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ZOOXANTHELLAE

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Synonyms

Algal symbionts; *Symbiodinium*

Definition

The term “zooxanthellae” refers to a paraphyletic group of yellow-brown microalgae, including certain dinoflagellates, diatoms, cryptophytes, chrysophytes (golden algae), and rhodophytes (red algae), that are found in mutualistic symbiosis with a variety of invertebrate and protist hosts. “Zooxanthellae” is a plural noun (singular: zooxanthella) derived from the Greek words *zoo* (animal), *xanthos* (yellow), and *ella* (diminutive): “yellow animal cells.” On coral reefs, vernacular usage almost exclusively refers to the symbiotic dinoflagellates in the genus *Symbiodinium* that are commonly found in certain corals, anemones, jellies, clams, worms, sponges, and other reef organisms.

Introduction

Zooxanthellae are ubiquitous and critical members of coral reef ecosystems (Taylor, 1974; Muscatine and Porter, 1977; Trench, 1993; Rowan, 1998). They are normally abundant, with healthy reefs typically containing $>10^9$ cells per m^2, but due to their small size (10 μm diameter) their overall biomass on reefs is low. Because they are so important to the construction, evolution, and ecology of coral reefs, zooxanthellae can be regarded as keystone species on coral reefs – perhaps the only protists to play such a role.

Zooxanthellae provide significant nutritional benefits to their hosts in the form of translocated photosynthates, particularly glycerol and other water soluble compounds such as glucose. In a variety of scleractinian corals, photosynthates from dinoflagellate zooxanthellae (in the genus *Symbiodinium*) have been shown to account for 50–95% of the coral’s energy budgets. In addition, the presence of algal symbionts drives rapid calcification in the host organism, and allows scleractinian corals to accrete limestone skeletons, dominate as the principal builders of contemporary reefs, and compete for space in the shallow tropical seas where they are most commonly found.

Recently, coral–algal symbioses have become a major focus of research inquiry as a result of coral reef “bleaching,” in which reef corals and other zooxanthellate hosts lose their algal symbionts (or experience a reduction in their per-cell pigment concentrations) and become pale or white as the calcium carbonate skeleton becomes increasingly visible through the translucent coral tissue. In some cases, residual coral pigments result in bleached corals appearing pale blue, pink, yellow, purple, chartreuse or other colors, rather than the typical white appearance.

Bleaching events are become increasingly frequent as a result of rising sea surface temperatures, and have been responsible for widespread coral mortality in some reef regions (Hoegh-Guldberg et al., 2007). Moreover, with ocean acidification resulting in declining rates of coral calcification, the role of algal symbionts in influencing the response of their calcifying hosts appears poised to be a similarly active research field.

Diversity and distribution of zooxanthellae

In 1883, Karl Brandt first recognized that the “animal chlorophylls” he studied in radiolarians were, in fact, mutualistic algae (Figure 1). He introduced a new genus *Zooxanthella* to refer to these algae, but this name was quickly dropped, as the phylogenetic diversity of these algae (see Definition) became apparent.

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Zooxanthellae, Figure 1 Original drawings of "zooxanthellae" reproduced from Brandt (1883). Shown are the *Gelbe Zellen* ("yellow cells") isolated from the scleractinian coral *Cladocora caespitosa* ("21") and the upside-down jellyfish *Cassiopeia borbonica* ("24"). Both are *Symbiodinium* based on their appearance and host origin.

The first dinoflagellate zooxanthellae were cultured in the 1950s, and in 1962 Hugo Freudenthal introduced a new genus and species *Symbiodinium microadriaticum*, from the Greek words *symbion* ("living together") and *dinos* ("whirling"), to describe the gymnodinioid dinoflagellates isolated from the upside-down jellyfish *Cassiopeia xamachana* (Freudenthal, 1962). Because no further species in the genus were formally described for several decades (with eight species names eventually validated by formal description in 2000), it was generally assumed that all symbiotic dinoflagellates belonged to a single pandemic species *S. microadriaticum*, despite the fact that evidence pointing to significant diversity within the genus had begun to accumulate since the 1970s.

In fact, there are currently eight genera in four or five orders of dinoflagellate that are recognized as endosymbiotic zooxanthellae in marine invertebrates and protists (Banaszak et al., 1993; Trench, 1997). *Symbiodinium* is the most studied genus in this paraphyletic group and is commonly found in shallow water tropical and subtropical cnidarians. Cnidarian species reported to contain *Symbiodinium* include many representatives from the class Anthozoa (including anemones, scleractinian corals, black corals, zoanthids, corallimorphs, blue corals, alcyonacean corals, and sea fans) and several representatives from the classes Scyphozoa (including rhizostome and coronate jellyfish) and Hydrozoa (including milleporine fire corals). *Symbiodinium* has also been identified from gastropod and bivalve mollusks (including tridacnid [giant] clams, heart cockles, and conch), large miliolid foraminifera (in the subfamily Soritinae), sponges, and a giant heterotrich ciliate (see Trench, 1993; Baker, 2003 for review). Some records of "zooxanthellae" present in invertebrates and other hosts have been based on observations of just a handful of individuals, or are based on only cursory observations or anecdotal reports. Because systematic surveys of potential hosts have not been undertaken, it is likely that additional zooxanthellate hosts exist in nature which have yet to be been reported.

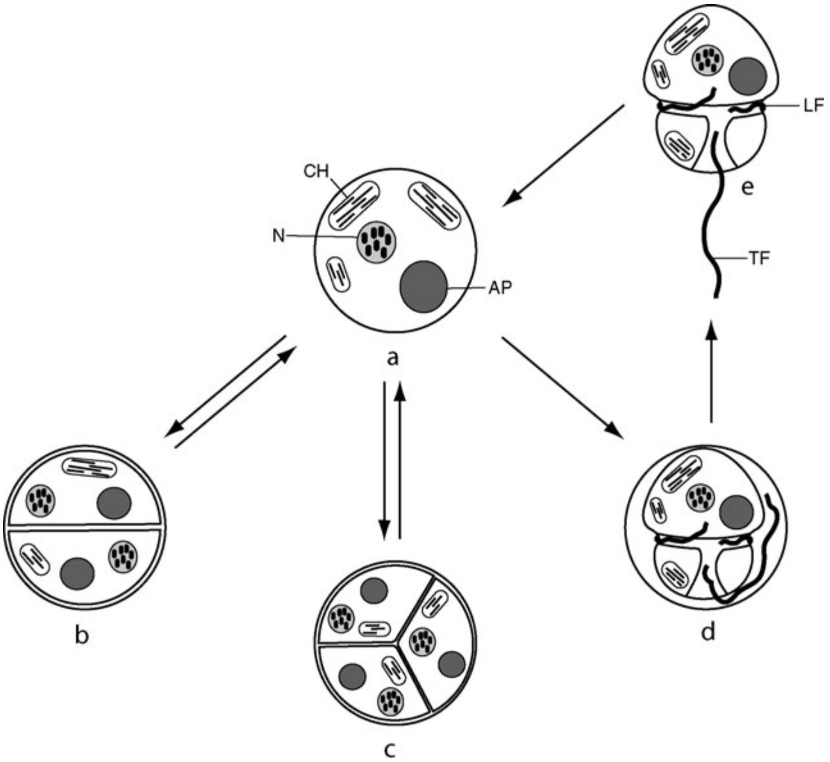
Although zooxanthellae can be found in a wide variety of hosts, algal symbiosis tends not to be the norm for any particular taxonomic group. For example, while scleractinian corals are the principal builders of contemporary coral reefs, the majority of species in the order Scleractinia are in fact deep water and azooxanthellate. Moreover, some individual species are facultatively zooxanthellate, able to survive indefinitely in both a symbiotic and non-symbiotic state, depending on environmental conditions (e.g., certain species in the scleractinian coral genus *Oculina*, which is zooxanthellate in shallow water, but azooxanthellate at depth). Together, these patterns indicate that symbiosis with algae has evolved independently multiple times, even within individual groups such as anthozoans.

The life cycle of *Symbiodinium* alternates between a vegetative cyst and a motile zoospore (Figure 2), with the vegetative stage being the dominant form in endosymbiosis. Relatively little is known of the diversity and ecology of free-living *Symbiodinium*, although they are now routinely identified in reef waters and/or sediments (Carlos et al., 1999; Gou et al., 2003; Lewis and Coffroth, 2004; Coffroth et al., 2006; Littman et al., 2008; Manning and Gates, 2008; Porto et al., 2008). It is not yet clear how much *Symbiodinium* diversity exists in these free-living pools, and what overlap and/or interactions exist between these algae and those in endosymbiosis. This is currently an active area of research.

Diversity and flexibility in coral–algal symbiosis

The dinoflagellate genus *Symbiodinium* is extraordinarily diverse, and consists of at least eight major clades (A-H, Santos and Coffroth and Santos, 2005; Pochon et al., 2006). Members of five of these clades (A, B, C, D, and F) have to date been documented in scleractinian corals. It is clear that additional diversity in *Symbiodinium* remains to be discovered, and that most species are uncultured and undescribed (Rowan, 1998; Santos et al., 2001). Moreover, in addition to the dominant populations of symbiotic dinoflagellates in these hosts, many unusual or novel variants may also occur as cryptic and unstable transients whose physiological or ecological importance is not yet clear (LaJeunesse, 2001; Santos et al., 2001; Toller et al., 2001). It is likely that additional diversity (at both the clade level and the subclade level) will be discovered with increased sampling of understudied zooxanthellate hosts, such as forams, anemones, sponges, and octocorals.

Scleractinian corals often show flexibility in the types of *Symbiodinium* they can host, both within and among clades (Baker, 2003). Although one symbiont type is usually dominant in any given coral species and environment (Rowan and Powers, 1991; LaJeunesse, 2002; LaJeunesse et al., 2003), the ability of some corals to host different symbionts in different environments or locations suggests



Zooxanthellae, Figure 2 Life cycle of *Symbiodinium* (**a**) vegetative cyst, (**b**) dividing vegetative cyst producing two daughter cells, (**c**) dividing vegetative cyst producing three daughter cells, (**d**) developing zoospore, and (**e**) zoospore. CH: chloroplast; N: nucleus; AP: accumulation product; LF: longitudinal flagella; TF: transverse flagella. (Adapted from Schoenberg and Trench [1980] and Freudenthal [1962], and reproduced with permission from Stat et al. [2006].)

that these corals may possess different physiological optima depending on the algal symbiont(s) they host. Moreover, because these corals appear able to change the dominant symbiont type in response to environmental changes (Rowan et al., 1997; Rowan, 1998; Baker, 2001, 2003; Little et al., 2004; Berkelmans and Van Oppen, 2006; Jones et al., 2008; LaJeunesse et al., 2009), it has been suggested that flexibility in coral–algal symbiosis is an important mechanism by which reef corals adapt or acclimatize to disturbances, including those resulting from climate change (Buddemeier and Fautin, 1993; Baker, 2001, 2003; Baker et al., 2004; Berkelmans and Van Oppen, 2006). Although evidence exists in support of these hypotheses, the large-scale implications for coral reef survival through the coming century have yet to be established (Hoegh-Guldberg et al., 2007). In addition, there are likely to be trade-offs between different symbiont types (Little et al., 2004) that have yet to be explored in detail. Diversity and flexibility in coral–algal symbiosis remain an active area of research for exactly these reasons.

Summary

The endosymbiosis between scleractinian (stony) corals and zooxanthellae (typically symbiotic dinoflagellates in the genus *Symbiodinium*) underpins the success of modern coral reefs. Reef corals (and other contemporary reef-builders) gain a twofold advantage by hosting zooxanthellae. First, they can function as autotrophs and use the photosynthates thus obtained as an energy substrate. Second, for reasons which remain unclear, they are able to calcify much faster than their azooxanthellate counterparts (Cohen and McConnaughey, 2003). Together these phenomena explain why coral reefs have become dominant ecosystems in shallow, oligotrophic tropical seas. They also explain why coral reef bleaching (the loss of zooxanthellae from reef-builders) as a result of environmental stress is a major threat to coral reef ecosystems, particularly as a result of climate change-related seawater warming. The potential role of zooxanthellae in mediating the response of reef builders to ocean acidification also illustrates their importance as a contemporary subject of research.

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Cross-references

Ocean Acidification, Effects on Calcification
Symbiosis
Temperature Change: Bleaching