FEMS Microbiology Ecology, 2022, 98, 1–18
DOI: 10.1093/femsec/fiac081
Advance access publication date: 9 July 2022
Minireview

Effect of temperature on microbial reductive dehalogenation of chlorinated ethenes: a review

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One sentence summary: Temperature changes affect microbial dechlorination of chlorinated ethenes to a greater extent compared to competing and synergistic microbial processes such as fermentation, methanogenesis and sulfate reduction, however, data gaps prevent final conclusions.

Editor: Marcus Horn

Abstract

Temperature is a key factor affecting microbial activity and ecology. An increase in temperature generally increases rates of microbial processes up to a certain threshold, above which rates decline rapidly. In the subsurface, temperature of groundwater is usually stable and related to the annual average temperature at the surface. However, anthropogenic activities related to the use of the subsurface, e.g. for thermal heat management, foremost heat storage, will affect the temperature of groundwater locally. This minireview intends to summarize the current knowledge on reductive dehalogenation activities of the chlorinated ethenes, common urban groundwater contaminants, at different temperatures. This includes an overview of activity and dehalogenation extent at different temperatures in laboratory isolates and enrichment cultures, the effect of shifts in temperature in micro- and mesocosm studies as well as observed biotransformation at different natural and induced temperatures at contaminated field sites. Furthermore, we address indirect effects on biotransformation, e.g. changes in fermentation, methanogenesis, and sulfate reduction as competing or synergetic microbial processes. Finally, we address the current gaps in knowledge regarding bioremediation of chlorinated ethenes, microbial community shifts, and bottlenecks for active combination with thermal energy storage, and necessities for bioaugmentation and/or natural repopulations after exposure to high temperature.

Keywords: organohalide respiration, reductive dechlorination, chlorinated ethenes, temperature, groundwater contamination

Introduction

Organohalides comprise a diverse group of chemicals, which are used in various industries globally. However, its widespread industrial application also serves as an entry point into the environment. In fact, organohalides such as chlorinated solvents are amongst the main contaminant groups that are commonly occurring in the urban groundwater environment; the majority of these are derived from anthropogenic sources (Rittmann et al. 2000). Some of them can be highly persistent and toxic and are, therefore, listed as priority groundwater contaminants in the European Union and the USA (https://www.epa.gov/dwreginfo/chemical-contaminant-rules) or in the Stockholm Convention on Persistent Organic Pollutants (Kalnins et al. 2019).

Chlorinated ethenes (CE), such as tetrachloroethene (PCE), trichloroethene (TCE), and the partially dechlorinated metabolites dichloroethene isomers (DCE), and vinyl chloride (VC) are of a major concern mainly due to their frequent occurrence in the environment (Squillace 2004, Carter 2008, Weatherill et al. 2014). While PCE and TCE originate from anthropogenic sources, *cis*-DCE and VC tend to be associated with biotic transformation *in situ* (Hartmans 1985, Vogel and McCarty 1985, Nijenhuis et al. 2007). Although PCE and TCE are used in a variety of industrial and commercial applications, such as industrial solvents or degreasing agents, improper usage or disposal resulting in accidental spillage or leakages are notably amongst the main sources of these contaminants into the subsurface (Bishop 1993).

Groundwater contaminations including organohalides and urban areas usually overlap due to urban-related industrial activities (Rivett et al. 2012). Hence, mitigation strategies must be incorporated within the scope of the subsurface urban groundwater management. PCE and TCE form dense nonaqueous phase liquids and tend to sink, and migrate through the permeable aquifers before reaching a nonpermeable zone, resulting in plumes that are usually long due to the low abiotic and biotic degradation rates (OSWER Directive 1999, Fiedler and Gilbert 2013). Given the persistence of PCE, TCE, as well as DCE, and VC in the environment and their toxicity to human health, ensuring the complete conversion of these CE to the relatively harmless ethene or mineralization to CO_2 is paramount (National Research Council 2000, Huang et al. 2014).

Natural attenuation (NA) is one common mitigation strategy for organic groundwater contaminants (OSWER Directive 1999). Both abiotic and biotic transformations of CE depend on a multitude of factors such pH, temperature, and presence of electron donors/acceptors that can mediate or hamper dechlorination (Zhuang and Pavlostathis 1995, Lai and Lo 2007, Shapiro 2017). Although NA can proceed abiotically, such reactions tend to be limited and usually occur alongside biotransformation by dechlorinating bacteria (Wiedemeier et al. 1998, Dolinova et al. 2017). For organohalides, which include PCE and TCE, organohalide respiration is the main mode of biotransformation in anoxic environments (Adrian and Löffler 2016, Dolinova et al. 2017). CE are

Received: January 27, 2022. **Revised:** June 30, 2022. **Accepted:** July 7, 2022

used as an electron acceptor with hydrogen as electron donor provided by fermentation of substrates such as lactate and pyruvate, or direct oxidation of low-weight organic compounds (Schink and Stams 2006, Fiedler and Gilbert 2013). Anaerobic transformation of PCE and TCE generally progresses via sequential dechlorination to *cis*-DCE, one of the three isomers of DCE (*trans*-DCE and 1,1-dichloroethene are less common intermediates) and further dechlorination to VC before yielding ethene (Fig. 1; OSWER Directive 1999). Overall, more bacterial species are known to be capable of utilizing PCE and TCE as electron acceptors generating the end product DCE when compared with those that are capable of transforming DCE or VC (Fig. 1 and Table 1; Table S1, Supporting Information; Dolinova et al. 2017). Probably as a consequence of the low cell number and diversity of species possessing genes, which confer the ability to dechlorinate DCE or VC, or unsuitable environmental conditions for the biochemical reaction, these compounds are typically accumulated at sites with PCE and TCE contamination (Fiedler and Gilbert 2013, Dolinova et al. 2017). Meanwhile to date, only a few bacterial strains belonging to the genera *Dehalococcoides* (i.e. *Dehalococcoides mccartyi*) and '*Candidatus* Dehalogenimonas etheniformans' are known to dechlorinate PCE or TCE completely to ethene while others are only capable of partially dechlorinating PCE or TCE to either DCE or VC (Tables S1, Supporting Information).

Temperature is one of the crucial factors affecting microbial activity and ecology in the environment (Dettmer 2002, Fiedler and Gilbert 2013, Jesußek et al. 2013, Shapiro 2017), and temperature changes may affect rates of other processes e.g. nitrogen and carbon cycling significantly (Hantschel et al. 1995, Yvon-Durocher et al. 2010, Jung et al. 2011). Temperature can also influence rates of other processes such as fermentation or acetogenesis, which can indirectly support dechlorination by supplying electron donors (e.g. hydrogen) or carbon sources (e.g. acetate). On the contrary, temperature can enhance growth of microorganisms within the community, which compete with dechlorinating bacteria for the same electron donors and carbon sources, examples being methanogens or sulfate reducers (Smatlak 1996, Chambon et al. 2013, Wei et al. 2016). In general, there are limitations to which increasing temperatures can affect rates of biochemical reactions. Rates of processes driven by microbes are highest within a certain temperature range at the temperature optimum, beyond which rates usually rapidly decline (Mohr and Krawiec 1980, Huang et al. 2011). Once a threshold temperature is exceeded, irreversible damage can occur to cell components such as proteins and cell membranes resulting in the ceasing of activity. Similarly, below a certain temperature, activities will decrease significantly and stop (Mohr and Krawiec 1980, Huang et al. 2011).

Microbial growth and activity temperatures are characteristic for each microorganism, and microorganisms and microbial communities are able to tolerate temperature changes to a certain extent (Madigan et al. 2018). Typically, the growth range for psychrophiles, mesophiles, thermophiles, and hyperthermophiles can be roughly defined as 0–20°C, 8–48°C, 40–70°C, and 65–90°C, respectively (Madigan et al. 2018) and these microorganisms are usually adapted to temperature ranges of their habitat. However, some taxonomic groups within the Gram-positive bacteria develop spores resistant to extreme hot or cold temperatures, allowing them to survive long periods at unfavorable temperature conditions. Owing to the fact that most enrichment cultures and isolates have been obtained using material from 'mesophilic' habitats, most described cultures are actually mesophiles. While there have been attempts to establish dechlorinating cultures from materials from hot and cold environments these were mainly unsuccessful and are not in published literature (see section 'Effect of temperature on microbial reductive dehalogenation by microbial communities at laboratory and field conditions').

In general, the temperature of groundwater is stable and correlated to a given depth, becoming constantly higher in direction of the earth center (Goldscheider et al. 2006, Griebler and Lueders 2009); groundwater temperatures may only fluctuate annually in a relatively narrow range in shallow aquifers depending on factors such as annual seasonal average temperature changes at the surface and aquifer recharge (Benz et al. 2017, Moeck et al. 2020). It has also been observed to respond, albeit with some delay and at a small degree, to climate change (Menberg 2014, Menberg et al. 2014, Benz et al. 2017, Previati and Crosta 2021). Notably, other anthropogenic activities, including inputs from local heat sources (e.g. subways; Menberg et al. 2013), or the use of the subsurface, e.g. for thermal energy storage (Fleuchaus et al. 2018), can affect the temperature of groundwater locally in larger magnitudes. Currently, two main types of underground thermal energy storage systems (UTES) are implemented for heating and cooling of buildings (Fleuchaus et al. 2018): borehole thermal energy storage (BTES), where heat or cold is extracted from a volume of rock or soil, and aquifer thermal energy storage (ATES), from which heat or cold is extracted from groundwater whilst being pumped from one well to another (Fleuchaus et al. 2018, 2020). For ATES, national regulations require a balance in temperature over a certain period and limit the upper and lower temperatures of groundwater injected, e.g. between 5 and 25°C, however, other systems such as High Temperature ATES (HT-ATES), which introduce temperatures above 50°C do exist (Fleuchaus et al. 2018, 2020, Todorov et al. 2020).

Currently, there is a demand for application of ATES in urban areas, e.g. in redeveloped former brown field sites, which can be contaminated where this increased use of the subsurface for areas to fulfill high energy storage demands can overlap with organohalides-contaminated groundwater. For CE bioremediation, temperatures exceeding a certain maximum (~ 45°C) may halt or disrupt biotransformation resulting in accumulation of the toxic parent compounds PCE/TCE or its dechlorination reduction intermediates, DCE or VC. On the other hand, higher temperatures may trigger other effects such as increased rates of volatilization or abiotic CE degradation by reaction with iron compounds such as pyrite (FeS_2) or zero-valent iron (Costanza and Pennell 2007, Lai and Lo 2007, O'Carroll et al. 2013, Badin et al. 2016, Schaefer et al. 2017, Koproch et al. 2019). Since increasing temperatures in the subsurface are mainly due to anthropogenic activities (Menberg 2014), there is a need to revisit the current status of temperature-related research pertaining to the isolates, enrichment cultures, and *in situ* field sites experiments to allow conclusions on the effect of temperature on microbial dehalogenation and subsequent management of these temperature impacted contaminated sites.

In this review, we aim to summarize the current knowledge of the temperature range of microbial reductive CE dechlorination, compiling data for dechlorinating bacterial isolates (Table 1; Table S1, Supporting Information), microbial consortia, column studies, as well as field sites (Table S2, Supporting Information). We derived general upper and lower temperature limits for reductive CE dechlorination from the published studies, for both the direct dechlorination reaction as well as for processes indirectly affecting dechlorination. Finally, we outline research gaps and questions that need to be addressed for a better understanding on the effects

Table 1. Overview of optimal temperatures and temperature ranges for growth or activity of isolates and selected enrichment cultures capable of reductive dehalogenation of CE. For more information and details see Table S1 (Supporting Information). References for the corresponding strains/isolates are available in the Supporting Information (N.A. not available).

Microorganisms/culture	Strains	Temperature range	Final dechlorination products	References
Chloroflexota: *Dehalobium, Dehalogenimonas*, and *Dehalococcoides*				
'Dehalobium chlorocoercia'	DF-1	10–35°C	PCE → *trans*-DCE + *cis*-DCE	Wu et al. (2000, b, 2002a), Miller et al. (2005), Kittelmann and Friedrich (2008), May et al. (2008), May and Sowers (2016)
Dehalogenimonas	'*Candidatus* Dehalogenimonas etheniformans' *strain GP*	20–30°C	TCE → ethene	Yang et al. (2017b)
	Dehalogenimonas sp. strain WBC-2	RT	*trans*-DCE → VC	Jones et al. (2006), Manchester et al. (2012), Molenda et al. (2016)
Dehalococcoides mccartyi	195, BTF08, CBDB1, BAV1, VS, FL2, GT, MB, ANAS1, ANAS2, 11a, 11a5, DCMB5, CG1, CG4, CG5, 11G, CG3, SG1, GEO12, NIT01, IBARAKI, GY50, UCH007	15–35°C	PCE / TCE → ethene; some partial to *cis*-/*trans*-DCE or VC	Maymo-Gatell et al. (1997), Adrian et al. (2000), Richardson et al. (2002), Cupples et al. (2003), He et al. (2003, 2005), Muller et al. (2004), Sung et al. (2006a), Bunge et al. (2008), Cheng and He (2009), Cheng et al. (2010), Cichocka et al. (2010), Lee et al. (2011, 2013), Löffler et al. (2013), Wang et al. (2014b, 2019), Uchino et al. (2015), Yohda et al. (2015), Adrian and Löffler (2016), Ding et al. (2017, 2020), Ismaeil et al. (2017), Zhao and He (2019), Yan et al. (2021), Asai et al. (2022)
Bacillota: *Dehalobacter, Acetobacterium*, and *Desulfitobacterium*				
Dehalobacter	*Dehalobacter restrictus* PER-K23^T, TEA	10–37°C	PCE/TCE → *cis*-DCE	Holliger et al. (1993,1998), Wild et al. (1996), Nelson et al. (2014)
	Dehalobacter sp. strains 12DCB1, 13DCB1, TCP1	25–30°C	PCE → TCE; main product of strain 12DCB1 + *cis*-DCE	Nelson et al. (2011, 2014), Wang et al. (2014a)
Acetobacterium	WB1	30°C	PCE → TCE	Balch et al. (1977), Egli et al. (1988), Damborský (1999)
Desulfitobacterium	*Dsb. hafniense* strains DCB-2^T, PCE-S, TCE-1, TCP-A, Y51, G2, JH1 *Dsb. dehalogenans* strains PCE-1, JW/IU-DC1 *Dsb. metallireducens* strain 853-15A^T *Dsb.* sp. strains B31e3, KBC1, PR, Viet-1, PCP-1	13–45°C	PCE → DCE; some to TCE	Madsen and Licht (1992), Utkin et al. (1994), Bouchard et al. (1996), Christiansen and Ahring (1996), Gerritse et al. (1996), Loffler et al. (1997), Miller et al. (1997), Dennie et al. (1998), Damborský (1999), Gerritse et al. (1999), Tiedje (1999), Breitenstein et al. (2001), Suyama et al. (2001), Finneran et al. (2002), Shelobolina et al. (2003), Tront et al. (2006), Tsukagoshi et al. (2006), Villemur et al. (2006), Yoshida et al. 2007, Fletcher et al. (2008), Ding et al. (2014), Goris et al. (2015)
Thermodesulfobacteriota: *Desulfuromonas* and *Geobacter*				
Desulfuromonas	*Dsm. chloroethenica* strain TT4B *Dsm. michiganensis strains* BB1, BRS1	10–35°C	PCE/TCE to *cis*-DCE	Krumholz et al. (1996), Krumholz (1997), Sung et al. (2003)
Geobacter lovleyi	SZ^T, KB-1, LYY	10–40°C	PCE → *cis*-DCE	Duhamel and Edwards (2006), Sung et al. (2006b), Wagner et al. (2012), Lihl et al. (2019), Liang et al. (2021)
Campylobacterota: *Sulfurospirillum*				
Sulfurospirillum multivorans	Strain K	15–33°C	PCE/TCE→ *cis*-DCE	Scholz-Muramatsu et al. (1995)
Sulfurospirillum halorespirans	Strain PCE-M2	Opt: 25–30°C	PCE/TCE→ *cis*-DCE	Luijten (2003)
Sulfurospirillum sp.	Strains JPD-1, ACS $_{TCE}$, ACS $_{DCE}$	JPD-1: 1.5–40°C ACS $_{TCE}$: 21°C ACS $_{DCE}$: 21°C	PCE to TCE; strain ACS $_{TCE}$ PCE to *cis*-DCE; strains JPD-1 and ACS $_{DCE}$	Laanbroek et al. (1977), Pietari (2002), Yang et al. (2017a), Huo et al. (2020)
Actinomycetota: *Propionibacterium*				
Propionibacterium	*strains HK-1 and HK-3*	30°C	Dechlorination to ethene	Stackebrandt et al. (2006), Chang et al. (2011)

Abbreviations: CE; chloroethenes; DCE; dichloroethene; N.A.; not available; PCE; perchloroethene; RT; room temperature; T; temperature; TCE; trichloroethene; and VC; vinyl chloride.

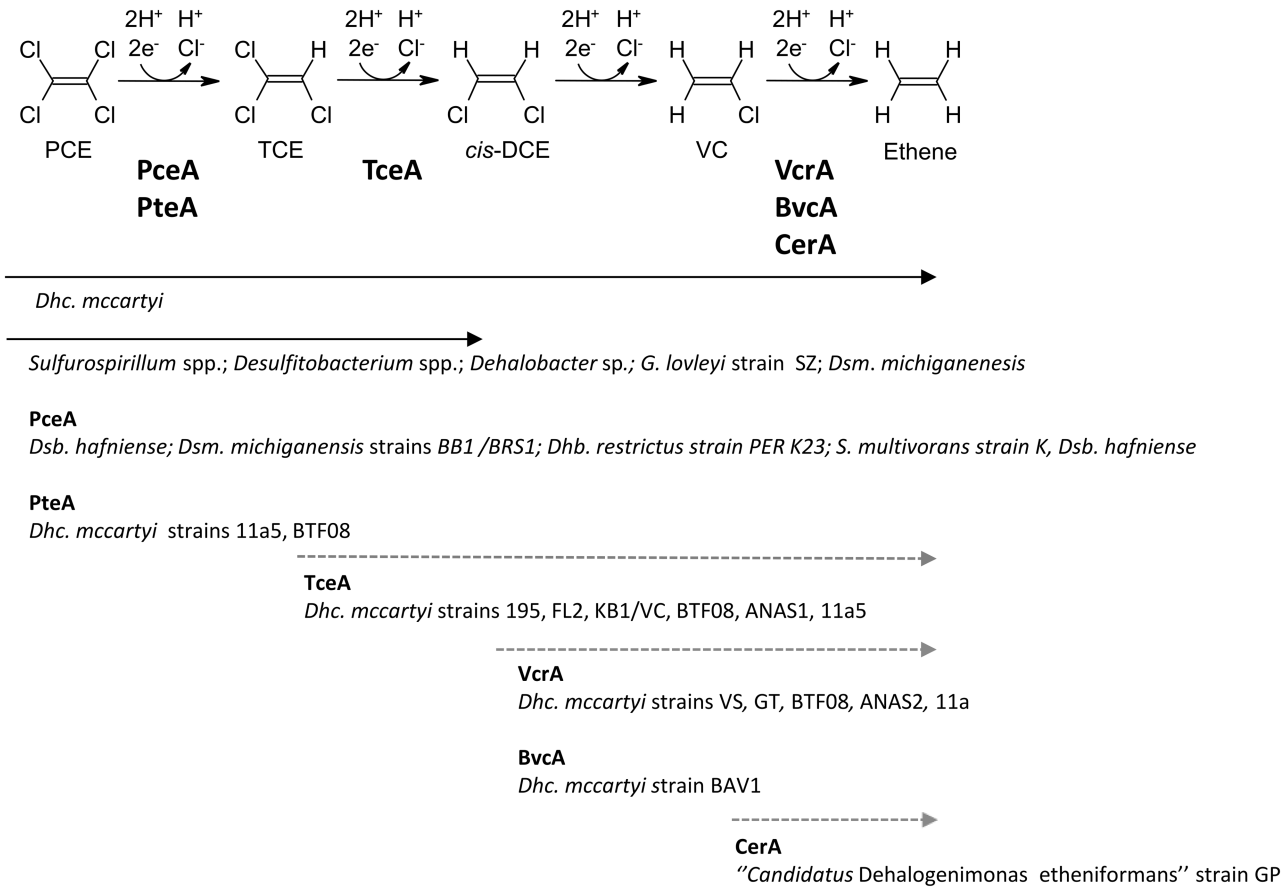

Figure 1. Overview of reductive dehalogenation of PCE; via TCE, DCE, and VC to ethene, with respective enzymes; PceA, PteA, TceA, VcrA, BvcA, and CerA and some of the reported microorganisms capable of the partial reaction.

of temperature on microbial dehalogenation and a combined application of ATES with bioremediation.

Temperature optima and growth ranges of organohalide-respiring bacterial isolates

Organohalide-respiring bacteria (OHRB) have been isolated from a variety of sources, many of which originated from chlorinated hydrocarbon contaminated sites from various continents and mainly coming from temperate climate zones (Table S1, Supporting Information). However, isolation was particularly targeted at obtaining isolates with dehalogenating capability for the purpose of further characterization; this process is usually related to availability of incubation temperatures in laboratories, e.g. room temperature (~20–25°C) or with a focus on the *in situ* temperature at the sampling sites. Hence, few studies investigating the effect of temperature shifts on the dechlorination potential of the isolates have been published. Notwithstanding that, not all the studies contain information on temperature range for growth, optimal temperature, or temperature at which dehalogenation was observed. While a number of the genera and strains have been substantially characterized [e.g. *Dehalococcoides (Dhc.) mccartyi*, *Desulfitobacterium (Dsb.) hafniense*, and *Sulfurospirillum multivorans*; Goris et al. 2015, Futagami and Furukawa 2016, Goris and Diekert 2016, Zinder 2016; also see Table S1 (Supporting Information)], information on temperature effects on dehalogenation potential as well as growth conditions seems to be unavailable for a significant number of the strains (Table S1, Supporting Information). Overall, not much has been described for the specific temperature-related limitations towards dehalogenation, which would be an important aspect for bioremediation purposes, and for assembling dehalogenating consortia for bioaugmentation applications.

According to our current knowledge, OHRB are distributed across several phyla: Chloroflexota, Bacillota, Thermodesulfobacteriota, and Campylobacterota. Amongst these, most OHRB capable of dechlorinating CE that have been isolated so far belong to the two genera: *Dehalococcoides* (phylum: Chloroflexota), where at least 20 strains have been reported affiliated with *Dhc. mccartyi* (Table S1, Supporting Information); *Desulfitobacterium* (phylum: Bacillota) with at least seven strains reported for *Dsb. hafniense*. These genera are amongst others described in the following Phylum subsections, with a focus on those capable of organohalide respiration using CE as electron acceptors.

Chloroflexota: within the phylum Chloroflexota, at least three genera with dehalogenating activity have been described: *Dehalogenimonas* and *Dehalococcoides and Dehalobium*. So far, only one isolate has been reported for the genus '*Dehalobium*', assigned *Dehalobium chlorocoercia* strain DF-1 (May and Sowers 2016, Oren and Garrity 2022). In addition to its ability to selectively dechlorinate certain chlorinated polychlorobiphenyls (PCBs) and highly chlorinated benzenes, *D. chlorocoercia* strain DF-1 can also dechlorinate PCE and TCE to yield, albeit incompletely, higher amounts of *trans*-DCE than *cis*-DCE, when supplemented with H_2 or formate as an electron donor (Miller et al. 2005, May et al. 2008). *Dehalobium chlorocoercia* strain DF-1 grows optimally at 30–33°C, while no growth was reported at 10°C or 35°C (Wu et al. 2000, 2002a, b,

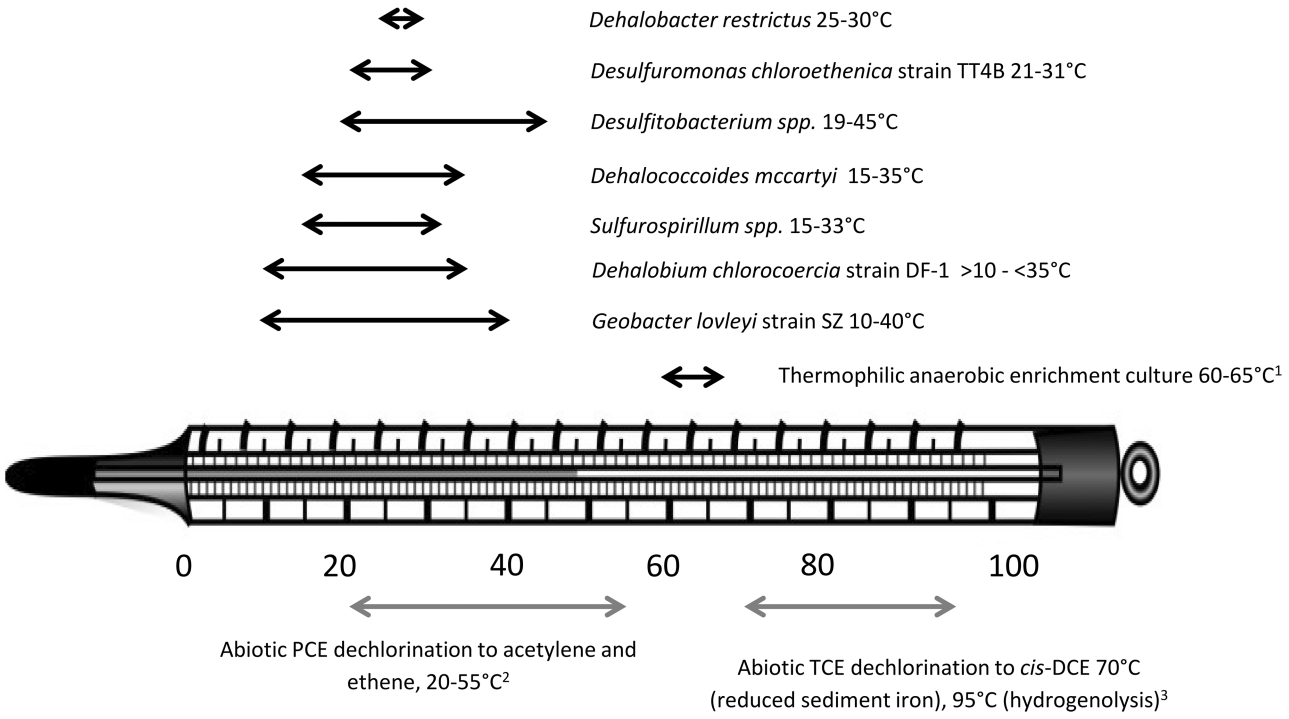

Figure 2. Overview of the temperature activity range for a select group of CE-dechlorinating bacteria and the range of temperature for some examples of abiotic dechlorination processes of the CE (1) Kengen et al. (1999), (2) Schaefer et al. (2017), and (3) Costanza and Pennell (2007) and Truex et al. (2007). References for the temperature range of microorganisms can be found in Table 1 and Table S1 (Supporting Information).

Miller et al. 2005, Kittelmann and Friedrich 2008, May et al. 2008). Within the genus *Dehalogenimonas (Dhgm.)*, the two well described species, *Dhgm. lykanthroporepellens* and *Dhgm. alkenigignens* were only capable of dehalogenating a variety of organohalides such as 1,2-dichloroethane and 1,1,2-trichloroethane but not any of the CE (Moe et al. 2009, Yan et al. 2009, Bowman et al. 2013). However, at least two strains have since been reported: '*Candidatus* Dehalogenimonas etheniformans' and *Dehalogenimonas* sp. strain WBC-2, which could dechlorinate one the CE (Table S1, Supporting Information). '*Candidatus* Dehalogenimonas etheniformans' strain GP, which dechlorinates TCE, DCE, and VC grows between 20 and 30°C with hydrogen (Yang et al. 2017b). *Dehalogenimonas sp.* strain WBC-2, which was enriched from the West Branch Canal Creek (WBC-2) culture dechlorinates mainly *trans*-DCE to VC at room temperature (Jones et al. 2006, Manchester et al. 2012, Molenda et al. 2016).

Most bacterial isolates within the phylum Chloroflexota capable of organohalide respiration belong to the genus *Dehalococcoides* (Table S1, Supporting Information). Many *Dhc.* strains can dechlorinate CE, some of them completely to ethene. *Dehalococcoides mccartyi* strain 195^T (formerly known as *Dhc. ethenogenes*) is the type strain for this genus (Maymo-Gatell et al. 1997, McMurdie et al. 2009, Löffler et al. 2013), dechlorinate PCE and TCE to VC, and cometabolically to ethene, with hydrogen as the electron donor (Maymo-Gatell et al. 1997, 1999, Yan et al. 2021). In general, *Dhc. mccartyi* strains are grown under mesophilic conditions with most strains cultivable between 15 and 35°C (Fig. 2; Maymo-Gatell et al. 1997, Rosner et al. 1997, He et al. 2003, Muller et al. 2004, Sung et al. 2006a, Cheng and He 2009, Löffler et al. 2013, Adrian and Löffler 2016). *Dhc. mccartyi* strain 195^T has an optimum growth temperature of 35°C, while above this dechlorination activity only persisted temporarily, and no dechlorination occurred at 40°C (Maymo-Gatell et al. 1997, McMurdie et al. 2009, Löffler et al. 2013); strains CBDB1, BAV1, VS, FL2, and GT grow at optimum temperatures between 25 and 30°C (Adrian et al. 1998, 2000, He et al. 2003, Sung et al. 2006a, Löffler et al. 2013, Adrian and Löffler 2016). Other strains such as MB, ANAS1, ANAS2, 11a, and DCMB5 possess optimum temperatures of 30°C (Richardson et al. 2002, Cheng and He 2009, Lee et al. 2011, Low et al. 2015).

Bacillota: CE dehalogenating species of this phylum belong to the genera *Dehalobacter (Dhb.)*, *Desulfitobacterium* (*Dsb.*), *Sporomusa*, and *Acetobacterium* (Table S1, Supporting Information). A total of two strains of *Dhb. restrictus*, strain PER-K23^T and strain TEA, are non spore-forming and have optimum growth temperatures of about 30°C (PER-K23: 25–30°C with no growth above 35°C; Holliger et al. 1993, 1998, Wild et al. 1996, Nelson et al. 2014). Meanwhile, several strains have been described within the genus *Dehalobacter,* such as strains 12DCB1, 13DCB1, and TCP1 (Table S1, Supporting Information). All *Dhb.* strains reported here have growth temperatures of 25–30°C (Holliger et al. 1993, 1998, Yoshida et al. 2009, Nelson et al. 2011, 2014, Wang et al. 2014a). Strains belonging to the genus *Desulfitobacterium* (*Dsb.*) are facultative OHRB, which enable them to use a wide spectrum of electron donors and acceptors. Within this genus, several strains are capable of dechlorinating at least one of the CE, comprising the species *Dsb. hafniense*, *Dsb. dehalogenans*, and *Dsb. metallireducens* including several which are categorized under *Dsb.* spp. (Table S1, Supporting Information). *Dsb. hafniense* strains DCB-2 (the type strain; Madsen and Licht 1992, Christiansen and Ahring 1996) and TCP-A can dechlorinate mainly PCE but not TCE (Breitenstein et al. 2001), while strains TCE-1 and PCE-S can utilize both PCE and TCE (Miller et al. 1997, Gerritse et al. 1999, Milliken et al. 2004, Ye et al. 2010, Goris et al. 2015). Temperature range of growth is between 13 and 45°C, varying between strains (Table S1, Supporting Information). *Dsb. hafniense* DCB-2^T was cultivated at 37°C (Madsen and Licht

1992, Christiansen and Ahring 1996), while *Dsb. dehalogenans* PCE-1 grows between 19 and 42°C (optimum: 34–37°C). *Dsb. metallireducens* strain 853-15A^T grows between 20 and 37°C, and no growth was observed at 4, 15, or 50°C (Finneran et al. 2002). Some strains can form spores, suggesting their capability to survive at higher temperatures, such as *Dsb. hafniense* strains DCB-2^T and PCE-S, and *Dsb*. sp. strain B31e3 are spore-forming (Madsen and Licht 1992, Christiansen and Ahring 1996, Löffler et al. 1996, Sanford et al. 1996, Kunapuli et al. 2010), while others such as *Dsb. hafniense* strain JH1, *Dsb. dehalogenans* strain JW/IU-DC1^T, and *Dsb. metallireducens* strain 853-15A^T are not spore-forming (Utkin et al. 1994, Finneran et al. 2002).

Thermodesulfobacteriota: to date, two several bacterial genera within this phylum were capable of reductive dehalogenation: *Desulfuromonas* and *Geobacter*. The genus *Desulfuromonas* (*Dsm.*) comprises two species with dehalogenating capabilities namely *Dsm. chloroethenica* and *Dsm. michiganensis*. *Dsm. chloroethenica* strain TT4B utilizes PCE and TCE as electron acceptors in the presence of the electron donors acetate or pyruvate, to yield *cis*-DCE (Krumholz et al. 1996, Krumholz 1997, Sung et al. 2003). This non spore-forming strain has a growth range of 21–31°C (optimum: 30°C) and did not dechlorinate at 16 or 35°C (Krumholz et al. 1996, Krumholz, 1997). *Dsm. michiganensis* strains BB1 and BRS1 are capable of dechlorinating PCE and TCE as electron acceptors (Sung et al. 2003), with a growth range between 10 and 35°C and an optimum growth temperature of 25°C (Table S1, Supporting Information). The second genus, *Geobacter* includes several *Geobacter lovleyi* strains (SZ, KB-1, and LYY), which can utilize PCE and/or TCE as electron acceptor, with *cis*-DCE as a major end product (Table S1, Supporting Information). *Geobacter lovleyi* strain SZ, the type strain, grows between 10 and 40°C (optimum: 35°C), does not form spores, and uses pyruvate, acetate, or hydrogen as electron donors (Sung et al. 2006b, Wagner et al. 2012), while *G. lovleyi* strains KB-1 and LYY grow at 22–25°C and 30°C, respectively (Duhamel and Edwards 2006, Lihl et al. 2019, Liang et al. 2021).

Campylobacterota: *Sulfurospirillum* (formerly *Dehalospirillum*) is the only known dehalogenating genus within this phylum comprising mainly *S. multivorans* and *S. halorespirans* (Table S1, Supporting Information). A number of these strains are mesophilic, growing between 20 and 30°C (Table 1; Table S1, Supporting Information) and are capable of metabolically dechlorinating PCE or TCE to *cis*-DCE (e.g. *S. multivorans* strain K, *S. halorespirans* strain PCE-M2, and *Sulfurospirillum*. sp. strain JPD-1; Laanbroek et al. 1977, Scholz-Muramatsu et al. 1995, Campbell et al. 2001, Pietari 2002, Luijten 2003). Spore formation was not described. One of the best described species, *S. multivorans* (formerly *Dehalospirillum multivorans* strain K), is able to dechlorinate PCE and TCE to *cis*-DCE, with electron donors such as hydrogen, formate, or pyruvate, grows between 15 and 33°C but optimally at 28–30°C and does not grow above 37°C (Scholz-Muramatsu et al. 1995). There are also several strains within the *Sulfurospirillum* sp. (strains JPD-1, ACS $_{TCE}$, and ACE$_{DCE}$) and *S. carboxydovorans* (strain MV) with optimal growth temperatures within the mesophilic growth range (~21–30°C; Table S1, Supporting Information; Laanbroek et al. 1977, Campbell et al. 2001, Pietari 2002, Jensen and Finster 2005, Yang et al. 2017a, Huo et al. 2020).

Reductive dehalogenation at thermophilic conditions

Overall, there is a lack of reports describing reductive dehalogenation processes by microbial isolates at thermophilic conditions (above 45°C; Table S1, Supporting Information), suggesting that higher temperatures may hamper reductive dehalogenation. However, it should be noted that enrichment and isolation of dehalogenating bacteria has generally been done at 20–30°C, thus resulting in isolates adapted to these temperatures. To our knowledge, there are no reports about enrichment of thermophilic dehalogenating microbes from natural hot habitats such as volcanic areas, hot springs, oil reservoirs, or deep aquifers. It is possible that since these habitats do not contain halogenated organics in higher concentrations, and were hence not the main focus in investigations. Nevertheless, it is an open question whether these hot natural habitats are inhabited by thermophilic dehalogenating microorganisms. Notably, the solubility of CE is slightly decreasing from 20 to 40°C, but again increasing at temperatures above 40°C (Koproch et al. 2019), hence reductive dehalogenation reactions should not be limited by physical–chemical constraints at higher temperatures.

Kengen et al. (1999) describe a thermophilic anaerobic enrichment culture from PCE-polluted sediment from Rotterdam harbour containing relatives of *Dhb. restrictus* and *Desulfotomaculum thermosapovorans*, capable of dechlorinating PCE to *cis*-DCE at 65°C (Table 1), indicating that microbial reductive dehalogenation, which was likely attributed to *Dhb. restrictus*, is principally feasible at thermophilic conditions. Therefore, more studies are needed to be done at higher temperatures to better understand the limits at which microbial growth and dechlorinating ability can persist, as well as remain resilient during a temporary period of high temperature exposure.

Nevertheless, strains possessing a temperature range of ≥ 25°C for growth are probably more tolerant to environmental temperature fluctuations, e.g. *G. lovleyi* strain SZ (10–40°C), *Dsb. frappieri* strain PCP-1 (15–45°C), and *Dsb. hafniense* strain PCE-S, which has a growth range between 20 and 45°C (optimal: 37–38°C) respectively (Table S1, Supporting Information). At contaminated sites exposed to elevated temperatures, a succession of microbial communities may result in a dominance of spore formers; however, this is expected to lead to partial dechlorination to DCE (Keynan et al. 1964, Berg and Sandine 1970, O'Sullivan et al. 2015). Spores which are usually resistant to high (boiling) temperatures confer the members of this respective community with the ability to reestablish themselves post heat exposure (O'Sullivan et al. 2015, Chan et al. 2021). For example, the growth and activity of the spore-forming *Dsb. chlororespirans* strain Co23 recovered 1 week post incubation at 80°C, after being returned to 30°C (Sanford et al. 1996).

Effect of temperature on microbial reductive dehalogenation by microbial communities at laboratory and field conditions

The effect of temperature shifts on microbial dehalogenation has been investigated mainly in the context of thermal treatment of contaminated field sites, as well as, more recently, with the combination of ATES and bioremediation in mind (Table S2, Supporting Information). However, only few studies have been published systematically investigating the effect of temperature.

Over the years, several consortia have been established including BDI, OW, KB-1, WBC-2, and SDC-9 (Table S2, Supporting Information). Consortium BDI comprises *Dhc. mccartyi* strains BAV1, FL2, and GT with a cultivation temperature of 24°C; ethene was produced at 30°C, but VC accumulated at 35 and 40°C, however, cultivation at 45°C resulted in a loss of dechlorination activity

(Fletcher et al. 2011a). Consortium OW was cultivated at 30°C and consists of multiple *Dehalococcoides* strains as well as *Dehalobacter*, *Geobacter*, and *Sulfurospirillum* (Fletcher et al. 2011b). Similar to BDI, dechlorination activity was lost at 45°C while VC accumulated at 35 or 40°C (Fletcher et al. 2011a). Consortium KB-1, which consists of *Dehalococcoides* and phylotypes affiliated to the genus *Geobacter*, was cultivated at room temperature and completely dechlorinated TCE between 10 and 30°C, but it accumulated *cis*-DCE outside the mentioned temperature range; no dechlorination activity was observed at 50 and 60°C (Friis et al. 2007b). Consortium SDC-9, which comprised *Dehalococcoccoides* and *Desulfitobacterium* as the two most abundant genera, were cultivated between 21 and 30°C, but have been reported to dechlorinate at 5°C and up to 40°C (Vainberg et al. 2009, Vainberg and Steffan 2014, Kucharzyk et al. 2020). Consortia WBC-2 and DehaloR 2 were cultivated at 19°C and 30°C, respectively, however, no further range of temperatures were described (Table S2, Supporting Information; Jones et al. 2006, Lee and Lee 2016).

The lowest temperature at which reductive dehalogenation of TCE to DCE and VC was reported is 4°C, proven by formation of [^{14}C]-VC and [^{14}C]-*cis*-DCE from [^{14}C]-TCE, in microcosms prepared with contaminated sediments from Alaska (Bradley et al. 2005). Incubations with consortium KB-1 below 10 or 15°C, with lactate or propionate as electron donor, respectively, in batch culture, or at 15°C in a column system, accumulated *cis*-DCE, suggesting comparatively lower activity of *Dhc. mccartyi* at lower temperature (Friis et al. 2007b, Marcet et al. 2018b). However, it should be noted that these experiments were done with consortium KB-1, which was continuously cultivated at room temperature, probably leading to a loss of slow-growing reductive dechlorinators adapted to lower temperatures in the original inoculum. Meanwhile, in other studies with consortium KB-1, complete reductive dechlorination to ethene was observed in laboratory studies at temperatures as low as 4°C with lactate (Heimann et al. 2007) and up to 43°C in KB-1 bioaugmented column experiments (Marcet et al. 2018a; Table S2, Supporting Information). In these studies, an increase in temperature resulted in a complete dechlorination to ethene. Contrastingly, a laboratory study by Nagymate et al. (2020) observed dehalogenation of TCE to ethene with corresponding presence of *Dhc. mccartyi* at 8°C (Nagymate et al. 2020), stressing the importance of the temperature used for cultivation, especially in the case of bioaugmentation.

However, it is important to note that the upper limits differ for different systems, could instead hamper complete dechlorination past *cis*-DCE. For example, the upper limits for the dechlorination of PCE to ethene was 43°C in a column system (Marcet et al. 2018b), while in another study batch cultures with the same KB-1 consortium an upper limit of 30°C was reported (Friis et al. 2007b, Heimann et al. 2007). The highest currently reported temperature for dechlorination of PCE to *cis*-DCE is 65°C, by a thermophilic anaerobic enrichment culture containing relatives of *Dehalobacter restrictus* and *Desulfotomaculum thermosapovorans* (Kengen et al. 1999; Table S2, Supporting Information).

With that, it seems that complete dechlorination to ethene is more temperature sensitive when compared to incomplete dechlorination. However, there are many studies that do not provide information on temperature ranges and/or its effects on reductive dechlorination (Table S2, Supporting Information). Regardless, temperature ranges reported in the laboratory studies do not necessarily reflect the potential temperature range for dechlorination present in natural systems, since the diversity of dechlorinators are likely to be broader than currently known. The diversity in the temperature optima and ranges of the consortium members enable the consortium to adjust to the temperature whilst performing their dechlorination function especially during bioaugmentation. This may be useful in the event where different members of the consortium (each with different growth temperature ranges and optima), which are either involved in different steps of the reductive dechlorination, or contribute indirectly either via fermentation of substrates to supply carbon source and electron donor, can carry out the steps when temperatures are non-inhibitory.

A majority of the enrichment cultures were cultivated under mesophilic growth conditions such as KB-1 (room temperature) and OW (30°C; Friis et al. 2007b, Fletcher et al. 2011a; Table S2, Supporting Information). However, temperature-influenced loss of dechlorination activity could cause the accumulation of the toxic *cis*-DCE and VC outside the optimal temperature window (Fletcher et al. 2011b).

In a study done by our lab, which investigated dechlorination of TCE in CE-contaminated sediment in the temperature range between 10 and 60°C, a higher accumulation of VC at 30°C and *cis*-DCE at 40°C was observed when compared to replicates incubated at 10°C and 20°C where the major product was ethene (unpublished). In general these results fit with published results, the dechlorination to ethene occurred in the presence of *Dehalococcoidia* related phylotypes in experiments between 10 and 30°C, while this was absent at 40°C (Ni et al. 2015, Zhang et al. 2015, Yamazaki et al. 2020).

To our knowledge, at least two studies of tests directly at field sites have been published. A field pilot test in the Czech Republic was performed in which the groundwater at the contaminated field site was heated from the original temperature of 12–13°C to 35–40°C and amended with whey as electron donor (Nemecek et al. 2018). Ethene and methane were observed as products after heating and a rapid increase of the number of organohalide-respiring genera (*Dehalococcoides* and *Dehalobacter*) and reductive dehalogenase genes (*vcrA* and *bvcA*) was observed. Another study tested high temperature heating of groundwater from 10 up to 70°C at the Fort Lewis field site (Truex et al. 2007). While at lower temperatures *cis*-DCE was observed as a product from presumably biological dehalogenation, ethene, and acetylene were observed at higher temperatures, likely a result from abiotic dehalogenation catalysed by the reduced iron in the sediments.

Nevertheless, several studies have also discussed the role of the microbial community following a period of more drastic temperature fluctuations from thermal treatments, e.g. electrical resistance heating (> 100°C) and steam injection (between 100 and 120°C; Friis 2006a, Friis et al. 2006). Friis et al. (2006) also mentioned the role of the temperature following thermal treatment in predicting the biological remediation potential since this temperature can either promote or inhibit dechlorination activity (Friis 2006b). For example, in the Danish site where steam injection was applied followed by cooling, temperatures of 30–50°C were reported 1.5 months after completion (Friis 2006b, Friis et al. 2007a), whereas a longer duration was needed in the Fort Lewis site (> 100 d) before temperatures below 50°C were measured. Thus, these prolonged cooling times would require long periods before temperatures allow for growth of native or bioaugmented microbial communities and recovery of dechlorination activity. Another field study involved an analysis of a post-remediated PCE-contaminated site in Rødekro, southern Denmark, which underwent thermal remediation via steam injection in 2006. In their study, conducted 11 years after remediation, samples were obtained from wells drilled along the plume flowline to investigate parameters such as redox potential, CE concentrations, and iso-

topic compositions as well as qPCR for quantification of specific organohalide-respiring genera and reductive dehalogenase genes and microbial community analysis (Murray et al. 2019). Murray et al. (2019) observed the recovery of microbial PCE and *cis*-DCE dechlorination in the previously thermally remediated section of the field site, stimulated by the release of dissolved organic carbon (DOC) during steam injection. However, the investigations did not specifically ascertain if the recovery of dehalogenation activity was related to a microbial community surviving heat treatment or an inoculation from by-passing groundwater, which did not experience thermal remediation. The lack of information on the site's recovery potential following heat treatment further highlights the uncertainty towards the resumption of biotransformation activity in ATES-related heat storage cycles. Future studies should, therefore, elucidate the potential of recolonization from surrounding groundwater, regrowth of microbial communities surviving heat treatment, or the need for bioaugmentation for resumption of dehalogenation activity.

Effect of temperature on expression and activity of reductive dehalogenases

Temperature is a critical variable that affects enzyme stability and activity where this usually increases with increasing temperature before reaching an optimum followed by a decline in activity (Mohr and Krawiec 1980, Arcus et al. 2016). Typically the optimum temperature and thermal stability of enzymes is higher in thermophiles followed by mesophiles and psychrophiles, which is related to the corresponding 'lifestyles'. In the context of this review, the temperature behaviors of dehalogenating enzymes are of special interest. To date, several reductive dehalogenases (RDases) are described for organohalide respiration via carbon–chlorine bond cleavage (Fig. 1). PceA dechlorinates PCE and/or TCE to *cis*-DCE (Neumann et al. 1996). PCE reductive dehalogenase PteA was more recently classified in *Dhc. mccartyi* strain 11a5 and is believed to dechlorinate PCE to TCE (Jugder et al. 2016, Zhao et al. 2017, Franke et al. 2020). TCE reductive dehalogenase (TceA) dechlorinates TCE to VC via the intermediate *cis*-DCE (Major et al. 2002) and from VC to ethene (Magnuson et al. 1998, 2000, Yan et al. 2021). VC reductive dehalogenase (VcrA) is capable of dechlorinating TCE, *cis*-DCE, and VC to ethene while the BvcA dechlorinates VC to ethene. In addition, a new VC reductive dehalogenase, *cer*A, has also been reported which can dechlorinate TCE to ethene (Yang et al. 2017b).

A few of the purified CE reductive dehalogenases were characterized for their temperature optimum. Interestingly, higher temperature optima for the enzymes are reported when compared to the growth temperature optima of the respective microorganisms, e.g. PceA of *S. multivorans*, with growth optimum at 25–30°C, has its optimum at 42°C, and becomes thermolabile at 50°C (Neumann et al. 1996, Turkowsky et al. 2019). Similarly, the PceA from *Desulfitobacterium* sp. strain PCE-S has its optimum at 50°C, while the strain is optimally cultivated at 37–38°C (Miller, 1998).

A dependence of *tce*A expression on temperature in the ANAS enrichment culture was observed, with a 4-fold and 50-fold lower level of *tce*A expression (*tce*A transcripts per tceA gene) following 20 h of incubation at 22°C and 14°C, respectively, versus incubation at 30°C, while the quantity of *tce*A gene (normalized per ml) remained the same (Johnson et al. 2005). However, upregulation of expression does not necessarily equate to dechlorination activity. For example, Fletcher et al. (2011b) showed that although *vcr*A gene transcript abundances at 35 and 40°C were one order of magnitude higher compared to at 30°C, dechlorination still stalled at VC at the higher temperatures while complete dechlorination to ethene was observed at 30°C. Their study suggests that higher gene expression does not correlate with dechlorination activity, but instead a stress response to heat (Fletcher et al. 2011b). Nonetheless, while VC dechlorination activity of culture BDI was lost at 45°C, VC dechlorination activity recovered upon returning to 24°C following incubation at 40°C for 24 d, but incubations at 40°C for longer periods resulted in the loss of dechlorination activity (Fletcher et al. 2011b). These findings exemplify how a small temperature shift can impact bacterial growth, inducing a stress response or affecting dechlorination activity.

Indirect effects of temperature on biotransformation: competing/synergetic microbial processes

Temperature can influence synergistic or competing microbial processes either by supporting, enhancing, limiting, or inhibiting dehalogenation processes or its kinetics (Fig. 3). These include production of hydrogen as electron donor and acetate as carbon source for OHRB, respectively, during fermentation, competition with the activity of methanogens and sulfate-reducing bacteria for electron donors and carbon sources, and production of cofactors (corrinoids) essential for functionality of the RDases. Generally, these processes have been reported at high temperatures (Fukui et al. 1964, Kallmeyer and Boetius 2004, Gieg et al. 2010, Verhaart et al. 2010, Piceno et al. 2014, Straub et al. 2018), however, thermophilic or thermotolerant microbial representatives may be absent in shallow aquifers. Additionally, high temperatures may result in mobilization of DOC as well as volatile contaminants (Griebler et al. 2016, Koproch et al. 2019). The increase in volatile organic compounds (VOC) concentration by mobilization from sediments may favour the faster conversion of PCE to *cis*-DCE due to better bioavailability (Ni et al. 2016); conversely, high concentrations of VOC such as PCE and TCE can be toxic to OHRB or other bacteria which support dechlorination (such as fermenters; Yang and McCarty, 2000, Huang and Becker 2011, Yoshikawa and Zhang 2020).

To our knowledge, studies which correlate temperature or temperature changes to effects which indirectly influence dechlorination are available but limited. Nonetheless, these will be described in the following subsections below.

Fermentation and production of electron donors and carbon sources for OHRB: fermentation of complex substrates, with production of hydrogen and acetate, by hyperthermophile and extremely thermophilic archaea and bacteria has been described and studied [for a review see Verhaart et al. (2010)]. Heimann et al. (2007) determined fermentation rates of lactate and pyruvate (as fast and slow hydrogen-releasing sources, respectively) at different temperatures to support anaerobic microbial dechlorination of TCE by the KB-1 consortium. Hydrogen production was observed between 4 and 40°C and the overall higher dechlorination rates of TCE to ethene could be related to the higher rates of hydrogen supply. Besides being a product of fermentation, acetate was suggested to be produced by hydrogenotrophic homoacetogenesis in lactate-amended cultures at temperatures between 4 and 30°C. No lactate fermentation was observed at temperatures above 40°C (Heimann et al. 2007). Thus, temperatures of up to 40°C generally may not hamper production of suitable electron donors and carbon sources for dehalogenation, however, it is

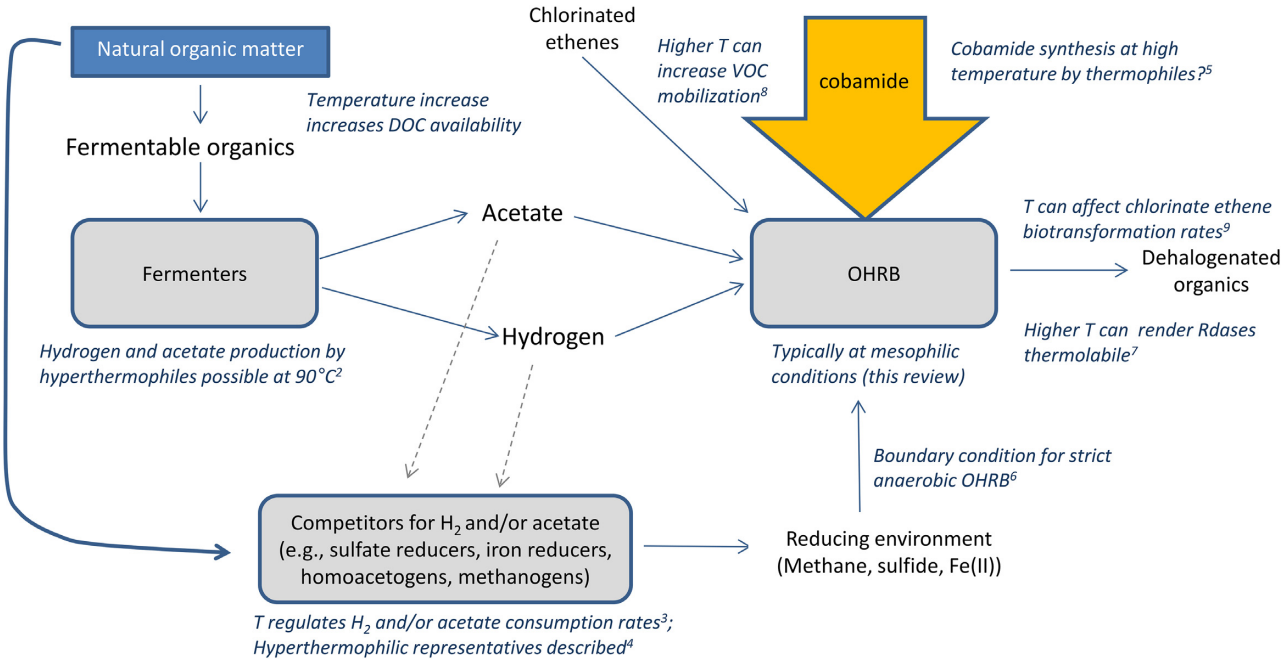

Figure 3. Summary of catabolic interactions and temperature-related bottlenecks indirectly affecting the processes; modified from Richardson (2016). (1) Friis et al. 2005, Tabuchi et al. (2010), Jesußek et al. (2013), Saito et al. (2016), and Bertolet et al. (2018), (2) Verhaart et al. (2010), (3) Conrad and Wetter (1990), Miyajima et al. (1997), Nozhevnikova et al. (2007), Tabuchi et al. (2010), Bin Hudari et al. (2020), and Metze et al. (2021), (4) Straub et al. (2018), (5) Fukui et al. (1964) and Fang et al. (2018), (6) Adrian and Löffler (2016), (7) Neumann et al. (1996) and Turkowsky et al. (2019), (8) Ni et al. (2016), and (9) Fletcher et al. (2011a, b).

questionable how and if aquifer microbial communities can retain the ability for dehalogenation at temperatures higher than 40°C and if shallow aquifers contain thermotolerant or thermophilic strains naturally.

Competition by methanogenic archaea, sulfate reducing, and iron reducing bacteria

Methanogens, sulfate reducing bacteria (SRB) and iron reducing bacteria (IRB), which may compete with OHRB (specifically CE dechlorinating bacteria) for hydrogen and acetate, have been reported to be active at psychro-, meso-, and thermophilic conditions, including extremely thermophilic archaeal representatives active at temperatures above 70°C [for reviews see e.g. Lovley et al. (2004), Gieg et al. (2010), Straub et al. (2018), Zheng et al. (2019), Lin et al. (2020)]. Nevertheless, several studies show how temperature can enhance or impede rates for methanogenesis (Sansone and Martens 1982, Schulz et al. 1997, Lettinga et al. 2001). Zhuang and Pavlosthatis (1995) described that methanogenesis and TCE dechlorination were both affected by temperature but methanogenesis was more sensitive to temperature. However, both processes showed similar temperature optima of ∼ 35°C, with both members competing for the same resource pool (e.g. electron donor and carbon source; Zhuang and Pavlostathis 1995). In contrast, in a study by Fletcher et al. (2011a) involving thermal treatment showed that temperatures > 5°C impeded reductive dechlorination, but instead a majority of the reducing equivalents were utilized in methanogenesis, which was considered one of the possible cause for the incomplete dechlorination.

As with all (bio)chemical reactions, sulfate reduction rates are temperature dependent (Okabe and Characklis 1992, Elsgaard et al. 1994, Meier et al. 2005, Bonte et al. 2013, Bin Hudari et al. 2020, 2022). To our knowledge, only one study simultaneously correlated temperature and its effect on sulfate reduction and dechlorination. Guerrero-Barajas et al. (2011) observed higher rates for sulfate reduction and TCE biotransformation at 37°C compared to 70°C, however, dechlorination was thought to be cometabolic with sulfate/sulfur reduction and fermentation (Guerrero-Barajas et al. 2011).

Meanwhile, the impact of biological Fe(III) reduction on reductive dehalogenation rates is less understood (Paul et al. 2015, Di Curzio 2019, Murray et al. 2020), as well as any temperature effects on this relationship.

The role of temperature on cofactor production

Reductive dechlorination undertaken by bacteria such as *Dhc. mccartyi* strain 195, requires cobamides such as vitamin B12 for growth and as cofactor in reductive dehalogenases (Maillard et al. 2003, Butler and Kräutler 2006, He et al. 2007, Schipp et al. 2013, Fang et al. 2017). Reductive dehalogenation with vitamin B12 (cyanocobalamin) can proceed abiotically or biotically, by generating a cobalt(I) supernucleophile using a strong reductant or catalyzed corrinoid-dependent reductive dehalogenases, respectively (Kim and Carraway 2002, He et al. 2007, Heckel et al. 2018, Yan et al. 2018). OHRB are either capable of producing cobamides *de novo*, either aerobically or anaerobically or use salvage pathways such as *Dehalococcoides*, which relies on exogenous cobamides (e.g. vitamin B12) in the growth medium (Schipp et al. 2013, Balabanova et al. 2021). Variations in the lower Coα base of the cobamide can impact microbial reductive dechlorination rates and growth of *Dhc. mccartyi* strains (Yan et al. 2018), resulting in varying rates or a complete loss of dechlorination activity as well as substrate utilization (Yan et al. 2015). This can be crucial for dechlorinators such as *Dehalococcoides*, which rely on exoge-

nous cobamide, where the loss of cobamide resulting from thermal treatment could instead result in utilization of less favourable cobamides affecting the extent and rates of dechlorination. Besides, higher concentrations of vitamin B12 have been described to improve the growth of *Dehalococcoides* sp. (He et al. 2007, Fang et al. 2017), and temperature can also promote growth of reductive dehalogenase-dependent cobamide producers. One study mentioned thermophilic cobamide production (Fukui et al. 1964), however, to our knowledge, there is no information on the effects of temperature on the cobamide producers supplying cofactors beneficial to the OHRB.

Other effects of high temperature

Temperatures above 45°C significantly mobilize dissolved organic carbon (DOC) from aquifer sediments (Griebler et al. 2016), also likely providing electron donors for reductive dehalogenation. For example, Marcet et al. (2018b) incubated 14 different solid materials at temperatures 30, 60, and 90°C, and reported an increase in the release of direct electron donors (such as acetate and H_2) and fermentable volatile fatty acids (e.g. lactate and propionate), highest at 90°C followed by 60°C when compared to 30°C higher temperatures. Friis et al. (2005) observed an increase of DOC in the aqueous phase after heating contaminated aquifer material up to 100°C (Newmark and Aines 1995, Friis et al. 2005). Marnette et al. (2010) attributed higher dechlorination activity to the increased mobilization of VOC (i.e. increased desorption) available to the dechlorinators. Abiotic reductive CE dechlorination can occur in parallel with biotic reductive dechlorination under field conditions to yield acetylene as well as ethene (Dong et al. 2009). Schaefer et al. (2017) investigated abiotic reductive dechlorination between 20 and 55°C in three clayey aquifer materials, an aquitard from PCE-impacted site in Puerto Rico, PCE-impacted site in the USA, and a TCE-impacted clayey layer from New Hampshire: acetylene and ethene generation followed the Arrhenius relationship and was putatively attributed to a higher ferrous mineral content. Costanza and Pennell (2007) incubated PCE contaminated soil and groundwater at 25, 55, 75, and 95°C. Aqueous phase PCE concentrations increased with higher temperatures which is attributed to PCE mass transfer from solid to aqueous phase. TCE hydrogenolysis to *cis*-DCE occurred at higher rates at 95°C compared to 55°C (Costanza and Pennell, 2007).

Potential for active combination of thermal energy storage and bioremediation: challenges

ATES becomes increasingly relevant in urban areas due to growing energy demands in combination with the transition to sustainable, CO_2 reduced energy systems (Fleuchaus et al. 2018). On the other hand, chlorinated solvents are typically contaminants of urban industrial and residential areas and since ATES applications results in water exchange between locations during input and output the potential migration of toxic contaminants may become problematic. Besides, one should also consider other effects (e.g. chemical) on pipes in sulfidic groundwater such as pipe clogging from iron sulfide precipitates (Li et al. 2017) or pipe corrosion (Lerm et al. 2013). However, a combination of ATES with bioremediation could allow a simultaneous contamination removal while fulfilling heating and cooling demand and supply, killing two birds with one stone. Clearly, integrating thermal treatment or thermal energy storage with bioremediation requires an understanding of microbial activity and adaptation to shifting temperatures.

Combinations with LT-ATES, with temperatures up to 25°C, would likely promote biotransformation as most described strains and consortia used for bioremediation purposes are adapted to these temperatures. Nevertheless, there are demands for storing higher temperatures (HT-ATES) due to the higher energy density per volume (Drijver et al. 2012). This is particularly interesting for urban areas where heat management requires storage in smaller volumes in the subsurface. HT-ATES systems in combination with bioremediation would have several added challenges. One of the probable scenarios following the use of high temperature either in thermal treatment or HT-ATES is that these may leave the subsurface void of the native microbial community and/or the necessary microorganisms that contribute towards contaminant biotransformation (Griebler et al. 2016). As shown in Table 1 and Tables S1 and S2 (Supporting Information), most CE-dechlorinating bacteria and consortia are cultivated in mesophilic conditions, while only a limited number are capable of spore formation, allowing survival under harsh conditions. While high temperature can induce the release of DOC containing putative electron donors and carbon sources for OHRB, and thereby stimulating microbial reductive dehalogenation, these populations may not survive the high temperatures (> 50°C) of the heating phase. Thus, natural inflow of native reductive dechlorinators with the surrounding groundwater from cooler regions or bioaugmentation with laboratory-grown reductive dechlorinating cultures may be necessary. Bioaugmentation, ideally in combination with biostimulation, is a useful strategy to restore dechlorinating ability at a contaminated site (Harkness et al. 1999, Ellis et al. 2000, Lendvay et al. 2003, Friis et al. 2005, 2006, Morrill et al. 2005, Lookman et al. 2007, Fletcher et al. 2011a, Ni et al. 2014). Bioaugmentation of heat-inactivated PCE/TCE contaminated sediments with the *Dehalococcoides*-containing, PCE to ethene dechlorinating consortium OW resulted in dechlorination of at least 85% of the PCE/TCE in a microcosm study, albeit to *cis*-DCE, which was further dechlorinated to ethene after biostimulation with hydrogen gas (Fletcher et al. 2011a). However, cyclic high temperatures regimes may then similarly require a cyclic bioaugmentation regime.

Key open questions and conclusion

This review observed several gaps that would need to be addressed with respect to reductive dechlorination at higher temperatures. The first gap pertains to the lack of information on thermophilic or thermotolerant reductive dechlorinators native to the subsurface. Thus far, a majority of isolates and enrichment cultures capable of reductive dechlorination comprise of mesophiles, derived from temperate zones and cultivated at common laboratory incubator temperatures (20–30°C). There are exceptions though, such as the non-CE dechlorinating *Dsb. chlororespirans* that grows between 15 and 37°C (optimum: 37°C); while no growth was reported above 45°C, residual activity was observed to persist up to 55°C, e.g. Sanford et al. (1996), observed dechlorinating activity in resting cells for up to 11 h when incubated at 50°C (Löffler et al. 1996, Sanford et al. 1996). Therefore, in order to diversify CE-dechlorinating bacteria (OHRB in general) to include thermophiles, perhaps there should be a greater attempt to isolate thermophiles, in addition to targeted enrichments for reductive dechlorinators at naturally hot sites. While there have been efforts to explore thermophilic reductive dechlorination, these have yet to yield any cultures from such habitats. In addition, searches for sequences of reductive dehalogenases from hot environment

did not generate many outputs (if any). Second, there is a lack of comprehensive information on some isolates and strains in the presented studies, particularly with respect to the temperature range for growth, the electron donor/acceptor profile, as well as whether they are capable of spore-spore formation (Table S1, Supporting Information). Spore formation could be crucial for resumption of dechlorination following a period of higher temperatures, or is essential for putative thermophilic reductive dechlorinators being inactive but alive at temperate or cold regions. Third, for a successful combined heat storage/thermal treatment and bioremediation approaches at contaminated sites, knowledge seems to be lacking on the direct effects of temperature perturbations on the microbial community, especially the dechlorination potential and recovery of dechlorination capacity. Fourth, unlike the extensive studies done to characterize isolates and enrichment cultures, much fewer studies pertaining to field site applications are available to our knowledge; perhaps, these studies were not made public for commercial or legal reasons. The fifth gap pertains to the very limited information available about the indirect effects of temperature on dechlorination, e.g. effects on syntrophic partner organisms or competitors of electron donors. The role of temperature on DOC and associated release of electron donors or toxicity from increased VOC mobilization for reductive dechlorination should also be investigated in greater detail. The penultimate gap, seems to be a lack of knowledge on the consortia applied for dechlorination for bioaugmentation [for e.g. KB-1 see Table S2 (Supporting Information)], and whether they are resilient to temperature shifts. Lastly, based on our literature search (Table S2, Supporting Information), very little information documenting dechlorination potential in ATES is available, with only a few studies related to thermal treatment.

In summary, there has been significant progress in the isolation and characterization of OHRB, as well as consortia for the purpose of bioremediation. This review highlights the gap when bioremediation is coupled with thermal energy storage and the need for resilient, active thermophilic OHRB sustaining biodegradation reactions at high temperatures. However, it is also important to note that other parameters can also directly and indirectly affect dehalogenation. Above all, since bioremediation is also site-specific and dependent on the type of contaminants and the native microbial community present, a comprehensive site survey is firstly necessary prior to establishment of bioremediation coupled to thermal energy storage.

Supplementary data

Supplementary data are available at *FEMSEC* online.

Acknowledgements

The authors acknowledge the support of the Federal Ministry for Economic Affairs and Energy (BMWi) within the funding initiative 'Energiespeicher', project ANGUS II, grant number 03ET6122, and of the Bundesministerium für Bildung und Forschung (BMBF) within the funding initiative 'Forschung für Nachhaltige Entwicklung (FONA3)', project TestUM-Aquifer, grant number 03G0875B.

Conflict of interest. None declared.

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