain tail and enter the environment through direct production or degradation of precursors. The long-chain perfluoroalkyl carboxylic acid (PFCAs) and perfluorosulfonic acids (PFSAs) with a general alkyl chain formula of C_nF_{2n+1} , ($n \geq 6$) have been a major target of global regulations [9]. In contrast, polyfluorinated compounds contain fluorine substitutions along the carbon chain and are generally more reactive because the C-H bonds act as a weak point for initiation of biotic and abiotic degradation. Since biodegradation of polyfluorinated compounds has been documented more extensively [7,8,10,11], this review focuses on the more recalcitrant PFAAs.

Our review identifies the most significant discoveries in the biodegradation of PFAAs by highlighting prominent microbes, degradation pathways, and enzymes associated with the degradation of PFAAs. We will review and discuss lines of evidence for PFAA biodegradation, including intermediate production, and compare aerobic versus anaerobic conditions to determine the current state of PFAA biodegradation by itself and in combination with physical and chemical conditions.

Microorganisms and per- and polyfluoroalkyl substances

The rarity of naturally fluorinated compounds, combined with the relatively late environmental presence of PFAS, and fluoride (F^-) toxicity, leaves microbes with an evolutionary disadvantage for PFAA degradation [12–15], which is challenging because the dense hydrophobic layer around the alkyl chain is not easily accessible to microbes [10]. Toxicity studies suggest that PFAAs can cause cell membrane disruption, morphological changes, increased extracellular polymeric substance secretion, and oxidative damage of DNA. Microbial community studies in the presence of PFAAs evince shifts towards proteobacteria abundance in the presence of carboxylic acid PFAAs, and sulfur-cycling bacteria in the presence of sulfur-containing PFAAs [7,16]. As such, microbes for biological degradation of PFAAs are typically sourced and isolated from PFAS-contaminated sites such as wastewater treatment plant biosolids, soils, and industrial sediments where positive selection for PFAA-degrading microbes occurs [15,17]. Biotransformation and removal of PFAAs by isolated strains and mixed microbial consortia have been reported.

Perfluorinated alkyl acids

Perfluorooctanoic acid (PFOA), a PFCA, and perfluorooctane sulfonic acid (PFOS), a PFSA, were

categorized as industrial persistent organic pollutants by the Stockholm Convention and listed in Annex A (elimination) and Annex B (restriction), respectively. Despite their phaseout by manufactures and elimination efforts by regulators, PFOA and PFOS remain persistent in the environment [18].

Bacterial strains associated with biodegradation of perfluoroalkyl acids

Perfluorocarboxylic acids

Recent studies provide varying degrees of evidence of PFOA biodegradation with PFOA removal, detection of transformation products, detection of F^- , and expression of relevant enzymes. Prominent examples and degradation efficiencies are included in Table 1A, Table 1C. In 2016, Yi et al. reported that *Pseudomonas parafulva* strain YAB-1 removed 48.1% PFOA over 96 h with the addition of 1 g/L of glucose to the inorganic salt culture medium [19]. A follow-up study in 2018 conducted genome shuffling to obtain a modified YAB-1 mutant (strain F3-52) that exhibited enhanced PFOA degradation, up to 58.6%, and displayed an improved tolerance to PFOA (1200 mg/L). These studies do not comment on specific mechanisms, intermediates, or F^- production [20].

Acidimicrobium sp. strain A6 (A6) was shown to co-metabolize PFOA during oxidation of ammonium under iron reduction (Feammox) in both pure and enrichment cultures. Over 100-day incubations, up to 60% removal of 100 mg/L or 0.1 mg/L PFOA was observed in an enrichment culture of A6, concomitant with buildup of shorter PFCAs, including perfluoroheptanoic acid (PFHpA), perfluorohexanoic acid (PFHxA), perfluoropentanoic acid (PFPeA), and perfluorobutanoic acid (PFBA), and an overall a good fluorine balance. PFOA removal was not observed in the abiotic controls [32]. Additional work by this group showed the formation of H-PFOA, indicating that reductive defluorination may be initiated at the alpha-carbon [33]. Notably, increased reactivity of the $-CF_2-$ group at the alpha carbon has also been observed in advanced reduction processes with hydrated electrons [3]. A6's co-metabolism of PFOA was further exemplified in PFOA-contaminated biosolids augmented with an A6 enrichment culture and ferrihydrite as an iron source. Over 150 days, removal of PFOA in excess of 50% (total, dissolved, and solid associated) and production of shorter carbon chain PFAAs and F^- were observed for incubations amended with A6 and ferrihydrite, but not for the control groups [24]. Biodegradation of PFOA with buildup of F^- and shorter PFAAs was also observed when A6 was grown in microbial electrolysis cells, where the Fe(III) is substituted for an anode as the electron acceptor [23]. Subsequent research used polyacrylic acid (PAA)-coated ferrihydrite to enhance PFOA degradation, as evinced by an increase in PFOA removal, F^- production, and buildup of short-

chain intermediates, concomitant with an increased ammonium removal. Similar to the case discussed above, this study too reported a good fluorine balance [28].

Within a lab-scale constructed wetland system, PFOA biotransformation was supported by a buildup of short-chain PFCAs, hydrogen-substituted perfluoroalkanes, and other partially fluorinated carboxylic acids. *Dechloromonas* and *Pseudomonas* were identified as possible PFAA-degrading species, and dehalogenase genes were upregulated in the constructed wetlands over time [27].

Perfluorosulfonic acids

Elevated concentrations of sulfonated substances, which include PFOS and its shorter-chained derivatives, have been found in soil, surface- and groundwater, drinking water, and biosolids in most countries. Ochoa-Herrera et al. studied the microbial toxicity and biodegradability of PFOS and concluded that PFOS was not reductively dehalogenated by the microbial consortia used in their study [34]. This conclusion was put to question when Kwon et al. reported 67% removal of 1400–1800 $\mu\text{g/L}$ PFOS by *Pseudomonas aeruginosa* strain HJ4 within 48 h. The strain was isolated from a mix of soil and activated sludge. Decrease in PFOS concentration was the primary evidence provided. Although no F^- was detected and abiotic controls were not mentioned, the intermediates perfluorobutanesulfonic acid (PFBS) and perfluorohexanesulfonic acid (PFHxS) were detected [35]. Other strains have been reported to degrade PFOS and are included in Table 1B, Table 1C.

Pseudomonas plecoglossicida strain 2.4, isolated in 2017 by Chetverikov et al., was reported to use PFOS as a carbon source. These authors report biotransformation of PFOS to perfluoroheptane accompanied by a release of F^- ions up to 150 mg/L. Total PFOS removal was 75% in 6 days; PFOS decrease was not observed in the medium control. Desulfonation was the proposed first step, supported by the presence of an ion with $m/z = 363$ amu after 3 days, identified as perfluoroheptane [50]. Most recently, Sharipov et al. isolated *Ensifer adhaerens* M1 from a fire extinguishing agent testing area. M1 biodefluorination of PFOS was observed to transform 1000 mg/L of PFOS, evinced by the formation of PFHpS and 152 mg/L of F^- [40].

Microbial consortia associated with biodegradation of perfluoroalkyl acids

PFOA and PFOS removal have also been documented in systems with microbial consortia. Microbial consortia originating from two river sediments with long-term PFOS and PFOA pollution were used to decrease PFOA by 16% with chemoorganoheterotrophic bacteria and 36% with a consortium of yeast and mold over 28 days. Their untargeted LC/MS analysis shows the production

Table 1A

PFOA biodegradation studies.

Compound	Organisms/enzymes	Removal efficiency	Degradation products/comments	Aerobic or anaerobic	Experimental conditions	Reference
PFOA	<i>Pseudomonas</i> YAB-1 (NR040859)	48.1% decrease over 96 h	Not reported	Aerobic	1 g/L glucose	Yi et al. [19]
PFOA	<i>Pseudomonas</i> YAB1 mutant F3-52	58.6% degradation	Not reported	Aerobic	Initial concentration: 1200 mg/L PFOA	Yi et al. [20]
PFOA	<i>Pseudomonas plecoglossicida</i> strain DD4	Complete removal over 96 h	Fluoride (132 mg/L), perfluoroheptane acid	Aerobic	Initial concentration: 1000 mg/L PFOA	Chetverikov and Sharipov [21]
PFOA	Activated sludge bacteria: <i>Stenotrophomonas</i> , <i>Bacillus</i> , <i>Pseudomonas</i> , and <i>Brevundimonas</i>	Removal from microbial tests showed 46.6 ± 5.7% removal, phytoremediation showed 49.0 ± 7.2% removal, synergistic system showed 69.3 ± 5% removal over 700 min	PFHpA and PFHxA were detected in the synergistic condition but not in the individual photocatalytic or biological conditions.	Aerobic	Combination of photocatalysis and aerobic biological remediation under low PFOA (500 ppb) conditions. PFAA removal was compared between pure sorption, biological remediation, photocatalysis, and synergistic systems. Synergistic systems had the highest removal rate. A6 as electron acceptor, NH ₄ ⁺ as electron donor	Ding et al. [22]
PFOA	<i>Acidimicrobium</i> sp. strain A6, microbial electrolysis cells	77% decrease with A6 highly enriched culture; 48.1% decrease in A6 enrichment culture	Fluoride, PFHpA, PFHxA, PFPeA, PFBA	Anaerobic		Ruiz Urigüen et al. [23]
PFOA	<i>Acidimicrobium</i> sp. strain A6, biosolids	37-68% decrease of PFOA over 150-day biosolid incubations (WAS, AS, and FC)	Fluoride (0.31-0.37 mg/L for 10 mg/L PFOA; 0.023-0.099 mg/L for 0.2 mg/L PFOA) and buildup of shorter-chain PFCAs (PFHxA, PFHpA)	Anaerobic	Augmentation with A6 and/or ferrihydrite, autoclaved controls included, waste-activated sludge, activated sludge, and filter cake	Huang et al. [24]
PFOA	Haloacid dehalogenase enzyme (DeHa I) from <i>Deiflia acidovorans</i> engineered for expression in <i>E. Coli</i>	Not reported, fluoride produced after 4 h	Fluoride (~1.25 µM for <i>E. Coli</i> with DeHa I)	Aerobic	Initial concentration: 100 ppm; PFOA used as energy source for <i>D. Acidovorans</i>	Harris et al. [25]
PFOA	Bacterial consortium from anaerobic digestion	Biochemical degradation of 20.4-38% of the initial PFOA	Not reported	Anaerobic	Higher biodegradation observed with higher PFOA concentration, up to 3 mg/L PFOA used	Xie et al. [26]
PFOA	Microbial consortia in constructed wetland, including <i>Pseudomonas</i> and <i>Dechloromonas</i>	PFOA removal observed	Short chain PFCAs, perfluoroalkyl alcohols/aldehyde, unsaturated/saturated organic fluorine, fluoride not detected	Aerobic	Initial concentration: 100-1000 µg/L, T = 25°C; proposed mechanism: decarboxylation, hydroxylation, hydrolysis, dehydrogenation, and dehalogenation	Xiao et al. [27]
PFOA	<i>Acidimicrobium</i> sp. strain A6, with PAA-coated ferrihydrite	Enhanced PFOA removal over 40 days with PAA (6 K and 450 K) coated ferrihydrite compared to control with bare ferrihydrite	Fluoride, PFHpA, PFHxA, PFPeA, PFBA	Anaerobic	Initial concentration: 1 mg/L PFOA; fluoride production reported highest for 450 K-coated ferrihydrite (~0.005 mM at end of incubations)	Park et al. [28]
PFCAs (C7-C10)	<i>Pseudomonas mosselii</i> with possible genes for haloalkane			Aerobic	PFCAs as sole source of carbon, proposed mechanisms:	Chetverikov et al. [29]

Table 1A (continued)

Compound	Organisms/enzymes	Removal efficiency	Degradation products/comments	Aerobic or anaerobic	Experimental conditions	Reference
	dehalogenase gene (<i>dhaA</i>), haloacetate dehalogenase H-1 gene (<i>dehH1</i>), fluoride ion transporter (<i>crcB</i>) and alkane sulfonate monooxygenase gene (<i>ssuE</i>)	Removal of PFDA, PFNA, PFOA, PFHpA, and PFOS over 7 days	Fluoride, PFHpA, PFHxA as major product for all compound, PFHxS, PFHxS		decarboxylation, desulfonation, reductive defluorination at the alpha-carbon of PFOS followed by shortening of carbon chain	
PFMeUPA (unsaturated C6 perfluoro-4-methylpent-2-enoic acid)	Acetobacterium species with functional fluoride efflux pump (<i>crcB</i>) and electron bifurcating caffeate reduction pathway (CarABCD E)	Removal of PFMeUPA over 3 weeks	Intracellular defluorination at the α -carbon yielded defluorination intermediates	Anaerobic	Initial concentration: 100 μ M PFMeUPA, bacteria grown on fructose	Yu et al. [30]
PFOA, TFA	Bacterial consortium with anaerobic bacteria, proteobacteria and bacteroidetes	13.52% removal of PFOA, 8.03% removal of TFA	Fluoride production, PFHxA, PFHpA, TFA, and pentafluoropropionic acid	Anaerobic	Initial concentration: 5 mg/L PFOA or 10 mg/L TFA; fluoride production not observed in sterilized control for blank; 10-month incubations	Tang et al. [31]

of monofluorinated fatty acids that were not present in the control. The study posits that fluorination of the microbial fatty acids stabilizes the fluorine [43].

In 2023, Tang et al. investigated the biodegradability of PFOA and trifluoroacetate (TFA) using aquifer solids from a fluorochemical plant under anaerobic conditions. They showed 13.52% biological removal of 5 mg/L PFOA accompanied by 0.119 mg/L of F^- production, PFHxA, and PFHpA in 10-month incubations. For TFA, they observed 8.03% removal of 10 mg/L TFA with 0.166 mg/L of F^- production over the 10-month incubation period. No F^- production was detected in the sterilized control or the active blank with no PFAS added. For the PFOA incubations, TFA and pentafluoropropionic acid were detected in the biodegradation groups. They posit that decarboxylation, followed by hydrolytic elimination and H/F exchange, is responsible for the observed intermediates. The most prominent phyla present in the incubations with TFA and PFOA were Proteobacteria and Bacteroidetes [31].

Another investigation of PFOA removal in anaerobic digestion by Xie et al. attributed 36.1–61.2% of PFOA removal to sludge adsorption and 10.4–28.2% to biological degradation [26]. Among the mentioned studies using microbial consortia, the strongest lines of evidence come from reports of transformation products, fluorine balances, and PFAA removal. Thus far, results presented in the study by Tang et al. and Huang et al. provide the most thorough evidence of PFAA degradation by microbial consortia, namely PFAA concentration decrease coupled with F^- production and degradation product formation [31,33].

PFAA degradation experiments with an anaerobic microbial consortia, WBC-2, in the presence of chlorinated volatile organic compounds (cVOCs) indicate that 46.4% PFOA removal was attained over 45-day incubations. Sulfate reducer abundance increased, and a buildup of PFHxS, PFFeS, and PFBA was observed. This study posits that PFOS degradation was initiated by desulfonation followed by sequential reductive defluorination to produce short-chain PFSAAs [49]. Fluoride production was not reported.

Synergetic combined systems for the biodegradation of perfluoroalkyl acids

Given the challenge of PFAA biodegradation, researchers have also focused on combining physical and chemical technologies with biological systems to initiate defluorination to make the partially fluorinated compounds more susceptible to degradation by microorganisms capable of degrading polyfluorinated compounds. Although not the focus of this review,

Table 1B

PFSA biodegradation studies.

Compound	Organisms/enzymes	Removal efficiency	Degradation products/comments	Aerobic or anaerobic	Experimental conditions	Reference
PFOS	<i>Pseudomonas aeruginosa</i> strain HJ4	67% removal of 1400-1800 µg/L PFOS within 48 h; PFBS and PFHxS detected	No fluoride detected	Aerobic	T = 30-37°C, pH 7-9, abiotic controls not mentioned	Kwon et al. [35]
PFOS	<i>Pseudomonas plecoglossicida</i> 2.4-D	75% removal in 6 days	Fluoride (up to 150 mg/L), perfluoroheptane	Aerobic	Initial concentration: 1 g/L PFOS, T = 26-30°C, pH 6.8-7.2, NaCl concentration within 5%, proposed mechanism: desulfonation, PFOS used as carbon source, no PFOS decrease in medium control	Chetverikov et al. [36]
PFOS	Marine, Gammaproteobacteria and Roseobacter, Flavobacteria	<i>In situ</i> PFOS decreased by 31% over 6 days. 85% decrease in PFOS when PFOS and PFOA present. No PFOA removal was observed	No defluorination was observed, sulfate reducer bacteria and enzymes were prominent and the formation of perfluorooctanol was postulated but not observed	Aerobic	Experiments performed using Antarctic water both with in situ concentrations and spiked concentrations of PFOA and PFOS in a 1:0.6 ratio, respectively, proposed mechanism: desulfonation supported by increase in sox genes, sulfate monooxygenase, DMSP-related genes, and sulfohydrolases.	Cerro-Galvez et al. [37]
PFHxS	<i>Pseudomonas</i> species (PS27 & PFMF10)	24% removal by PS27 and 15% removal by PFMF10, 5-day incubations	Not reported	Aerobic	Proposed mechanism: bioaccumulation, PFHxS did not serve as carbon or energy source, maximum bioaccumulation occurred in the presence of an ethanol-octane mixture	Presentato et al. [38]
PFOS	<i>Ensifer Moralensis</i> H16 (gram negative, aerobic rods)	88% PFOS removal	Fluoride (removal of 4 F- ions per PFOS molecule), PFHps	Aerobic	Initial concentration: 1000 mg/L, PFOS used as sole carbon source, batch fermentation, T = 28°C, pH 6.8-7.2, proposed mechanism: monooxygenase elimination of sulfonate group	Chetverikov and Hkudaigulov [39]
PFOS	<i>Ensifer adahaerens</i> M1	Complete removal	Fluoride (152 mg/L), PFHps	Aerobic	Initial concentration: 1000 mg/L PFOS, 140 h incubations, proposed mechanism: monooxygenase elimination of sulfonate	Sharipov et al. [40]
PFOS	Anaerobic microbial consortia	24% PFOS removal over 10 days	2,2,3,3,4,4,5,5,5-nonafluoropentanol	Anaerobic	Initial concentration: 1000 µg/L PFOS, T = 35°C, pH 6 m cometabolism was observed with simulated sewage as a co-substrate	de S. Furtado et al. [41]
PFOS	Bacterial consortium with <i>Paracoccus</i> , <i>Hyphomicrobium</i> , and <i>Micromonosporaceae</i> from activated sludge enclosed in capsules	70% PFOS reduction, 6-week incubations	PFBS, 3,3,3-trifluoropropionic acid	Aerobic	Microbial membrane capsule increased biological degradation, bacterial consortia from activated sludge, initial PFAS concentration: 2 mg/L	Sorn et al. [42]

Table 1C

Multiple PFAA biodegradation studies.

Compound	Organisms/enzymes	Removal efficiency	Degradation products/ comments	Aerobic or anaerobic	Experimental conditions	Reference
PFOA, PFOS	Chemoorganoheterotrophic bacteria AND consortia of yeast and mold	16% decrease for bacteria; 36% removal with consortia of yeast and molds over 28 days	Monofluorinated fatty acid, fluoride not detected	Aerobic	Initial concentration: 1 µg/mL	Beškoski et al. [43]
PFOA, PFOS	<i>Acidimicrobium</i> sp. strain A6	60% removal over 100 days	Fluoride, shorter PFCAs (PFBA, PFPeA, PFHxA, and PFHpA)	Anaerobic	Initial concentration: 100 mg/L PFOA, 100 mg/L PFOS, reductive defluorination, pH 4.5	Huang and Jaffé [32]
PFOA, PFOS	Activated Sludge Reactor at Laboratory Scale	21–42%, removal for PFOA; 15–27% removal for PFOS over 24 h	Not reported	Aerobic	Initial concentrations: 100–500 ng/ L PFAAs, biodegradation observed after adsorption of PFAAs	Chiavola et al. [44]
PFOA, PFOS	<i>Ensifer adhaerens</i> strain M1	Degradation of PFOS completed in 6 days, degradation of PFOA in 4 days	PFHpA and fluoride	Aerobic	Bacteria from fire-fighting foams contaminated soil, used PFOA and PFOS as sole carbon source and energy, decarboxylation and desulfonation, T = 26–28°C.	Chetverikov and Loginov [45]
PFOA, PFOS	<i>Phaenerochaete chrysosporium</i> (fungi) with possible genes for laccase, lignin peroxidation, and manganese peroxidase	69.23% removal in 35 days	Partially fluorinated aldehydes, alcohols, and aromatic rings	Aerobic	Proposed mechanism: decarboxylation and rearrangement of short-chain fluorinated free radicals	Zhou et al. [46]
PFOS, TFA	Bacterial consortia from anaerobic granular sludge and anaerobic digester sewage sludge	Unsuccessful, incubation run for 3.4 years	Not detected	Aerobic and anaerobic tested	PFAAs not reductively dehalogenated, initial PFAS concentration: 200 mg/L	Ochoa-Herrera et al. [34]
PFOA, PFOS	<i>Pseudomonas aeruginosa</i> , <i>Pseudomonas putida</i>	27.9% removal PFOS and 47.3% removal PFOS (<i>P. aeruginosa</i>), 19.0% PFOA removal and 46.9% PFOS removal (<i>P. putida</i>) over 96- hour incubation	PFOA degradation products: PFHxA with <i>P. aeruginosa</i> ; PFPeA, PFHxA, PFHpA with <i>P. putida</i> ; PFHxA and PFHpA from both strains for PFOS degradation	Aerobic	Initial concentration 10, 1, or 0.1 mg/L, proposed mechanisms: desulfonation for PFOS, removal of CF2 groups for PFOA	Chiriac et al. [47]
PFOA, PFOS	Iron cycling microbial consortia in constructed wetland, primarily <i>Proteobacteria</i>	Percent removal due to biodegradation not specified	Not reported	Anaerobic	Microbes and enzymes related to electron transfer during iron cycling increased; carbohydrate metabolism and acetate decarboxylation were linked to PFOA and PFOS degradation.	Kang et al. [48]
PFOA, PFOS	Microbial consortia in constructed wetland, primarily <i>Proteobacteria</i> , <i>Firmicutes</i> , <i>Bacteroidetes</i> , <i>Planctomycetes</i> , <i>Chloroflexi</i> , and <i>Actinobacteria</i>	Percent removal due to biodegradation not specified	Not reported	Aerobic and Anaerobic	Conclude iron minerals (magnetite and siderite) promote electron transfer that enhances PFAS removal by microorganisms	Ma et al. [21]

Table 1C (continued)

Compound	Organisms/enzymes	Removal efficiency	Degradation products/ comments	Aerobic or anaerobic	Experimental conditions	Reference
PFOA, PFOS	Dehalogenating culture WBC-2 and native microbes from AFFF-contaminated site	46.4% PFOS removal over 45 days	PFHxS, PFPeS, and PFBS; fluoride not measured	Anaerobic	Initial concentrations: 100 µg/L PFOS, 50 Mg/L PFOA, T = 22-23°C, pH= 7, 5 mM lactate, incubations with chlorinated volatile organic compound co-contaminants, Desulfosporosinus (Firmicutes) and Sulfurospirillum (Campilobacterota) increased with PFOS decrease, suggesting desulfonation.	Lorah et al. [49]
TFA, trifluoroacetate.						

Table 1D provides examples of these synergetic combined systems [51,52].

Enzymes/genes associated with biodegradation of perfluoroalkyl acids

Specific microbial machinery is necessary for PFAA degradation, including mechanisms for PFAS transfer across the cell membrane, PFAS degrading enzymes, and fluoride detoxification [15]. Some key enzymes have been linked to PFAA biodegradation. Studies with fungi and cyanobacterium have pointed to laccase, lignin peroxidation, and fluoroacetate dehalogenase enzymes [57,55,53,58], but removal by laccase has been debated; some studies suggest that adsorption in laccase mediator systems mimic substrate loss [59]. In terms of bacterial enzymes, examples are included in Table 1D. Harris et al. showed that *Delftia acidovorans*, an aerobic bacterium found in PFAS-contaminated soil, was able to grow with PFOA as the sole carbon source. They engineered a haloacid dehalogenase enzyme from this organism for expression in *Escherichia coli* (*E. Coli*). When *E. Coli* contained the engineered dehalogenase plasmid and was grown in 100 ppm PFOA-spiked media, F⁻ release was observed [25].

Genes encoding a reductive dehalogenase homolog (*RdhA*), a fluoroacetate dehalogenase homolog (*FceA*), two putative haloacid dehalogenases (*dhl_1* and *dhl_2*), and two putative F⁻ pumps (*CrcB*) were identified in the genome of *Acidimicrobium* sp. strain A6. Expression of the *rdhA* gene had a significant correlation to F⁻ production and PFAA removal over the incubation period, while expression of *dhl_1* and *dhl_2* was related to dechlorination and did not change in the presence of PFAAs. The *CrcB* enzyme is expected to play a crucial role in removing F⁻ from inside the cell, thus mitigating the toxic building of F⁻. Gene knockout experiments further confirmed that the enzyme encoded by the *rdhA* gene plays a key role in the defluorination of PFAAs by A6, while the *FceA* gene may just be co-expressed and plays no direct role in the PFAA defluorination [60].

Chetverikov et al. investigated the biodegradation of C7-C10 PFCAs by *Pseudomonas mosselii*. The *Pseudomonas* strain grew on mineral media with PFCAs as the sole carbon sources. Over the course of one week, the concentration of PFHpA, PFOA, perfluorononanoic acid (PFNA), and perfluorodecanoic acid (PFDA) decreased, and PFHxA was observed as the predominant degradation product accompanied by F⁻ production. This study also found reduction defluorination at the α-carbon for PFOS, which they attributed to the haloacetate dehalogenase H-1. The dehalogenation was followed by carbon-carbon bond elimination that resulted in buildup of PFHpS. This cycle continued to produce PFHxS after 4 days. Subsequently, they posit that an alkane

Table 1D

Enzymes and synergistic systems studies.

Compound	Organisms/enzymes	Removal efficiency	Degradation products/comments	Aerobic or anaerobic	Experimental conditions	Reference
PFOA	Enzyme catalyzed oxidative humification reactions (ECOHFRs) with soybean mediator	In water 24% removal in 36 days; in soil slurry 40% removal in 150 days	Detected partially fluorinated organic compounds	Aerobic	Proposed mechanism: free radical chain reactions identified as main mechanism	Luo et al. [53]
PFOS, PFOA	Enzyme catalyzed oxidative humification reactions (ECOHFRs)	Up to 30% removal under different ECHOR enzyme and mediator dosage in the presence of Laccase and 4-methoxy-phenol	Not reported	Anaerobic	Initial concentration: 1-30 µM PFOA	Huang et al. [54]
PFOA	<i>Synechocystis</i> sp. PCC 6803 (cyanobacterium) with possible genes for laccase, fluoroacetate dehalogenase, sodium symporters, ABCs associated proteins, fatty acid CoA ligases, and aquaporins identified as potential PFOS gateway	37% removal PFOA at 0.36 mg/L/d; 88% removal PFOS at 0.15 mg/L/d	No detected	Aerobic	Aerobic continuous batch reactor with 1 mg/L PFOA or PFOS supplied	Marchetto et al. [55]
PFOA, PFOS	Synergistic diatom (<i>Chaetoceros muelleri</i>) and iron nanoparticle system	Defluorinated up to 93% PFOA and 89% PFOS in 24 h	intermediates were produced such as PFPA and PFPrA	Aerobic	Synergistic diatom (<i>Chaetoceros muelleri</i>) and iron nanoparticle system in which the ROS produced by the diatoms are used to stimulate the Fenton reaction and defluorinate PFAAs	Albert et al. [51]
PFOA and PFOS	Prominent bacteria on the biofilm were <i>Cupriavidus</i> (7%–49%), <i>Mesorhizobium</i> (1%–9%), and <i>Dokdonella</i> (1%–8%)	97% PFOA and PFOS removal in 50–70 h	Defluorinated PFOS with 1-9 fluorines replaced with Hydrogen atoms after MCfR treatment and various intermediate carbon chain PFOS from C2 to C6 PFOS intermediates after MBfR treatment	Aerobic	Paired Pd-based bimetallic catalyst membrane biofilm reactors in series with the effluent of a H ₂ -based membrane catalyst-film reactor (MCfR) acting as the influent of a O ₂ -based membrane biofilm reactor (MBfR). The reactor shows that MCfR resulted in defluorination while MBfR resulted in a shortening of the carbon chain	Rittman et al. [52]
PFOA	Microbial consortia in dual biocatalyzed microbial electrosynthesis system, <i>Methanosarcina</i> and <i>Petrimonas</i> were enriched	91% removal (1 ppm), 85% removal (5 ppm), and 76% removal (10 ppm) in 120 h	Propionic acid, short-chain PFCAs, acetate were produced and then disappeared	Anaerobic	Initial concentration: 1, 5, and 10 ppm, T = 35°C, proposed mechanisms: decarboxylation, H/F exchange, chain shortening, radical formation	Tahir et al. [56]

sulfonate monooxygenase cleaved the C-S bond to release SO_3^- to form PFHxA by day 7. They point to a haloalkane dehalogenase gene (*dhaA*) and haloacetate dehalogenase H-1 gene (*dehH1*) for defluorination, a F^- ion transporter gene (*crcB*) for F^- export out of the cell, and alkane sulfonate monooxygenase gene (*ssuE*) for desulfonation. This study concludes that these genes may be important for PFAA defluorination in their system [29]. Another study with an *Acetobacterium* species exhibited reductive defluorination via an α, β -unsaturated perfluorocarboxylic acids. In this experiment the bacterium also utilized a fluoride efflux transporter (*crcB*) [30].

Discussion

Various lines of evidence have been provided for PFAA biodegradation under both aerobic and anaerobic conditions, ranging from a decrease in PFAA concentration to PFAA decrease accompanied by the detection of F^- and other degradation products (e.g. shorter PFAAs), which gives more confidence that the decrease in concentration is due to biodegradation. For environmental samples, proper controls must be included to ensure that these products are not from the degradation of other PFAS that might be present in these samples.

So far, isolated bacterial phyla showing the most promise of PFAA biodegradation include *Pseudomonas*, *Ensifer*, and *Acidimicrobium*, all of which show significant PFAS removal backed by the production of F^- and PFAA intermediates [20,50,60,29]. Studies with anaerobes typically involve a consortium of anaerobic bacteria, except for *Acidimicrobium* sp. strain A6, although, for this strain too, a higher activity and overall PFAA degradation is observed when it is grown in enrichment cultures [32]. Among the degradation products identified, shorter-chain PFCAs and PFSAAs are commonly reported. The most prominent mechanisms of PFAA degradation are decarboxylation, desulfonation, and stepwise defluorination along the alkyl chain. Although fluorine balances are challenging for PFOS degradation studies, in part due to possible analytical interferences, detection limits, and possible formation of complexes [33], the detection of F^- production is a valuable indicator of defluorination.

Enzymes identified as key players in the PFAA degradation are typically of the dehalogenase category and include reductive dehalogenase (*rdhA*), haloalkane dehalogenase (*dhaA*), and haloacetate dehalogenase H-1 (*dehH1*) enzymes [25,33]. Finally, a key aspect of PFAS degradation, in general, is the removal of toxic by-products, especially F^- , from the cell [12,13,61]. Examples include F^- exporters or stabilization via incorporation into cellular components [43]. Both Jaffé

et al. and Chetverikov et al. have identified specific F^- ion transporter genes responsible for removing the toxic F^- ions from the cells of the bacteria degrading PFAAs [43,60,29].

To date, researchers have established links between PFAA biodegradation, specific bacterial communities and/or organisms, and specific gene expression for both aerobic and anaerobic conditions. Although some experiments have been conducted with natural sediments or sludges, the papers reviewed discuss laboratory experiments. Little to no research has been reported on PFAA biodegradation in the natural environment or at contaminated sites. This review indicates that there is still a large knowledge gap in our understanding of PFAA biodegradation mechanisms, identification, and characterization of relevant enzymes, the applicability of laboratory findings to field conditions, and potential applications for bioremediation.

CRediT authorship contribution statement

Chiara M Smorada: Investigation, Writing – original draft, Visualization. Matthew W Sima: Investigation, Assisting in writing. Peter R Jaffe: Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Summarizes findings of *Acidimicrobium* sp. strain A6 PFAA degradation, gene expression, and avenues for application.