Symbioses of Methanotrophs and Deep-Sea Mussels (Mytilidae: Bathymodiolinae)

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1 Introduction

Symbioses between marine invertebrates and methanotrophs provide the bacteria with access to methane and oxygen and other substrates necessary for metabolism and the invertebrate host with a source of organic carbon. Methanotrophic bacteria utilize methane for generating ATP through oxidative phosphorylation and for the net synthesis of organic compounds used in cellular metabolism. Because methane is typically produced in anoxic environments, through either biological (the action of methanogenic Archaea) or inorganic processes, free-living aerobic methanotrophs are limited to the microaerophilic interface between oxic and anoxic zones (Anthony 1982). But in methanotrophic symbioses the invertebrate host acts as a “bridge” across the oxic-anoxic interface (as in chemoautotroph symbioses; see previous chapter), facilitating access to both oxygen and methane for the endosymbionts (Cavanaugh 1985; Cavanaugh et al. 2005). The methanotrophs in turn consume methane and provide the host with a sustainable carbon source not directly available to metazoans. The host derives other essential elements (e.g., N, P, S) from the symbiont and/or environmental sources.

The symbioses between mytilid mussels in the genus *Bathymodiolus* (family Mytilidae; subfamily Bathymodiolinae) and type I methanotrophic bacteria are the most prevalent, widespread, and best understood of the aerobic methane-based associations. Bathymodioline symbioses are globally distributed at deep-sea hydrothermal vents and cold seeps (Fig. 1, Table 1; von Cosel et al. 1994; O’Mullan et al. 2001; van Dover et al. 2001; Fiala-Médioni et al. 2002) and depending on the host mussel species, harbor either methanotrophs, chemoautotrophs (that oxidize reduced inorganic compounds accompanied by CO_2 fixation; see previous chapter), or both of these two metabolically and phylogenetically distinct gamma Proteobacteria

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endosymbionts simultaneously (e.g., Distel et al. 1995; Dubilier et al. 1999). Methanotrophs and chemoautotrophs share the ability to synthesize organic compounds from C_1 compounds, utilizing both energy and carbon sources otherwise unavailable to their animal hosts. As these symbiotic bacteria have not yet been isolated in pure culture, much of the work has focused on characterizing these symbioses from physiological and phylogenetic perspectives. Recent advances in molecular techniques are permitting higher resolution examinations into symbiont distributions, evolution, and diversity.

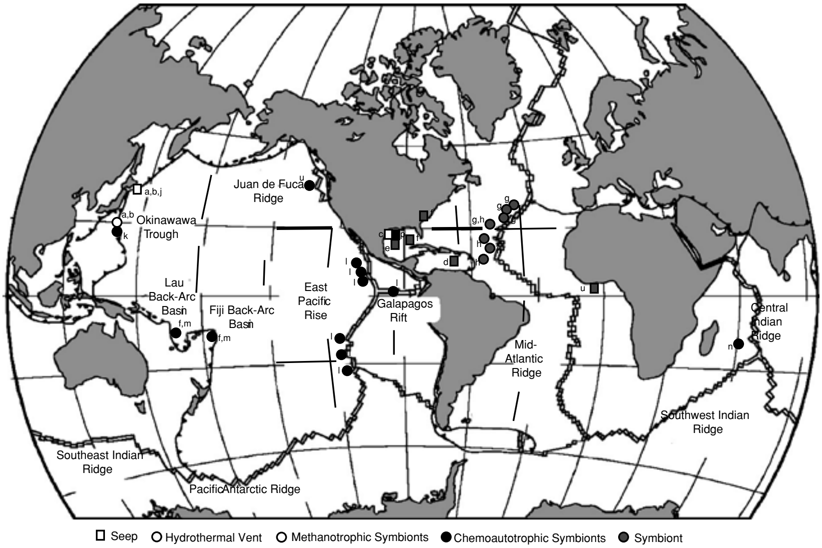

Fig. 1. Distribution of *Bathymodiolus* mussels and occurrence of methanotrophic and/or chemoautotrophic endosymbionts (modified from van Dover et al. 2002). Sites are shaded depending on the type of symbiont(s) hosted by *Bathymodiolus*. The biogeographic provinces are labeled for reference.

2 Methanotrophic Symbioses

Methanotrophic endosymbioses have only been characterized in a few marine invertebrate taxa and deep-sea habitats. Symbioses involving methanotrophs were first described in bathymodioline mussels inhabiting deep-sea cold seeps (Childress et al. 1986; Cavanaugh et al. 1987) and subsequently found in other bathymodioline mussels, a pogonophoran