



## Establishment of endosymbiosis: The case of cnidarians and *Symbiodinium*

David Fransolet <sup>a,1</sup>, Stéphane Roberty <sup>b,1</sup>, Jean-Christophe Plumier <sup>a,\*</sup>

<sup>a</sup> Laboratoire d'Ecophysiologie et Physiologie Animale, Département de Biologie, Ecologie et Evolution, Université de Liège, Boulevard du Rectorat 27 (Bat. B22), 4000 Liège, Belgium

<sup>b</sup> Laboratoire d'Ecologie Animale et d'Ecotoxicologie, Département de Biologie, Ecologie et Evolution, Université de Liège, Boulevard du Rectorat 27 (Bat. B22), 4000 Liège, Belgium

### ARTICLE INFO

#### Article history:

Received 4 October 2011

Received in revised form 16 March 2012

Accepted 17 March 2012

Available online 3 May 2012

#### Keywords:

Coral bleaching

Lectins

Rab family

Recognition molecules

Symbiosis

### ABSTRACT

The symbiosis between cnidarians and *Symbiodinium* algae (dinoflagellates) is the keystone responsible for the formation of the huge and important structures that are coral reefs. Today many environmental and/or anthropogenic threats compromise this tight relationship and lead to more frequent events of drastic loss of *Symbiodinium* pigments and eventually of algae themselves from cnidarians, better known as cnidarian bleaching. While the mechanisms underlying the collapse of the algae–coral symbiosis are progressively getting unraveled, the understanding of the mechanisms involved in the de novo infection of bleached cnidarians by *Symbiodinium* remains elusive. In this review, we describe the various steps needed to establish a stable symbiotic relationship between *Symbiodinium* and cnidarians. We review the mechanisms implicated in host–symbiont recognition and in symbiosome formation and persistence, with a special emphasis on the role played by lectins and Rab proteins. A better understanding of these molecular mechanisms may contribute to the development of strategies to promote post-bleaching recovery of corals.

© 2012 Elsevier B.V. All rights reserved.

### Contents

1. Introduction . . . . .	1
1.1. The diversity of the symbiosis . . . . .	2
1.2. From the free-living state to the symbiosis . . . . .	2
2. Establishment of the symbiosis . . . . .	3
2.1. Making contact . . . . .	3
2.1.1. Lectin/glycan interactions . . . . .	3
2.1.2. Other proteins . . . . .	4
2.2. Symbiosome formation . . . . .	4
2.3. Towards a functional symbiosome . . . . .	5
3. Ecology of the symbiosis . . . . .	5
4. Conclusions . . . . .	5
Acknowledgments . . . . .	5
References . . . . .	6

### 1. Introduction

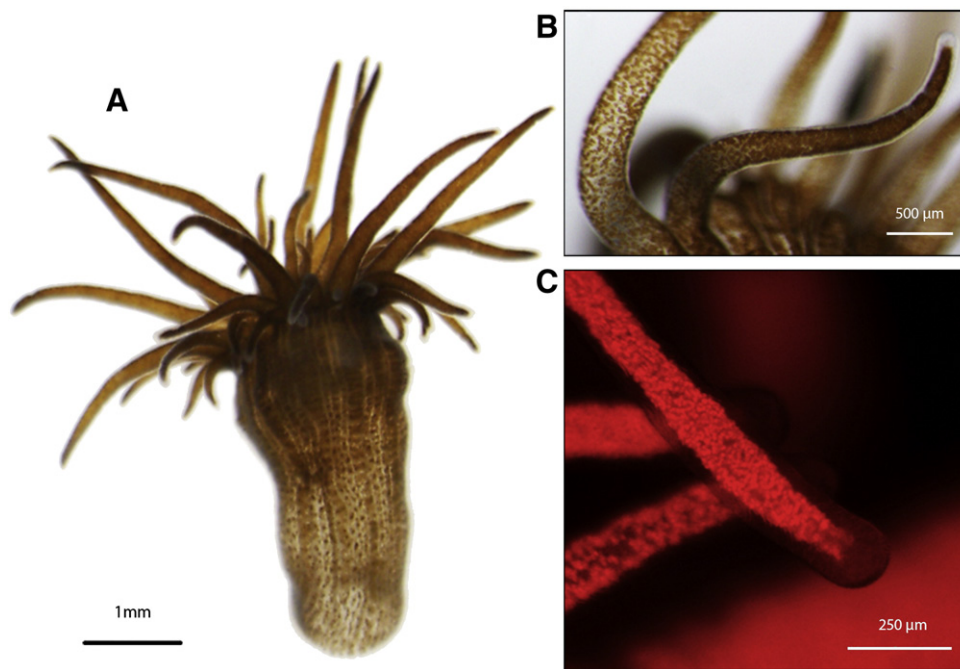
The foundation of coral reefs, one of the most diverse and productive marine ecosystems, relies on the mutualistic relationship between invertebrate hosts (scleractinian corals) and their photosynthetic dinoflagellates of the genus *Symbiodinium* (commonly referred to as zooxanthellae; Fig. 1). In the cnidarian–*Symbiodinium* associations, photosynthetic algae are located in host-derived vacuoles (symbiosomes)

within gastrodermal cells of the host (Wakefield and Kempf, 2001). Once in symbiosis, the symbiont provides up to 95% of its photosynthetic products (glycerol, glucose, amino acids or lipids) to the host (Muscatine, 1990), thus contributing massively to its energy demands (Gattuso et al., 1999). A significant part of the photosynthetically fixed carbon is translocated through processes controlled by host release factors (HRFs) which are yet to be clearly identified (Yellowlees et al., 2008). High O<sub>2</sub> concentration due to *Symbiodinium* photosynthesis also helps maintaining the high ATP level needed for the calcification process (see Jokiel, 2011). In return, the host ensures protection to the zooxanthellae and provides a source of inorganic nutrients (CO<sub>2</sub>, NH<sub>3</sub> and PO<sub>4</sub><sup>3-</sup>; see Yellowlees et al., 2008 for review). This mutual

\* Corresponding author. Tel.: +32 4 366 3843; fax: +32 4 366 3847.

E-mail address: [jc.plumier@ulg.ac.be](mailto:jc.plumier@ulg.ac.be) (J.-C. Plumier).

<sup>1</sup> Both authors equally contributed to this article.



**Fig. 1.** Illustration of the distribution of symbiotic algae in a sea anemone *Aiptasia pallida*. A. Overall view of *A. pallida* shows the general distribution of zooxanthellae. B. Closer view of some tentacles revealing the patchy distribution of brown zooxanthellae within the gastrodermis. C. The lack of chlorophyll autofluorescence in the ectodermis of a tentacle tip confirms the gastrodermal distribution of zooxanthellae.

relationship continuously adjusts to subtle changes in the environment to optimize the survival of the holobiont (entity including the host, the symbionts and the whole associated microbial fauna). In the current context of global changes threatening symbiotic cnidarians, especially reef building corals, it is critical to understand the mechanisms controlling the symbiosis in order to develop new management strategies to help preserve or improve the health of coral reefs. In this review, we describe the mechanisms involved in the various steps needed to establish a stable symbiotic relationship between *Symbiodinium* and cnidarians.

### 1.1. The diversity of the symbiosis

Although zooxanthellae were once all considered as members of a single pandemic species, *Symbiodinium microadriaticum* Freudenthal (1962), recent molecular and genetic analyses, based upon variation of nuclear ribosomal DNA (18s, ITS and 28s rDNA) and chloroplast 23s rDNA, have revealed that the genus *Symbiodinium* is divided into nine large clades (A to I), each comprising multiple strains or species (Coffroth and Santos, 2005; Pochon and Gates, 2010). Moreover, the ability for *Symbiodinium* to establish symbioses is not restricted to reef-building corals but also involves a variety of other cnidarians (octocorals, sea anemones and jellyfish) and some representatives of the Platyhelminthes, Mollusca, Porifera, Foraminifera and ciliates (see Stat et al., 2006 for review).

### 1.2. From the free-living state to the symbiosis

Under normal conditions, *Symbiodinium* densities in symbiotic corals reach a steady state wherein neither partner outgrows the other (Muscatine et al., 1989). The maintenance of this dynamic equilibrium suggests the existence of intrinsic and environmental factors that can potentially regulate algal density pre- or post-mitotically (Hoegh-Guldberg and Smith, 1989; Muscatine and Pool, 1979). This regulation involves a variety of mechanisms, like the limitation of algal nutrient supply (e.g. Falkowski et al., 1993), the digestion of algae (Jones and Yellowlees, 1997; Muscatine and Pool, 1979; Titlyanov et al., 1996), the expulsion of excess or dividing *Symbiodinium* (Baghdasarian and Muscatine, 2000; Hoegh-Guldberg and

Smith, 1989; Jones and Yellowlees, 1997), the accommodation of excess algae by division of host cells (Titlyanov et al., 1996) and possibly the production of growth inhibiting factors (Smith and Muscatine, 1999). This fine regulation of algal density also occurs on daily (Fitt, 2000; Hoegh-Guldberg et al., 1987; Jones and Yellowlees, 1997; Stimson and Kinzie, 1991) and yearly bases showing, for example, seasonal variations (Brown et al., 1999; Fagoonee et al., 1999; Fitt et al., 2000; Stimson, 1997). Expelled algae can then be recruited by gastrodermal cells or released to the ambient environment. Symbiotic algae that are released every day to the external environment, either through density regulation mechanisms (Hoegh-Guldberg et al., 1987; Stimson and Kinzie, 1991) or through survival of corallivorous species digestion (Bachman and Muller-Parker, 2007; Muller-Parker, 1984), may contribute to the maintenance of a free-living *Symbiodinium* population. Indeed, several studies report the presence of free-living *Symbiodinium* in the water column, within sediments (Adams et al., 2009; Carlos et al., 1999; Coffroth et al., 2006; Gou et al., 2003; Hirose et al., 2008a; Littman et al., 2008; Manning and Gates, 2008; Pochon et al., 2010) and in association with macroalgae beds in the vicinity of coral reefs (Porto et al., 2008). Nevertheless, the density distribution of free-living *Symbiodinium* seems to be highly heterogeneous between and within reefs (Littman et al., 2008).

Nevertheless, the symbiotic relationship is highly sensitive to environmental or anthropogenic disturbances and may be disrupted, thus leading to a phenomenon, commonly referred to as coral bleaching, in which *Symbiodinium* densities are drastically reduced (Brown, 1997; Douglas, 2003; Glynn, 1993). Debate still rages on whether expelled *Symbiodinium* following a stressful event remains viable and is able to contribute to the recovery of bleached corals. Some studies reported that a majority of expelled symbionts remained healthy (Bhagooli and Hidaka, 2004; Ralph et al., 2001, 2005; Sandeman, 2006), others claimed that *Symbiodinium* survival did not last (Hill and Ralph, 2007; Perez et al., 2001; Steen and Muscatine, 1987; Strychar et al., 2004). For instance, Hill and Ralph (2007) reported that *Symbiodinium* cells released in the water column after a thermal stress had a drastically reduced photosynthetic activity after 5 days, suggesting that their survival could be compromised. Therefore their contribution to the free-living stocks may then be limited.

Download English Version:

<https://daneshyari.com/en/article/4395974>

Download Persian Version:

<https://daneshyari.com/article/4395974>

[Daneshyari.com](https://daneshyari.com)