The cold shock response and adaptation have been extensively studied in Escherichia coli and Bacillus subtilis. Cytoplasmic membranes, RNA/DNA, and ribosomes are suggested to be the cellular thermosensors. The major effects of cold shock are a decrease in membrane fluidity and the stabilization of secondary structures of RNA and DNA, which may affect the efficiency of translation, transcription, and DNA replication. The organisms overcome the membrane fluidity problem by decreasing the degree of saturation of fatty acids in the membrane phospholipids. In the case of B. subtilis and cyanobacteria, desaturases play an important role in alteration of the degree of saturation of fatty acids in the membrane phospholipids to restore the membrane-associated functions. Cold-inducible proteins overcome the deleterious effects of the cold shock on transcription and translation. CspA, the major cold shock protein of E. coli, is a β-barrel protein with two RNA-binding motifs. It is proposed to function as an RNA chaperone that facilitates translation at low temperature by preventing formation of secondary structures in RNA molecules. The expression of cspA at low temperature is regulated at the levels of transcription, mRNA stability, and translation. CspA-homologs are widely distributed in bacteria, and in some cases, these proteins are essential for survival even under optimal growth conditions.

Temperature is one of the major stresses that all living organisms face. In contrast to the heat shock response (see chapter 1) which has been extensively studied from bacteria to humans, the cold shock response has caught the attention of researchers recently. The study of the cold shock response and adaptation is important for our understanding of how microorganisms are able to live under low temperature stress and for improvement of cold tolerance in plants and useful microbes. In addition, the cold shock response and adaptation have important health implications. As refrigeration is a commonly used method for extending the shelf life of food, it is necessary to understand the cold shock response of food-spoilage bacteria. One such example is Listeria monocytogenes, an opportunistic food-borne pathogen. This bacterium causes listeriosis, a disease primarily affecting pregnant woman, neonates, and immunocompromised patients, such as those with AIDS or undergoing corticosteroid therapy (5). The study of the cold shock response and adaptation is also important in bacteria such as Lactobacillus, which are widely used in the dairy industry (13).

The cold shock response and adaptation have been studied in detail using Escherichia coli and Bacillus subtilis as model systems (see reviews in references 35, 39, 49, 66, 68, 84, 94, 95). As a result of excretion from animals, enterobacteria such as E. coli encounter sudden drastic temperature downshift. Thus, the cold shock response and adaptation in this bacterium confer a selective advantage of quick adaptation to the new environment. In this chapter, we will discuss two important aspects of the cold shock response: how bacteria sense the change in temperature (i.e., what the cellular thermosensors are) and how they cope with the cold stress. We will also discuss cold shock proteins, especially CspA and its homologs, with respect to the regulation of their synthesis and their structure and function.

CELLULAR THERMOSENSORS FOR COLD SHOCK

- The cytoplasmic membrane, nucleic acids, and ribosomes are implicated in sensing temperature changes. The cold shock response and adaptation in E. coli are summarized in Fig. 1.
scription and translation, have been indicated, but elaborate and extensive research is essential for thorough elucidation of functions of cold shock proteins. This lack of information has limited the design of strategies to identify the key regulatory factors responsible for survival of the organism after cold shock and for preventing cold adaptation of food-poisoning bacteria.

One of the important aspects of the study of the cold shock response and adaptation in bacteria is regarding health issues and economy of many industrial processes involving bacterial fermentations. As refrigeration is a commonly used method for extending the shelf life of food, it is necessary to understand the cold shock response and adaptation of food-spoilage bacteria, such as Clostridium (22), Enterococcus (83), Listeria (5), Pseudomonas (57), Vibrio (56), and Yersinia (33). Understanding the expression of cold shock proteins and designing means for decreasing their accumulation can potentially reduce the efficacy of the cold shock response and adaptation and prevent growth of bacteria at low temperatures. The knowledge acquired through the study of the cold shock response and adaptation in E. coli and B. subtilis as model systems can be applied to other organisms. It is reported that if B. subtilis cells are cold shocked before freezing, the viability during the freezing is enhanced. This is probably because the cold shock proteins somehow protect cells from the cold damage caused by freezing (93). On this basis, the food-spoilage bacteria can be sensitized to damage through direct freezing itself, and cold shock-induced cryotolerance may contribute to the development of processes that allow improved viability/activity of frozen or freeze-dried commercial lactic acid bacteria starter cultures (13, 51). In addition, Rhizobium isolated from arctic (psychrotrophic) legumes is of considerable interest in agricultural industry because of its potential to improve nitrogen fixation of legumes cultivated in temperate climate, where low temperature limits the efficiency of the symbiosis (14). Furthermore, a desaturase from cyanobacteria that plays an important role in maintaining the membrane fluidity after cold shock confers chilling resistance to tobacco plants (42). These instances imply that in the future the study of the cold shock response and adaptation is going to play a major role in biotechnology.

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REFERENCES

18. Echegaray, J.-P., and M. Inouye. 1999. CspA, CspB, and CspG, the major cold shock proteins of Escherichia coli, are


88. Vigh, L., D. A. Los, I. Horvath, and N. Murata. 1993. The primary signal in the biological perception of temperature: Pe-


