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Regulatory mechanisms and adaptive functions of small RNAs in extremophilic microorganisms

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Abstract Small RNAs (sRNAs) are important non-coding RNAs that usually play crucial roles in gene expression at the post-transcriptional level. The sRNAs have mostly been investigated in model microorganisms such as *Escherichia coli* and some pathogens. Nevertheless, microbial sRNAs from extreme environments such as the polar regions and deep sea have recently been discovered and analyzed for their unique roles in stress response, metabolic regulation and adaptation to extreme environments. These sRNAs fine-tune gene expression during oxidative and radiation stress, and modulate temperature and osmotic pressure responses. Representative sRNAs and their functions in thermophilic, psychrophilic, halophilic and radiation-tolerant bacteria are summarized in this review. Despite challenges in sample collection, RNA isolation, and functional annotation, the study of sRNAs in extreme environments provides opportunities for discovering novel regulatory mechanisms, applying them to biotechnology, and advancing our understanding of evolutionary adaptations. Looking ahead, high-throughput sequencing, synthetic biology, and multi-omics integration will bring new breakthroughs in discovering novel sRNAs and their functions and regulatory mechanisms. Such advancements are poised to enable comprehensive characterization of sRNA-mediated regulatory networks in extremophiles and unlock their biotechnological potential through mechanism-driven applications.

Keywords **small RNAs, extremophilic microorganisms, regulatory mechanisms, adaptive functions**

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1 Introduction

In nature, there exist a series of unique ecosystems known as extreme environments. While many organisms cannot survive under such harsh conditions, these places contain the mystery of biological evolution. Extreme temperature fluctuations (>60 ℃), oxidative damage from high concentrations of Reactive Oxygen Species (ROS), heavy metals, high-intensity radiation, and osmotic shocks are among the major stresses in these environments (Lui et al., 2018) (Figure 1). These combined stressors are way

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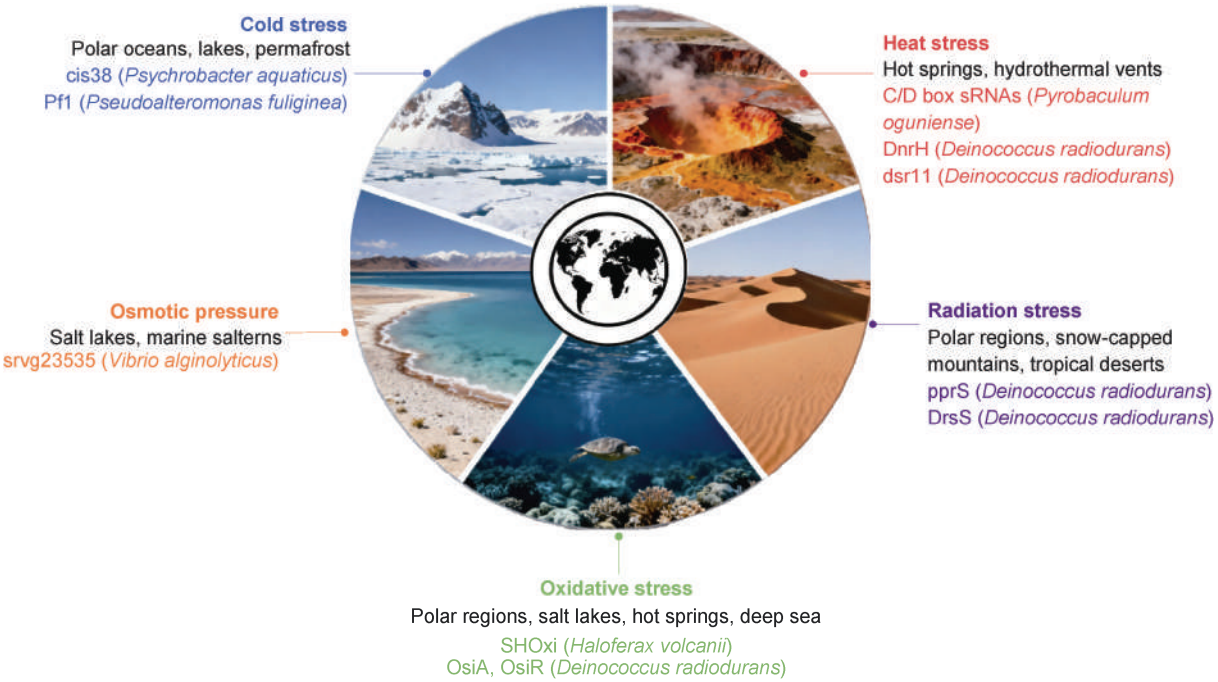

Figure 1 Typical extremophiles and their sRNAs in various extreme environments.

beyond the tolerance limits of ordinary organisms. However, they give rise to extremophiles such as thermophiles, psychrophiles, halophiles, radiation-resistant bacteria, and xerotolerant species (Schmid et al., 2020). These microbes thrive in harsh conditions with their unique survival strategies. Thus, extreme environments represent strategic resource repositories for discovering novel enzymes, biomaterials, and stress-resistance determinants.

Extremophiles have developed various mechanisms to tolerate and adapt to harsh conditions. For example, psychrophiles employ cold-adapted enzymes to sustain metabolism near the freezing point (Siddiqui et al., 2013) and produce antifreeze proteins to avoid freezing damage (Bar Dolev et al., 2016; Liao et al., 2025), while thermophiles reinforce protein stability to withstand >100 ℃ (Wang et al., 2015), halophiles rapidly resist osmotic shocks via compatible solute accumulation (Mukhtar et al., 2020), and radiation-resistant bacteria rely on ultra-efficient DNA repair machinery (Jung et al., 2017). Nevertheless, these adaptation strategies require sophisticated genetic regulation, including sRNAs that enable rapid induction of stress responses (Waters and Storz, 2009).

sRNAs, typically 50–500 nt in length, emerge as key post-transcriptional regulators (Waters and Storz, 2009). These sRNAs can be broadly categorized into two major classes based on their genomic origin and complementarity to target mRNAs. Typically, trans-encoded sRNAs are transcribed from genomic loci distant from their targets and exhibit only partial complementarity (Gottesman, 2005), allowing them to regulate multiple mRNAs through conserved seed regions (Waters and Storz, 2009). In contrast, cis-encoded sRNAs are transcribed from the opposite strand of their target genes and display perfect or near-perfect complementarity, leading to highly specific, often one-to-one, regulatory interactions (Waters and Storz, 2009). Additionally, some sRNAs can directly bind to and modulate the activity of regulatory proteins like CsrA, thereby exerting global regulatory functions (Timmermans and Van Melderen, 2010).

Unlike protein regulators, sRNAs are not translated but are rapidly induced by environmental or metabolic signals. Their primary function is to fine-tune target gene expression, thereby helping organisms adapt to stress, maintain homeostasis, and regulate metabolic pathways (Storz et al., 2011). A major advantage of sRNAs lies in their speed and efficiency, as they bypass complex processes such as translation and protein maturation. Upon transcription, they can act within minutes by modulating mRNA stability, interfering with translation, or interacting with RNA-binding proteins, thereby coordinating related gene networks (Waters and Storz, 2009).

The following sections will explore the specific roles and mechanisms of sRNAs in mediating responses to temperature, oxidative, radiation, and osmotic stresses. Through case studies of representative extremophiles, we illustrate how sRNAs coordinate cellular homeostasis and bolster environmental stress resistance.

2 Functional roles of sRNAs

2.1 Temperature stress and regulation

2.1.1 Heat stress

Thermophiles have optimal growth temperatures

higher than 45 ℃ and are widely distributed in hot springs and deep-sea hydrothermal vents (Schmid et al., 2020). To maintain essential functions such as translation under thermal stress, they employ specialized sRNA-guided modification systems, like stabilizing the secondary and tertiary structures of tRNA and rRNA, assisting in rRNA folding and ribosome assembly by acting as "molecular chaperones", and modifying tRNA to ensure translational accuracy.

A key example is the C/D box sRNA in *Pyrobaculum oguniense*, which was isolated from a hot spring in Japan (Bernick et al., 2012) and grows at temperatures up to 90 ℃ (Lui et al., 2018). The C/D box sRNA is approximately 50 nt in length and contains highly conserved C (RUGAUGA consensus) and D (CUGA) box sequences at the 5' and 3' ends of the molecule, respectively, and less conserved versions (designated C' and D') near the center of the molecule (Balakin et al., 1996) (Figure 2a). This structure first folds their conserved C/D and C'/D' motifs into K-turn and K-loop structures, which recruit the L7Ae/NOP5 complex. The L7Ae protein is responsible for recognizing K-turn and K-loop structures, while the NOP5 protein acts as a scaffold to link L7Ae and C/D box sRNAs and recruit fibrillarin, which exerts catalytic activity to carry out 2'-O-methylation modification on target RNAs (Omer et al., 2002). The dual guide sequences then simultaneously position target RNAs within 100 nt, where fibrillarin nucleolar methyltransferase catalyzes parallel 2'-O-methylation, raising the local melting temperature by ~1.5 ℃ and reducing hydrolysis and structural disorder to stabilize rRNA structures and ensure ribosome assembly under thermal stress (Su et al., 2013) (Figure 2b). This regulatory unit can further undergo retargeting through gene duplication and transposon-driven amplification, generating a versatile modification repertoire that accelerates genomic adaptation to the environment.

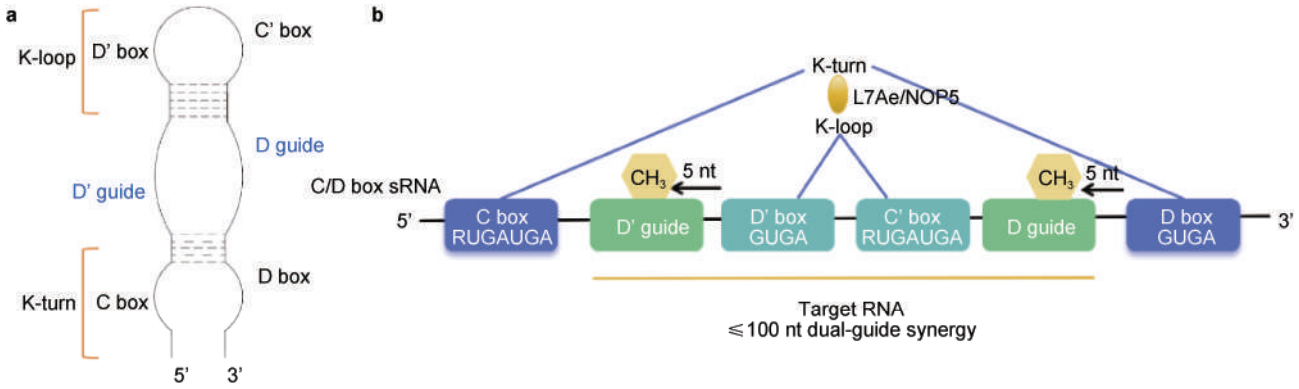

Figure 2 Schematic diagrams illustrating the structure (**a**) and the regulatory mechanism (**b**) of C/D box sRNA. **a**, the dashed lines represent base pairing. The C box and D box form a K-turn structure, while the C' box and D' box form a K-loop structure. **b**, a schematic diagram of the unfolded C/D box sRNA. The yellow oval represents the L7Ae/NOP5 complex, and the yellow lines represent the target RNA. The black arrows and the label "5 nt" refer to the position of the methyl group five nucleotides after the D and D' guide. The sRNA binds to the target RNA after undergoing 2'-O-methylation.

Deinococcus radiodurans, isolated from canned ground meat (Cox and Battista, 2005), is an extremely resistant bacterium that has evolved masterful strategies to survive under various environmental stress conditions. Under heat stress, sRNAs play important regulatory functions in *D. radiodurans*. Two heat-inducible sRNAs, DnrH and dsr11, have been identified as critical post-transcriptional regulators of thermotolerance (Xue et al., 2019, 2020). DnrH is strongly induced under thermal stress (e.g., 48 ℃), with its 28-nt sequence (nt 143–170) forming a 22-nt base pair with the Hsp20 mRNA (nt 91–117), thereby positively regulating its transcription and enhancing thermotolerance (Figure 3a). Knocking out DnrH or altering its pairing region significantly reduces thermotolerance (Xue et al., 2019). Similarly, dsr11 transcription is upregulated 4.2-fold under heat stress. This sRNA directly binds to the mRNAs of *trmE* (encoding tRNA-modifying GTPase) and *dr_0651* (encoding arginase). It regulates the expression of genes related to heat stress response, metabolism, and DNA repair, thereby ultimately enhancing the strain's tolerance to heat stress (Figure 3b). Knocking out dsr11 substantially impairs bacterial survival at high temperatures (Xue et al., 2020).

2.1.2 Cold stress

In extremely cold environments, microorganisms have evolved a set of survival strategies with the help of sRNA regulatory networks to achieve adaptation to low temperatures from multiple dimensions, covering the fine regulation of gene expression, RNA stability and metabolic pathways at multiple levels. Psychrophilic bacteria, adapted to cold environments like polar regions and glaciers, are essential in element cycling and energy flow (DeMaere et al., 2013).

Psychrobacter aquaticus, a psychrophilic, salt-tolerant, and non-motile bacterium isolated from cyanobacterial mats in the McMurdo Dry Valley, Antarctica (Bozal et al., 2003; Shivaji et al., 2005). In *P. aquaticus*, the well-characterized

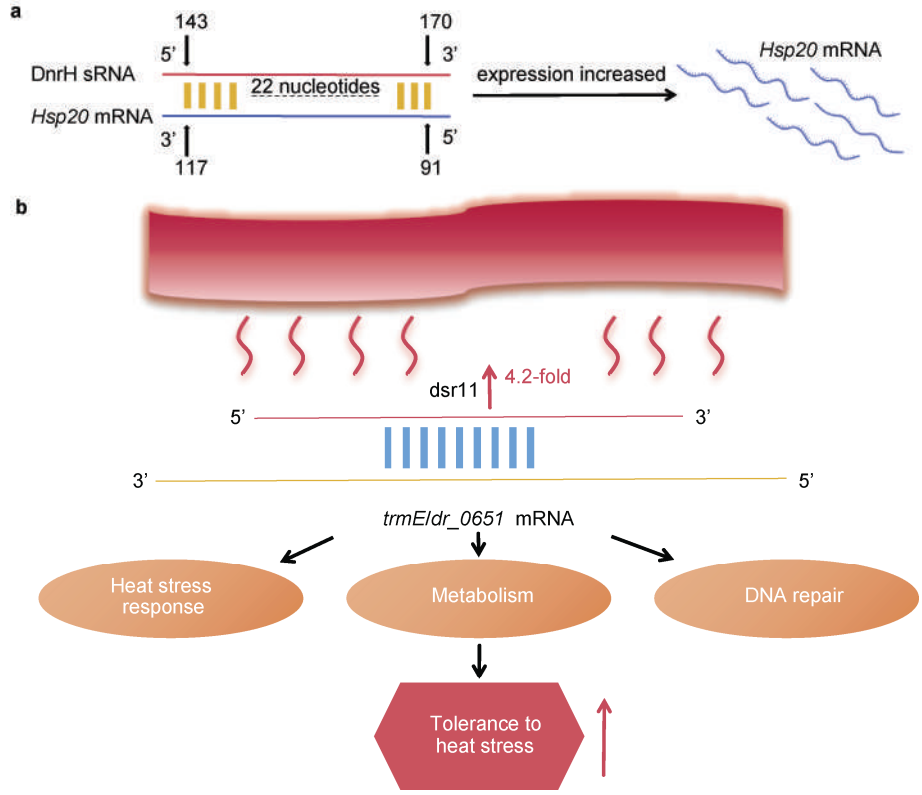

Figure 3 The regulatory mechanism of DnrH (**a**) and dsr11 (**b**) in *Deinococcus radiodurans*. In the diagram, the red lines represent sRNAs, the blue/yellow lines represent the target mRNAs corresponding to the sRNAs, the vertical lines between the two horizontal lines represent base pairing, and the orange ovals represent microbial physiological functions.

sRNA involved in cold adaptation is cis38 sRNA. It base-pairs with its target mRNA, *rhlB*, with perfect complementarity via a conserved and stable "seed region" (Nawaz et al., 2024) (Figure 4). By regulating *rhlB*, which encodes a cold-essential ATP-dependent RNA helicase, cis38 sRNA mediates RNA stability and translation efficiency at low temperatures. The complex formed by cis38 and *rhlB* mRNA exhibits an extremely low binding energy (−126.5 kcal·mol^{-1}) and high binding stability, which affects the structure of mRNA and thereby regulates gene expression.

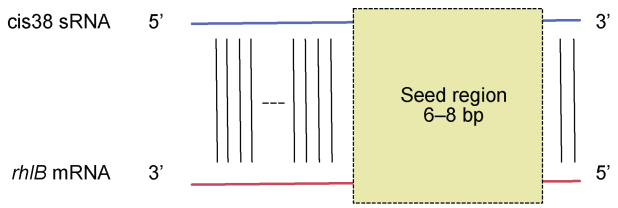

Figure 4 Interaction of cis38 with target genes in *Psychrobacter aquaticus*. The sRNA (blue line) forms complete base pairing (vertical lines) with target mRNAs (red lines) via the seed region (yellow rectangular area), with 6–8 bp involved in the interaction.

Beyond the example above, cold-adapted bacteria possess a broader repertoire of sRNAs that collectively underpin survival and fitness in the cryosphere. New CsrB-family sRNAs (Pf1–Pf3) have been identified in the cold-adapted bacterium *Pseudoalteromonas fuliginea*, a species widely distributed in polar oceans. These sRNAs regulate glycogen synthesis, carbon metabolism, and ion transport by sequestering CsrA proteins, thereby modulating stress responses (Duan et al., 2025; Wen et al., 2023). *Caulobacter crescentus* is capable of surviving at temperatures as low as −80 ℃ (Mazzon et al., 2008). When the temperature drops, the expression of a sRNA named CcnA, which regulates the cell cycle, is upregulated in *Caulobacter crescentus* (de Araújo et al., 2021). CcnA base-pairs with the 5' untranslated region (5' UTR) of target mRNAs to achieve dual control by masking or exposing the ribosome-binding site (RBS). It represses the translation of *gcrA* mRNA, an activator of DNA replication, and enhances the translation of *ctrA* mRNA, a key replication inhibitor (Beroual et al., 2022). This dual regulation results in cell cycle arrest at the G1 phase, reducing energy consumption and enabling the bacterium to adapt to extreme cold environments (de Araújo et al., 2021).

2.2 Oxidative stress

Extreme low temperatures, low water availability, frequent freeze-thaw cycles, strong winds, and ultraviolet radiation promote ROS production and induce oxidative stress (Abrashev et al., 2025). To survive under high levels

of ROS, extremophiles utilize sRNAs via a rapid and precise regulatory network to facilitate bacterial adaptation to oxidative damage and maintain intracellular homeostasis.

A case in point is the model archaeon *Haloferax volcanii*, which was first isolated from sediment samples of the Dead Sea in Israel (Mullakhanbhai and Larsen, 1975). This archaeon is frequently exposed to high levels of ROS in natural settings. Under oxidative stress, sRNA SHOxi is upregulated and binds to malic enzyme mRNAs, leading to their degradation. This reduction in NADH biosynthesis helps maintain NAD^+/NADH homeostasis, thereby limiting respiratory chain-derived ROS production and enhancing antioxidant capacity (Gelsinger et al., 2021). Similarly, the sRNAs OsiA and OsiR from *Deinococcus radiodurans* stabilize the mRNAs encoding catalases (*katA* and *katE2*), thereby enhancing the capacity to clear ROS (Chen et al., 2019).

Apart from direct regulation, sRNAs weave a broader regulatory network that indirectly enhances bacterial survival under oxidative stress. *Pseudomonas extremaustralis*, an Antarctic bacterium, is well-adapted to extreme environments (Tribelli et al., 2012). As a native inhabitant of Antarctica, it frequently encounters conditions like drought and high radiation, which inevitably induce oxidative damage. To counteract this stress, the expression of sRNA40 is significantly upregulated. This sRNA enhances bacterial resilience by targeting key components of the type II secretion system (T2SS), which is responsible for secreting antioxidant-related proteins. Through this mechanism, sRNA40 indirectly improves the adaptability to survive under oxidative stress (Solar Venero et al., 2022).

2.3 Radiation stress

Radiation-resistant bacteria living in nuclear reactors and outer space (Daly, 2009) are frequently exposed to radiation stress. However, they can endure high doses of ionizing radiation (typically exceeding 5,000 Gy) and still maintain viability (Cox and Battista, 2005). They rely on sRNAs to achieve rapid and precise stress responses and repair regulation at the post-transcriptional level, counteracting DNA double-strand breaks and oxidative damage induced by ionizing radiation, UV radiation, desiccation, and other stresses (Daly, 2009). Notably, *Deinococcus radiodurans*, a species originally isolated from canned ground meat, can endure radiation doses as high as 15,000 Gy, which ranks it among the most renowned extremophiles in this category (Cox and Battista, 2005).

In *D. radiodurans*, sRNA enhances cell viability through several mechanisms. Radiation exposure induces the production of DrsS sRNA, which directly interacts with the coding region of *katA* mRNA. This interaction promotes the expression of the *katA* gene (encoding catalase), leading to elevated intracellular catalase levels that scavenge endogenous ROS and mitigate radiation-induced oxidative damage (Figure 5a). Additionally, DrsS modulates intracellular metal ion homeostasis, elevating the cellular Mn (II) concentration and sustaining a high Mn^{2+}/Fe^{2+} ratio. This ion balance fosters the formation of a "protein protective shield", which mitigates protein carboxylation and alleviates oxidative damage to proteins (Figure 5b) (Rai and Dutta, 2024).

As the first identified sRNA involved in radiation stress repair in *D. radiodurans*, PprS functions by targeting and stabilizing *pprM* mRNA (Table 1) (Villa et al., 2021). This action, in turn, indirectly modulates the expression of DNA repair and oxidative stress-related genes (Ohba et al., 2009). Following radiation exposure, the reduced abundance of PprS leads to instability of *pprM* transcripts, reducing the expression of *pprM* (Villa et al., 2021). This alleviates the repression of PprA protein, which is responsible for DNA repair (Adachi et al., 2014). Concurrently, KatA acts synergistically to eliminate ROS (Figure 5c). Moreover, PprS functions in coordination with global transcriptional regulators like PprI (Gao et al., 2005) and DrRRA (Wang et al., 2012) to safeguard cellular repair and survival.

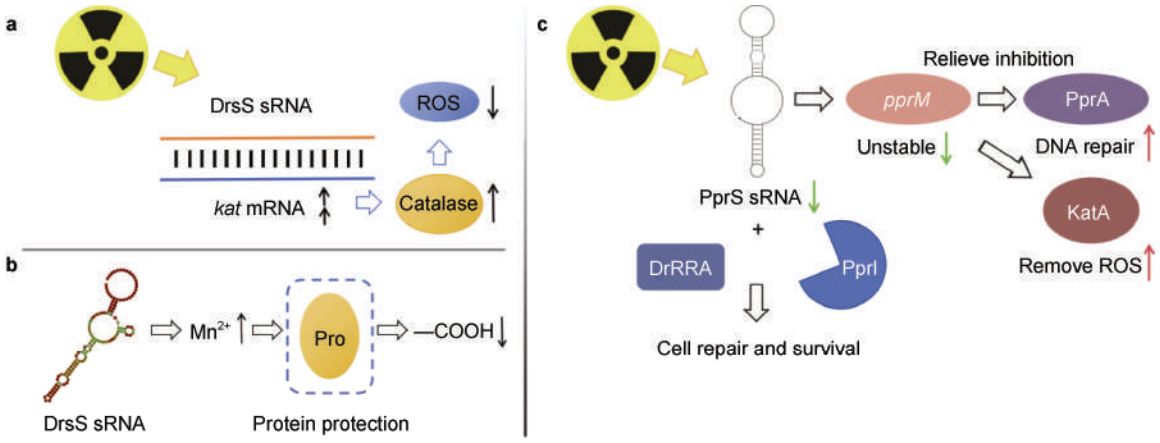

Figure 5 **a**, mechanism of DrsS sRNA regulation of catalase in response to oxidative damage under radiation; **b**, DrsS sRNA regulation of protein protection through Mn^{2+} to reduce oxidative damage. Among them, "–COOH" refers to reducing the carboxylation of proteins; **c**, model of PprS regulatory network in *Deinococcus radiodurans*.

2.4 Osmotic stress

Halophiles are microorganisms that grow and reproduce in high salt environments, such as salt lakes and salt flats (Schmid et al., 2020). They have evolved a series of strategies to adapt to a wide range of salt concentrations. In response to osmotic stress, sRNAs play an important role. sRNA synthesis consumes far less energy than protein transcription factors. Their rapid degradation relieves the burden of continuous expression, fitting the ATP-scarce metabolic state under high-salt conditions (Kliemt et al., 2019). By directly interacting with target mRNAs or proteins, sRNAs can fine-tune ion transport, compatible solute accumulation, and stress-response pathways (Gunde-Cimerman et al., 2018), thereby enabling microorganisms to dynamically adapt to osmotic challenges and balance the competing demands of growth and survival.

Vibrio alginolyticus, widely distributed in marine and estuarine environments (Koralage et al., 2012), employs sRNA-mediated post-transcriptional regulation to modulate osmotic stress tolerance at high NaCl and ethylene glycol concentrations (Deng et al., 2019a). Specific sRNAs (e.g., srvg23535) base-pair with target mRNAs to regulate the stability or translation efficiency of genes involved in metabolism and stress response. Deletion of srvg23535 significantly increases ethylene glycol tolerance, likely because its predicted target gene, *BAU10_15400*, encodes an ABC transporter permease. This protein facilitates the transport of small molecules across the membrane and may mitigate osmotic stress by regulating the cellular balance of ethylene glycol (Deng et al., 2018, 2019b).

Table 1 Examples of different types of sRNAs

Species	Strain type	sRNA	Target	Target function	Reference
Vibrio alginolyticus	Halophile	srvg23535	*BAU10_15400*	Osmotic stress	Deng et al., 2018
Deinococcus radiodurans	Radiation-tolerant bacteria	OsiA, OsiR	*katA, katE2*	Oxidative stress	Chen et al., 2019
Deinococcus radiodurans	Radiation-tolerant bacteria	DrsS	*katA*	Radiation stress	Rai and Dutta, 2024
Deinococcus radiodurans	Radiation-tolerant bacteria	pprS	*pprM*	Oxidative stress, radiation stress	Villa et al., 2021
Deinococcus radiodurans	Radiation-tolerant bacteria	DnrH	*Hsp20*	Heat stress	Xue et al., 2019
Deinococcus radiodurans	Radiation-tolerant bacteria	dsr11	*trmE, dr_0651*	Heat stress	Xue et al., 2020
Pyrobaculum oguniense	Thermophile	C/D box sRNAs	rRNA	Heat stress	Lui et al., 2018
Psychrobacter aquaticus	Psychrophile	cis38	*rhlB*	Low temperature resistance	Nawaz et al., 2024
Pseudoalteromonas fuliginea BSW20308	Psychrophile	Pf1	CsrA	Low temperature resistance	Wen et al., 2023
Caulobacter crescentus	Psychrophile	CcnA	*ctrA/gcrA*	Low temperature resistance	de Araújo et al., 2021
Pseudomonas extremaustralis	Psychrophile	sRNA40	T2SS	Oxidative stress	Solar Venero et al., 2022

3 Summarization and prospects

This review provides a systematic examination of sRNAs in adaptation of extremophilic microorganisms to extreme habitats such as hydrothermal vents, Antarctic subglacial lakes, and hypersaline basins. As pivotal regulatory molecules in extremophiles, sRNAs enable rapid, energy-efficient, and versatile ("one-to-many") responses to environmental stress. Under diverse extreme conditions, they fulfill distinct core functions: during thermal stress, they stabilize nucleic acid structures and modulate the cell cycle; under oxidative and radiation stress, they activate antioxidant systems and enhance DNA repair mechanisms; and in osmotic stress, they restore intracellular equilibrium by regulating ion channels and solute accumulation.

Despite significant progress in sRNA research, several critical challenges remain. First, identifying sRNAs in extremophiles remains challenging due to the limited genomic characterization of most extremophilic microorganisms and the general unculturability of these microorganisms. Second, although high-throughput sequencing has identified numerous sRNAs (Sharma and Vogel, 2014), functional annotation remains incomplete, especially for non-model species such as polar "microbial dark matter". Current research on sRNAs from extreme environments has merely scratched the surface, representing only the tip of a vast unexplored iceberg. Third, current studies often rely on mesophile-based knowledge and fail to capture extremophile-specific mechanisms, such as sRNA structural stability under extreme conditions and their interplay with RNA chaperones. Finally, certain extreme ecosystems, particularly polar environments, remain understudied despite harboring unique adaptive strategies.

To address these gaps, future research should focus on five interconnected dimensions. Technologically, optimized deep sequencing and single-molecule tracking, coupled with high-throughput functional validation, are needed to systematically identify and characterize extremophile sRNAs. Mechanistically, efforts should decode how sRNAs are synthesized and maintain structural integrity under extremes, as well as how they interact with cellular components in these environments. Evolutionally, studies should investigate the evolution and diversity of sRNAs across species and environmental contexts. Ecologically, the

intercellular roles of sRNAs merit exploration, including their potential transport via outer membrane vesicles and their function in cross-species signaling within extremophilic communities. Application-wise, extremophile sRNAs offer promising avenues for engineering biosensors, enhancing bioremediation, and fine-tuning the production of industrially relevant extremozymes.

Particular attention should be paid to polar ecosystems, which host a vast reservoir of microbial "dark matter" adapted to freezing temperatures, nutrient scarcity, and intense radiation. These environments likely harbor novel sRNA-mediated strategies, such as maintaining translational efficiency in the cold or regulating antifreeze protein synthesis that could provide fresh insights into extremophilic adaptation and inspire new tools for cold-active enzyme engineering and ecosystem monitoring.

Ultimately, advancing this field will require sustained technological innovation and interdisciplinary collaboration. By unraveling the regulatory logic of sRNAs in extremophiles, we can not only deepen our understanding of life's limits on Earth but also harness these molecules for biotechnology and environmental stewardship.

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