Roles of Bacterial Regulators in the Symbiosis between *Vibrio fischeri* and *Euprymna scolopes*

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1 Introduction

In a symbiosis, two or more evolutionarily distinct organisms communicate with one another in order to co-exist and co-adapt in their shared environment. The mutualistic symbiosis between the bioluminescent marine bacterium *Vibrio fischeri* and the Hawaiian squid *Euprymna scolopes* provides a model system that allows scientists to examine the mechanisms by which this communication occurs (McFall-Ngai and Ruby 1991). The squid, although *V. fischeri*-free (aposymbiotic) at hatching, rapidly acquires this bacterium and promotes its growth in a special symbiotic organ called the light organ (LO). In exchange for nutrients and a niche safe from competing bacteria, *V. fischeri* provides the bioluminescence used by *E. scolopes* to camouflage itself from predators.

In this chapter, we will give an overview of the early events in establishing the symbiosis and describe associated developmental changes triggered in each organism by the interaction. We will then discuss bacterial regulators and, where known, the traits they control that are necessary for a productive interaction between *V. fischeri* and *E. scolopes*. Finally, we will conclude by highlighting important directions for future investigation.

2 Early Events in the *Euprymna scolopes – Vibrio fischeri* Symbiosis

2.1 *Vibrio fischeri* strains are specifically recruited from the seawater

V. fischeri comprises less than 0.1% of the total bacterial population in the seawater inhabited by the squid (Lee and Ruby 1992), yet this organism alone

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Progress in Molecular and Subcellular Biology
Jörg Overmann (Ed.)
Molecular Basis of Symbiosis

is found in the light organ association (Boettcher and Ruby 1990). Furthermore, inoculation in the laboratory with bacteria closely related to *V. fischeri*, including *V. harveyi* and *V. parahaemolyticus*, fails to result in colonization (McFall-Ngai and Ruby 1991; Nyholm et al. 2000). In addition to this species-specific selection, strain-specific enrichment also occurs. Both visibly luminescent and non-visibly luminescent strains of *V. fischeri* co-exist in the seawater, but only the latter strains colonize the squid LO in nature (Lee and Ruby 1994b). This strict limitation on the species and strains of bacteria capable of colonizing the LO suggests that a specific exchange of signals must occur between the squid and the bacteria early during colonization.

Within hours of hatching, *E. scolopes* recruits *V. fischeri* from the surrounding seawater. The presence of bacteria or the bacterial cell wall component peptidoglycan in the seawater causes the squid to secrete mucus (Nyholm et al. 2002), allowing *V. fischeri* cells to aggregate near pores leading into the LO (Fig. 1). Other bacteria such as *V. parahaemolyticus* also exhibit the ability to aggregate in squid mucus, suggesting that *E. scolopes* does not distinguish between *V. fischeri* and other Gram negative bacteria at this stage (Nyholm et al. 2000). However, when both *V. parahaemolyticus* and *V. fischeri* are present, the latter organism becomes the dominant species in the aggregate (Nyholm and McFall-Ngai 2003), indicating that *V. fischeri* may participate in establishing specificity at this stage.

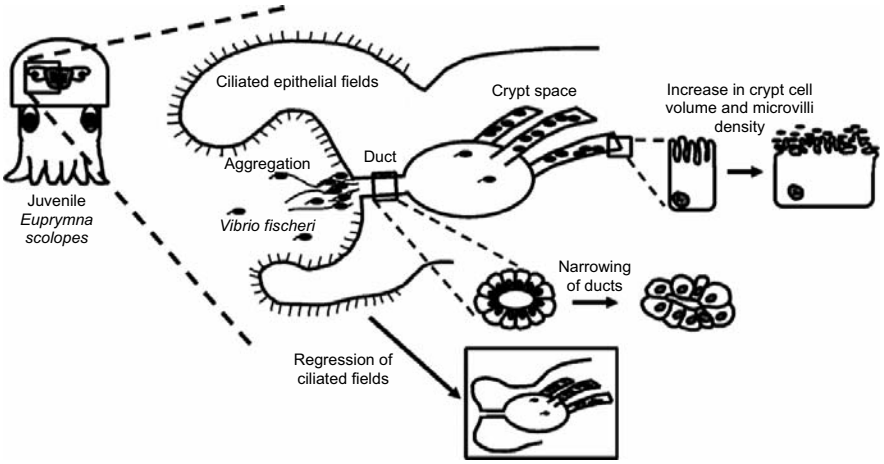

Fig. 1. Cartoon depicting the structure of and developmental changes in the juvenile squid LO during colonization. The position of the LO in a juvenile squid is shown on the *left*, while an enlarged cross section is shown on the *right*. The juvenile LO contains three pores on each side (six total), only one of which is depicted at the opening of the duct. *Arrows* indicate developmental events that occur within the first 4 days after exposure to *V. fischeri*. *Dashed lines* indicate an enlargement of the boxed area. *V. fischeri* cells are shown as *black ovals* aggregated in the mucus (depicted as *wavy lines*) outside the pore and in the crypt spaces (without flagella). This depiction of the light organ is based on Visick and McFall-Ngai (2000) and references described therein.