Regulating with RNA in Bacteria and Archaea
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It took time to realize, but now it’s clear: the field of prokaryotic RNA biology is here. The science of how RNA is made, processed, regulated, modified, translated, and turned over has established itself as a core discipline in molecular microbiology. A central aspect is the understanding that RNA molecules function as regulators and sensors across both the archaea and bacteria, often with striking similarity to the complex world of noncoding RNA of eukaryotes.

It has developed in waves, starting with the discoveries of basic mechanisms and factors of gene expression in the 1960s and 1970s, when bacteria were the workhorses of the emerging field of molecular biology. As molecular tools advanced, the 1980s and 1990s not only provided insights into the underlying molecular mechanisms but also saw bacteriologists stumble upon the first RNA molecules with regulatory functions, creating a sense that there might be more in the transcriptomes of these seemingly simple organisms than the established triumvirate of mRNA, tRNA, and rRNA.

As the old century gave way to the new, the next wave broke: systematic genome-wide searches unearthed small RNAs, riboswitches, and RNA thermometers in stunning numbers and diversity. Concomitantly, investigation of the mechanisms and cellular targets of these new cis- and trans-acting RNAs showed that they played by defined molecular rules and used protein cofactors such as the protein Hfq or, more recently, ProQ. It became increasingly obvious that there is a whole layer of gene expression control above that of transcriptional regulation. Again, bacteria were the trailblazers, but it soon emerged that their sister group in the noneukaryotic world, the archaea, were also full of interesting regulatory RNA molecules that share features with both bacterial and eukaryotic noncoding RNA. And of course, there was CRISPR (clustered regularly interspaced short palindromic repeat)-Cas, whose rise as a revolutionary genome-editing tool in
biomedicine and biotechnology originated in part in deciphering the function of particularly enigmatic noncoding RNAs in bacteria.

Many of these recent discoveries in prokaryotic RNA biology were made possible by new technology, be it genome sequencing, which fed global biocomputational searches, or technology for global transcript profiling—microarrays at first, now largely replaced by RNA deep sequencing. The latter now drives the next wave, in which RNA biology has gone global in new ways: through methodology that can track individual transcripts from birth to death, with high temporal resolution and in concert with the behavior of all other transcripts in the same cell; by drafting comprehensive RNA maps that can immediately highlight important RNA players under previously ignored physiological conditions or in an organism never looked at before; and global in the sense that we have so far investigated only a tiny sliver of the microbial world, and our attention is increasingly drawn to the astoundingly diverse bacteria of the human microbiota and environmental communities, promising new surprises for RNA biology.

Against the backdrop of this ongoing RNA revolution, the editors of Regulating with RNA in Bacteria and Archaea should be congratulated on having put together an excellent collection of chapters that in their sum easily convey the excitement of this field. Catering to principal investigators, postdocs, and advanced students alike, this book gives a comprehensive account of the state of the art of the prokaryotic RNA inventory and underlying molecular mechanisms. It also provides a sense of what the next decade may bring, with regard to global discovery on the genome scale, enhanced structural and molecular resolution, and a deeper mechanistic understanding of cellular RNA molecules; the reader will find all of these aspects covered. It is a pleasure to see that the author list is a healthy mix of established researchers known for their seminal contributions to prokaryotic RNA biology and young scientists who have only recently started independent work on regulatory RNA. On top of that, several chapters are focused on general aspects of bacterial gene expression that are crucially relevant to our understanding of the activities and consequences of RNA-based regulation. I hope the reader will find Regulating with RNA in Bacteria and Archaea as exciting as I, and the authors of the following chapters, do.

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In 1961, Jacob and Monod hypothesized that the regulator of the lac operon might be an RNA (1). When it was discovered that the Lac repressor was a protein, the possibility that an RNA could be a regulator was largely forgotten, with a few notable exceptions. The first “unusual” RNA regulators found included antisense RNAs that controlled plasmid replication as well as transposition (reviewed in references 2 and 3). Subsequently, a handful of chromosomally encoded small regulatory RNAs (sRNAs) that act by base-pairing with trans-encoded mRNAs were discovered in bacteria. Typically, identification was serendipitous, for example, due to overexpression phenotypes or the detection of bands by phosphate labeling or Northern blot analysis (reviewed in references 3 and 4). The realization that sRNAs are a large class of regulators came from bioinformatic searches for conserved intergenic regions as well as systematic sequencing of cDNAs corresponding to small transcripts (reviewed in references 5 and 6). Another major step in the appreciation that RNAs are widespread and important regulators was the discovery that the 5’ untranslated regions of mRNAs can function as sensory elements responding to the binding of tRNAs or small molecules with connections to the functions of the downstream genes (reviewed in references 7 and 8).

The initial characterization of individual RNAs on a “gene by gene” basis followed by the recent expansion to genome-wide analysis exploiting deep sequencing have made it clear that RNA regulators rival transcription factors with respect to their regulatory scope (reviewed in reference 9). These studies have been revealing that regulatory RNAs are part of an incredibly intricate regulatory network. For example, sRNAs frequently regulate multiple and sometimes dozens of transcripts. At the same time, sRNA concentrations can be affected by their binding to chaperone proteins as well as RNA “sponges,” which can be independent sRNAs, degradation products of mRNAs, or tRNA fragments. While many of the initial studies of regulatory RNAs were carried out in model bacterial organisms, the advances in
sequencing technologies have facilitated their discovery in a wide range of microbial species, indicating that regulatory RNAs are present in all organisms.

Given the amazing progress that has occurred in the study of regulatory RNAs in bacteria and archaea in the past 20 years, we thought a summary of current knowledge would be a useful resource. Thus, the chapters in this book cover well-characterized cis-encoded RNA thermometers, T-box regulators, riboswitches, and regulatory RNA elements within mRNA transcripts, antisense RNAs, as well as trans-encoded base-pairing and protein-binding sRNAs. These chapters illustrate how regulatory RNAs are an integral part of most microbial responses, including adaptation to stressful environments and changes in nutrient availability, and contribute to pathogenesis.

We hope the book also will focus attention on open questions in the field and stimulate further research in these areas. Despite the significant progress, there are aspects of regulatory RNAs in bacteria and archaea that are still poorly studied. The improved sequencing technology has revealed that much of bacterial and archaeal genomes is transcribed and that there are regulatory RNAs in “blind spots” that were previously ignored. For example, it is becoming increasing clear that 3′ untranslated region-derived transcripts are a major class of base-pairing sRNAs. There additionally are many RNA regulators about which less is known in general, including protein-binding RNAs, RNAs with dual functions, and larger RNAs whose structural complexity rivals that of ribosomes. Future studies should illuminate the molecular underpinnings of what distinguishes different classes of regulatory RNAs and whether clear distinctions are appropriate. New areas of research necessarily will involve not only the RNA components themselves and their modifications but also their associated protein partners and the spatiotemporal parameters underlying their interactions in the cell.

As for many fields of research, our understanding of microbial RNA-based gene regulation comes largely from a few model bacterial organisms such as *Escherichia coli* and *Bacillus subtilis*. Although it is tempting to apply lessons learned from these organisms to other species, it is likely that there are important differences. The availability of an exponentially increasing number of data sets for total RNA or RNAs that coimmunoprecipitate with particular proteins or associate with other RNAs in a wide range of organisms undoubtedly will uncover unique features as well as further common principles of RNA-mediated gene control in bacteria and archaea. Understanding and generalizing these principles will be key for the design of synthetic RNA regulators for applications in biotechnology and medicine. Cross-species comparisons also should facilitate the development of hypotheses about the evolution of regulatory RNA elements and whether the evolution differs from that of protein counterparts.

The final chapters of the book discuss how the remarkable expansion of data necessitates new ways of analyzing and visualizing the information. This includes new strategies to extract and present relevant information from genome-wide gene expression analysis, which should help to uncover common principles of RNA-mediated gene control in bacteria and archaea. Given that standard bacterial genome annotations typically fail to include regulatory RNAs, annotation is still incomplete and the number of microbial regulatory RNAs is unknown.

In summary, these are exciting times for microbiologists, particularly for those studying the regulatory RNA complement encoded by microbes. We think this book summarizes the most significant information gained from studies on RNA-based gene regulation in prokaryotes over the past few decades and will serve as a useful resource for researchers new to the field. Furthermore, the book summarizes open questions that hopefully will inspire new research directions and
approaches. We would like to conclude by thanking our many colleagues who so willingly contributed chapters and provided comments that significantly improved the content of this book.

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