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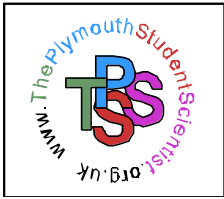
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The Role of Zooxanthellae in Marine Invertebrates

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Abstract

The importance of zooxanthellae in marine environments cannot be understated. Their role as a source of nutritive energy to corals underpins the success of reef-building systems worldwide, forming some of the most productive ecosystems on earth. The diversity of these unicellular symbiotic algae, which belong to the genus *Symbiodinium*, is enormous. Multiple hosts, multiple types of algae and the diverse habitats in which these organisms are found suggests a diverse reservoir of symbiont types in almost every region. This review focuses on the functional and genetic diversity of *Symbiodinium*, the specificity and flexibility of the host-algal association, and the implications they present. *Symbiodinium* types vary in their physiological response to environmental changes, and the possibility that hosts may alter their populations of symbiotic algae in response to external change might suggest zooxanthellae influence the ecological resilience of host species. This then raises the question of whether or not these changes are sufficient for hosts to tolerate climate change and other negative impacts on aquatic ecosystems worldwide.

INTRODUCTION

In marine environments, intimate relationships between unicellular algae and invertebrates are not uncommon. These algae, commonly referred to as zooxanthellae, predominately belong to the genus *Symbiodinium* in the phylum *Dinoflagellata* (Coffroth and Santos, 2005). Typically, zooxanthellae are associated with stony corals, which make up the majority of the world's reefs, but zooxanthellae form close mutualistic relationships with numerous hosts, including representatives of the Protista, Porifera, Cnidaria and Mollusca (Coffroth and Santos, 2005). Given that zooxanthellae are able to photosynthesise, and contain characteristic dinoflagellate pigments in addition to chlorophylls *a* and *b* (Muller-Parker and D'Elia, 1997), more often than not the basis for symbiosis is nutritional. In return for shelter, refuge, important inorganic nutrients (such as nitrates and phosphates, which the algae need to grow) and a steady supply of carbon dioxide for photosynthesis, zooxanthellae translocate enough photosynthetically fixed carbon (typically in the form of glycerol and other small molecules) to meet hosts' respiratory needs. Therefore, they playing a significant role in host nutrition and physiology (Santos, 2004). However, the dinoflagellates comprise a diverse group and thus exhibit a variety of feeding modes; in addition to photoautotrophy, there is some evidence that zooxanthellae take up dissolved organic carbon from host sea anemones, but photosynthesis is likely to contribute most of their carbon requirement (Muller-Parker and D'Elia, 1997).

Zooxanthellae reside exclusively in gastrodermal cells (Muller-Parker and D'Elia, 1997). In most cases, the algae are intracellular, residing in complex host-derived vacuoles, but some invertebrates (e.g. bivalves in the genera *Tridacna* and *Hippopus*) harbour their symbionts intracellularly in an elaborate tubular system (Coffroth and Santos, 2005). It is possible for zooxanthellae to live

independently of their animal host. Zooxanthellae living in animal cells are usually found in the non-motile, coccoid stage lacking flagella, which differs from the free-swimming motile stage that possesses two flagella and exhibits a characteristic swimming pattern (Muller-Parker and D'Elia, 1997). In laboratory culture, zooxanthellae alternate between motile and non-motile stages (Domotor and D'Elia, 1986), but once an organism is acquired by a host, the flagella are lost and the cell becomes coccoid.

LEVELS OF DIVERSITY WITHIN *Symbiodinium*

Overview

Only in the 1950s when members of the group were first successfully cultured and described did the phylogenetic diversity of the genus become apparent (Baker, 2004). Until then, the genus *Zooxanthella* referred to all algal mutualists, however, given the literal meaning of the word, this may seem inaccurate. Karl Brandt first coined the term in 1883, Gr. *zoo*=animal, *xanth*=yellow *ella*=diminutive; 'yellow animal cells', to refer to the tiny microscopic algae found in radiolarians which he suggested were mutualistic (Baker, 2004). But since not all symbiotic dinoflagellates are yellow or brown in colour (Dawson, 2007), and seeing as the term provides little taxonomic meaning (Blank and Trench, 1986), a new genus, *Symbiodinium*, was adopted (Baker, 2004). The term 'zooxanthellae' is still used, but only to describe yellow-brown endosymbionts of both dinoflagellate and diatom origin (Blank and Trench, 1986).

The genus *Symbiodinium* encompasses all dinoflagellate algal symbionts (Sampayo et al., 2007) and is exceptionally diverse (Baker, 2004). However it was once considered to be a single pandemic species, *Symbiodinium microadriaticum* (Stat et al., 2006), but as a result of research undertaken over the last few decades it is clear this is not the case. It is currently impossible to estimate how many

species of symbiotic dinoflagellates exist (Rowan, 1998), but thanks to the application of modern molecular techniques our understanding of defined symbiont diversity has radically improved (Apprill and Gates, 2007).

Since all of the data revealing symbiont diversity comes from molecular DNA studies, *Symbiodinium* is divided into different groups based on its members DNA sequences. This means that members of each group are more closely related to each other than they are to algae in other groups (Baker, 2003). The genus *Symbiodinium* is currently recognised as consisting of at least eight principle clades, A-H (Pochon et al., 2006), with each clade comprised probably of many species (Rowan, 1998).

However, the majority of these species have not been described. Because most of the different *Symbiodinium* have been documented from DNA work, and have not yet been formally described, given the vast amount of work involved, some clades have one or more named species, whereas others have none (Baker, 2003). Another reason as to why zooxanthellae are categorized into generalized groups or clades rather than defined ones is partly because there is a fundamental species problem in defining species of these algae (Rowan, 1998). There is a lack of readily discernible morphological features between different species of *Symbiodinium* (LaJeunesse, 2001), and although there is some evidence indicating that it does occur, sexual reproduction has not yet been directly observed in these organisms preventing application of the biological species concept (Baker, 2003; Blank and Trench, 1985), meaning there are lots of un-described and un-named types of *Symbiodinium*. As a result, LaJeunesse (2001) proposed that a phylogenetic species concept would be more appropriate for classifying *Symbiodinium*, whereby phylogenetic groupings are based on internal transcribed spacer (ITS) sequences, which exhibit a high degree of variation even between closely related species, providing greater systematic resolution.

SPECIFICITY AND FLEXIBILITY IN HOST-SYMBIONT PAIRINGS

Symbiont Acquisition

Hosts may acquire zooxanthellae either by maternal inheritance or from the surrounding seawater (Davy and Turner, 2003) at a variety of life history stages, depending on host species. The initiation of symbiosis in sexually produced offspring is known to occur by either of these methods whereas in clonal colonies, symbionts are primarily acquired vertically, i.e. maternally. In sexually produced animals, direct transmission of symbionts from parent to offspring takes place by way of incorporation of symbionts into the oocyte (Muller-Parker and D'Elia, 1997), guaranteeing the new host animal is provided with a complement of symbionts (Barneah et al., 2004). However, in clonal colonies, zooxanthellae are directly transmitted in fragments that form the basis of new colonies through the process of budding (Muller-Parker and D'Elia, 1997). Horizontal transmission, whereby offspring must acquire symbionts from the environment, is likely to happen as a result of positive chemotaxis of motile zooxanthellae to a suitable host. Zooxanthellae may also be supplied indirectly by ingestion of zooplankton prey or faecal material containing zooxanthellae (Muller-Parker and D'Elia, 1997) and subsequently reproduce by splitting apart. There is a risk, however, that environmental variability may prevent contact between symbiont and host, and the host may fail to establish a partnership, leaving it with severely reduced fitness (Barneah et al., 2004). Given that many cnidarian host species are obligately symbiotic with zooxanthellae, and are dependent on the association for their survival, it might be predicted that vertical transmission is the dominant mode of symbiont transmission (Schwarz et al., 1999). However, it has been shown, at least in scleractinian corals, that the majority of host species spawn gametes that are azooxanthellate (Richmond, 1996);

these are then fertilised within the water column and develop into azooxanthellate planula larvae that must acquire zooxanthellae at some stage of their development (Trench, 1987).

One advantage of this is the potential for colonization by zooxanthellae that are genetically distinct from parental symbionts (Muller-Parker and D'Elia, 1997), leading to a higher diversity of symbiont taxa in any one colony, and perhaps conferring an increased ecological resilience to the host. However, there is also the possibility that somatic mutation may produce genetic chimeras in colonial hosts, in which selection may result in functionally different symbionts in terms of their response to environmental parameters (Buddemeier et al., 2004).

Specificity

Our current understanding of diversity within *Symbiodinium* and their association with host taxa suggests there are varying degrees of host-symbiont specificity among partnerships (Coffroth and Santos, 2005). Some host species are highly specific, appearing to contain only one symbiont taxon, whereas others contain multiple symbiont types (Baker, 2004). For example, the described species *Symbiodinium microadriaticum* is apparently exclusive to the jellyfish *Cassiopeia xamachana* (LaJeunesse, 2002), whilst corals of the *Montastraea annularis* and *faveolata* complex host several different *Symbiodinium* types (Toller et al., 2001). Although host-specificity appears to vary between associations, members of the same host species generally harbour the same *Symbiodinium* taxa or species, and some symbiont types are consistently found in certain host taxa (Rowan and Powers, 1991). Studies of the fine-scale diversity and population structure of zooxanthellae in multiple host taxa of a single reef exemplified this, demonstrating that the majority of host species associated with a single symbiont type (LaJeunesse, 2002).

In other instances, some host species associate with a number of symbiont types

and some symbiont types are found within a range of hosts (Coffroth and Santos, 2005). Corals, anemones and other unrelated host taxa that contain *Symbiodinium*, such as foraminiferans and giant clams, have all shown intraspecific symbiont diversity. (Baker et al., 1997; LaJeunesse, 2002; Santos et al., 2003; Pochon et al., 2001; Rowan, 1998).

Flexibility

In many cases, external environmental conditions promote certain pairings between partners (Coffroth and Santos, 2005), and this diversity within single host species increases the physiological range of the resultant symbiosis (Rowan and Knowlton, 1995), providing hosts with an intrinsic flexibility to accommodate rapidly to changes in their environment.

Further studies are beginning to reveal the systematic, ecological and biogeographic underpinnings of this flexibility (Baker, 2003). The fact that closely related symbionts belonging to the same clade can be found in different hosts and environments indicates physiological variability between different symbionts (Baker, 2004), and suggests an interaction between specificity and local conditions (LaJeunesse and Trench, 2000). The distribution of symbiont types among hosts is unlikely to be random (Coffroth and Santos, 2005), since specific *Symbiodinium* types seem to associate with particular host species, and is much more likely to be determined by biogeographical constraints such as local symbiont availability (Wood, 1999).

If specificity between host and symbiont does not exist, then this perhaps confers an advantage on those hosts that are not dependent on a single symbiont type, suggesting a degree of selectivity could exist between some associations. The ecological resilience of a host or colony is dependent on the physiological resilience of its constituent colonies, and the huge diversity of *Symbiodinium* means that the genus is likely to exhibit significant physiological variation

(Baker, 2004). When hosts first establish or re-establish symbioses, they may actively select for more robust free-living symbionts in order to achieve a more novel phenotype that is better suited to the local conditions. Thus, selection pressure on a host to be resistant to ineffective symbionts may be an important factor that limits the host range of symbionts (Wood, 1999).

SIGNIFICANCE OF SYMBIONT DIVERSITY WITHIN SINGLE HOST SPECIES

Montastraea spp. of coral, which associate with a number of different *Symbiodinium* types (Rowan et al., 1997), zooxanthellae exhibit photic zonation (Baker, 2004), both vertically and horizontally, so that more light-tolerant zooxanthellae will be found towards the top of the coral colony whereas more shade-adapted genotypes will be found towards the bottom where irradiance is less intense, or in areas of reef which are regularly shaded or do not receive as much light. Thus, gradients of light and depth can shape the distribution of symbionts according to their photic optima. If a coral acquires zooxanthellae from its environment, it may acquire a species or type of symbiont that is more tolerant of high levels of light than those forming its current consortium. As a result, the coral will be better equipped to deal with higher levels of solar radiation such as during extreme low-tide events which coincide with high irradiances, to an extent to which other corals may not.

Such diversity among taxa of zooxanthellae may be associated with differences in physiological performance since it introduces critical variation into the gene pool of a zooxanthellae population, which is the basis for natural selection. Environmental pressures may result in mortality of the weaker genotypes and acclimation of the surviving ones. The ecological significance of polymorphisms like this is the flexibility in symbiotic association it creates, which may be an important

mechanism in coping with environmental variation (Lee, 1998).

The Adaptive and Bacterial Disease Hypotheses of Bleaching

The expulsion of algae from host tissues can have serious implications for host species. Bleaching, which is a consequence of environmental change at and above hosts' acclimatization capacities (Loya et al., 2001), can seriously impair the growth and reproductive capabilities of the hosts. As a result, bleached hosts cannot survive very long unless this process is reversed or the symbiosis re-established. The Adaptive Bleaching Hypothesis (ABH) (Buddemeier et al., 2004) uses a coral model to suggest that hosts may be capable of adjusting the relative abundance of their symbiotic algae when environmental circumstances change. The fact that the subset of *Symbiodinium* taxa that a host species may harbour can be sizeable means that this is possible; and reports of bleaching susceptibility, occurrence, and recovery further support it. The hypothesis posits that environmental conditions may cause the loss of one or more kinds of zooxanthellae, leading to the selection of the most advantageous holobiont, with different zooxanthellae that are better suited to the new conditions in the host's habitat (Kinzie et al., 2001). Coral bleaching is thus seen as an evolutionary mechanism to adapt to rising temperatures (Grimsditch and Salm, 2006).

More specifically, the Bacterial Disease Hypothesis of Coral Bleaching (Rosenberg, 2004) proposes that microbial infection may be responsible for mass coral bleaching. Rosenberg (2004) defines bleaching as a disease as it is an unhealthy condition, weakening the coral's capacity to survive. Over the last few decades, coral bleaching and other diseases of corals have increased dramatically (Rosenberg and Ben-Haim, 2002), causing widespread mortality among reef building corals.

Perhaps the most famous example of bacterial infection is the bleaching of *Oculina patagonica* by *Vibrio shiloi* (Ben-Haim et al.,

1999). Ben-Haim et al. (1999) found that the coral pathogen *V. shiloi* only adheres to and causes bleaching of *O. patagonica* at temperatures above 20°C. This means that during the winter *V. shiloi* fails to infect *O. patagonica*. In laboratory experiments, when corals were infected with *V. shiloi* at the permissive temperature of 28°C, the bacteria penetrated the coral and multiplied intracellularly, but as the infected corals were slowly shifted to lower temperatures, the bacteria died and the infection was aborted (Israely et al., 2001). An explanation for this is that at temperatures below 20°C, *V. shiloi* does not produce superoxide dismutase (SOD), which allows the bacteria to survive in the oxygen-rich coral tissue (Banin et al., 2003). As a result, the high concentration of oxygen in the coral tissue and resulting oxygen radicals produced by the zooxanthellae during photosynthesis is highly toxic to bacteria, and is proposed as one of the mechanisms by which corals resist infection to bacteria (Rosenberg, 2004).

The significance of these findings is that they provide strong evidence for the role of zooxanthellae in coral resistance to bacterial infection (Rosenberg, 2004). Both Buddemeier's and Rosenberg's hypotheses suggest that, by altering their population of symbiotic algae, hosts can adapt to changing environmental conditions, and are capable of potentially enhancing their long-term survival. This creation of new holobionts upon which selection can act provides continual opportunity for hosts to facilitate the uptake of more resistant types of zooxanthellae, which in turn provide a dynamic response of the symbiosis to changing environmental conditions.

However, these hypotheses are not universally accepted, and are the subject of considerable debate. Some experts are critical of the ABH arguing that the recombining of zooxanthellae, communities does not necessarily prove an evolutionary response is taking place, but is instead a phenotypic acclimatisation (Grimsditch and Salm, 2006), and that the current thermal resistance of corals evolved over a much

longer timeframe than predicted future climate change, which does not fit the hypothesis' rapid form of adaptation (Hughes et al., 2003). Despite this, most evidence gathered so far is consistent with, and much supportive of the ABH. Baker (2001) showed that corals bleach and recover with more tolerant combinations of zooxanthellae after being transplanted upwards to more stressful temperature and radiation conditions and Hill and Wilcox (1998) and Toller et al. (2001) showed that severe bleaching allows establishment of novel associations even if environmental conditions return to what they had been before bleaching (Fautin and Buddemeier, 2004). However, the molecular techniques used in these experiments have not been definitively proved to be capable of detecting subtle genotypic differences between zooxanthellae, so the same type of photosymbiont may be mistaken for a different one after bleaching, reflecting change and affecting the validity of some purported tests. Hoegh-Guldberg et al. (2002) also criticised Baker's experiment for not taking into account the difference in recovery potential between different depths.

When the ABH was first postulated, the diversity of *Symbiodinium* was thought to be small, but with the realisation of its actual genetic diversity, and the co-existence of multiple types of zooxanthellae in a single host, the ABH appears to be a valid working hypothesis.

Most experiments refuting the ABH are based on single experiments or limited observations. If occurrence of the same type of photosymbiont before and after bleaching is used to indicate recombination, then no change would be possible (or should be expected) in highly-specific symbioses, and in non-specific symbioses, the stochastic nature of the ABH must be taken into account (Fautin and Buddemeier, 2004). A host cannot 'predict' the future state of its symbiont community as it is not a deterministic process, and so the probability of change depends on variations in abundance and condition of potential partners, including the variety of symbionts in

the environment or the host. The greater the variability, the more likely it is that change will occur (Fautin and Buddemeier, 2004); therefore, bleaching need not lead to a changed symbiont flora (Buddemeier et al., 2004). Buddemeier et al. (2004) state that adaptive change may occur over the course of multiple repetitive stress events, and may take several generations to become established at the community or ecosystem level, so how can individual observations claim to measure this?

Further research is clearly needed to clarify the detailed mechanisms, environmental and evolutionary importance, and extent of the ABH. Grimsditch and Salm (2006) compiled a list of questions based on literature reviews that would need to be settled to address the evolutionary claims and consequences of the ABH. These include: (a) how do zooxanthellae community shifts in coral populations occur? (Lewis and Coffroth, 2004); (b) could adaptation occur via natural selection in corals and zooxanthellae? (CRC, 2005); (c) how long do these zooxanthellae community shifts last? (Baker et al., 2004); and, (d) is acclimation algal- or host- based? (Brown et al., 2002). But, if holobiont physiology is an emergent property, rather than being controlled by one of the partners, then the debate on which partner is responsible for observed tolerances is largely immaterial, as the resulting pattern will occur regardless of initiation by either algae or host (Fautin and Buddemeier, 2004).

The Bacterial Disease Hypothesis of Coral Bleaching also remains controversial. Ainsworth et al. (2008) conclusively state that *V. shiloi* is not the primary cause of the continued annual bleaching of *O. patagonica* in the Eastern Mediterranean, and that there is no evidence to support a primary role of bacteria in causing coral bleaching in the system used, as basis, for the Bacterial Bleaching Hypothesis. They state that not only did bleaching occur without the involvement of *V. shiloi*, but without any *Vibrio* sp. being present at all and with the only detectable microbial communities being members of the endolithic community. These

data raise further questions on hypotheses of bacterial mass coral bleaching and coral hologenome evolution.

Conclusion

While vertical transmission of symbionts ensures that offspring are provided with a complement of symbioses (Barneah et al., 2004), 'open' systems where members of a host species are provided with many opportunities to obtain different symbionts are surely better (Rowan and Knowlton, 1995). Host-algal flexibility allows hosts to switch or shuffle their symbionts in response to environmental parameters. If this adaptive strategy is indeed rapid enough to survive the challenge of acute stress, then it is possible that elevated sea surface temperatures due to global warming, widely believed to be the principle factor in large-scale coral reef bleaching, may simply have the effect of forcing corals to select for zooxanthellae that exhibit increased resistance to bleaching. By forming new symbiotic relationships with such algae, corals and other hosts may be able to mitigate the detrimental effects of rising sea surface temperatures (Baker, 2004).

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