Zooxanthellae: The Yellow Symbionts Inside Animals

Noga Stambler

Abstract Corals are associated with photosymbiotic unicellular algae and cyanobacteria. The unicellular algae are usually called zooxanthellae due to their yellow-brown color. The zooxanthellae are mainly classified as dinoflagellates to the genus Symbiodinium sp. The advantage of symbiosis is based on adaptations of transport and the exchange of nutritional resources, which allow it to be spread all over the tropical and some temperate oceans. Their existence over millions of years depends on the ability of the zooxanthellae, the host, and the holobiont as a whole unit to change, acclimate, and adapt in order to survive under developmental and stress.

Keywords Coral • *symbiodinium* • zooxanthellae • adaptation • carbon • host factor

1 Introduction

Corals are associated with photosymbiotic unicellular algae and cyanobacteria (e.g., as in the review of Venn et al. 2008 and Stambler 2010b). The unicellular algae are usually called zooxanthellae due to their yellow-brown color (Brandt 1883). The zooxanthellae are mainly classified as dinoflagellates to the genus *Symbiodinium* sp., to eight lineages (clades A–H, which are based on phylogenetic classification). Six of them (clades A–D, F, G) are found in scleractinian corals (LaJeunesse 2001; Coffroth and Santos 2005). This genetic diversity is part of the adaptation of the symbionts to the environment and, in many cases, they correlate with the diverse range of physiological properties in the host-symbiont assemblages (Stat et al. 2008b).

Photosynthetically fixed carbon is translocated from zooxanthellae to the host. Up to 95% of the fixed carbon may translocate under high-light conditions (e.g., Falkowski et al. 1984; Muscatine et al. 1984). The contribution of zooxanthellae to animal respiration (CZAR) is up to 100% of daily metabolic requirements and, in some cases, they provide even more than the total metabolic needs of the host animal (Muscatine et al. 1981, 1984; Davies 1984, 1991; Falkowski et al. 1984; Grottoli et al. 2006). However, it should be noticed that this contribution of the zooxanthellae to animal respiration decreased dramatically under bleaching in the case of *Porites compressa* (from 146% to 74%), *Montipora capitata* (from 132% to 41%), and *Porites lobata* (from 141% to 96%) (Palardy et al. 2008).

The advantage of symbiosis is based on adaptations of transport and the exchange of nutritional resources, which allow it to be spread all over the tropical and some temperate oceans. Carbon and nutrient fluxes between the host, the algae, and the environment are based on symbiotic relationships (Muscatine 1990; Yellowlees et al. 2008). These fluxes allow the corals and whole coral-reef communities to succeed at low concentrations of nitrogen (N) and phosphorus (P) in oligotrophic waters surrounding the reefs (Muscatine and Porter 1977). The assimilation of ammonium from the surrounding environment can be done by both the cnidarian host and the algae, as they both have the enzymes glutamine synthetase (GS) and glutamate dehydrogenase (Rahav et al. 1989). A variety of ammonium transporters, which are similar to bacterial transporters, exists in *Symbiodinium* (Leggat et al. 2007). Both symbiotic partners benefit from nitrogen recycling between animals and microorganisms. The host benefits from symbionts that act as a sink for potentially toxic nitrogenous waste compounds while the symbionts benefit from access to the N source for growth (e.g., Douglas 2008).

This symbiosis demands that the coral tolerates and recognizes the presence of the symbionts in its tissues, and that the algae will be able to survive in the tissue and develop some specific host–symbiont combinations (Weis 2008; Yellowlees et al. 2008). The algae and the host metabolism have to adjust to the conditions in order to increase their genotypic diversity even by lateral gene transfers between the endosymbionts and their cnidarian hosts (Furla et al. 2005). The success of the holobiont, the coral host, and the symbionts depends on the integrated physiological capacity of the symbiotic partners towards the environment (review: Trench 1993; Venn et al.

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Z. Dubinsky and N. Stambler (eds.), *Coral Reefs: An Ecosystem in Transition*,
DOI 10.1007/978-94-007-0114-4_7,

2008; Weis 2008; Yellowlees et al. 2008). Their existence over millions of years depends on the ability of the zooxanthellae, the host, and the holobiont as a whole unit to change, acclimate, and adapt in order to survive under developmental and stress conditions (review in Brown and Cossins 2011; Hoegh-Guldberg 2011; Lesser 2011; Stambler 2010a).

2 Geological History

The symbiotic scleractinian corals developed early in history, about 210 mya (Wood 1998, 1999). The coral taxa currently existing in symbiosis may or may not have been associated with dinoflagellates from that entire period (Trench 1993). Symbiosis with zooxanthellae evolved independently several times in the Triassic period; however, the first scleractinian corals did not form reefs and were solitary animals. The earliest true coral reefs date from the late Triassic period. At that time, the scleractinian corals that emerged in the warm waters of the Tethys Sea were predominantly zooxanthellate (Stanley and Swart 1995).

The *Symbiodinium* genus originated in the early Eocene period, 50 mya. The major diversification of extant *Symbiodinium* lineages started about 15 mya at the mid-Miocene, when Tethys Sea closure occurred and the ocean temperatures decreased (Pochon et al. 2006). *Symbiodinium* clades A and E were the first to initiate symbiosis (e.g., Karako-Lampert et al. 2004; Pochon et al. 2006; Stat et al. 2008b).

From an evolutionary point of view, in the later part of the Cenozoic era, the symbiotic algae in cnidarians were selected because of their reduced tolerance to elevated temperatures (Tchernov et al. 2004). However, the modern group of *Symbiodinium* sp. developed over millions of years and, as such, contains a broad diversity species that is differentiated physiologically (Tchernov et al. 2004).

3 Cellular Anatomy and the Symbiosome

Symbiodinium sp. size ranges from 6 µm to 15 µm diameter, and varies between genotype and host (see LaJeunesse 2001; LaJeunesse et al. 2005; Frade et al. 2008a). The morphological characteristics of *Symbiodinium* sp. were described by Freudenthal (1962) and appear in the outstanding works of Trench (and in review of Trench 1993). In *hospite* and in culture, the coccoid cells are limited by continuous cellulosic cell wall, which is external to the plasmalemma. There is a single chloroplast with thylakoids. The chloroplast thylakoids are stacked, and often arranged around the periphery of the cell. A pyrenoid body is connected to the chloroplast used for the storage of photosynthetic products, such as starch (Fig. 1). Specific crystalline material stores uric acid that can be mobilized rapidly and used as a nitrogen source, allowing the algal symbionts to grow in an N-poor environment (Clode et al. 2009). The nucleus has notable permanently condensed chromosomes, dinokaryon (the chromosome number varies among species 26–97). The cell contains 1.5–4.8 pg DNA (LaJeunesse et al. 2005). In *hospite*, the zooxanthallae are found only in the coccoid state and they divide mitotically. So far, coccoid cells from corals are found only in culture with flagellum, although the latter has been observed in algae of other hosts within a symbiosome (Trench 1993). The cells become motile either following karyokinesis and cytokinesis, or even without mitosis (Trench 1993). In addition to the lack of flagella, the zooxanthellae inside the coral tissue have slightly different cell-wall structure from the wall of the free-living *Symbiodinium* (Wakefield et al. 2000). In culture, the cells are motile swarmers, characteristic of gymnodinioid morphology (Figs. 2 and 3).

The zooxanthellae are located in vacuoles (symbiosomes) within the host's endoderm cells (Trench 1987). The symbiosome has been defined as the host-derived outer membrane together with the *Symbiodinium* cell and the space between the two. It also includes multilayered membranes derived from the *Symbiodinium* cell. Cultured zooxanthellae lack symbiosomes (Trautman et al. 2002). Following algal cytokinesis, each daughter cell is allocated to an individual symbiosome (Trench 1993). The symbiosome is composed of a zooxanthellae cell that rarely divides and is separated from the host gastrodermal cytoplasm by a symbiosome multimembrane complex (Wakefield et al. 2000; Kazandjian et al. 2008). In the sea anemone *Aiptasia pallida* and its endosymbiont *Symbiodinium bermudense*, the symbiosome membrane is a single, host-derived membrane, whereas the remaining membranes surrounding the algal cell are symbiont-derived

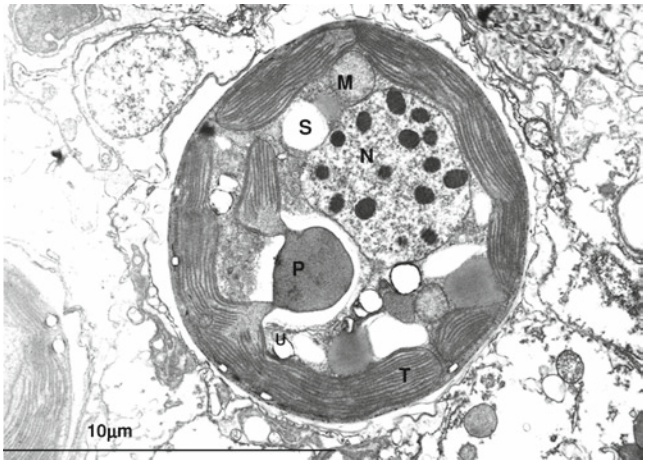

Fig. 1 Transmission electronic micrograph of zooxanthellae (*Symbiodinium* sp.). *T* thylakoid, *N* nucleus with condensed chromosomes, *M* mitochondria, *P* pyrenoid, *S* starch, *U* crystal of uric acid

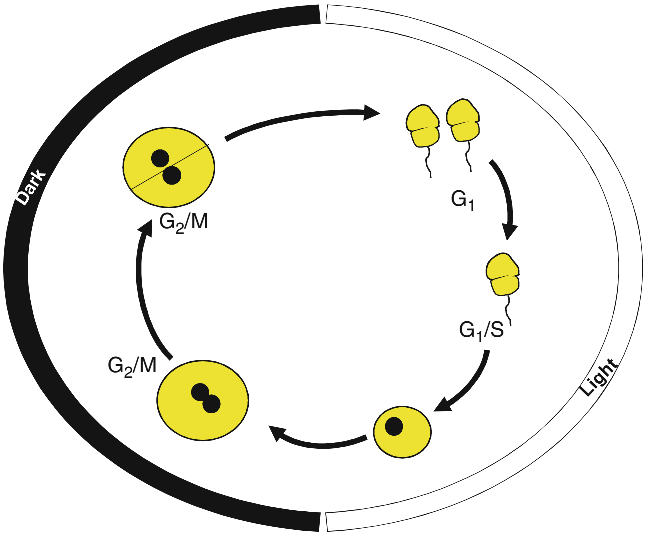

Fig. 2 The *Symbiodinium* cell cycle in culture during the light and dark cycle. G1, G1/S, G2/M phases (Based on Wang et al. 2008)

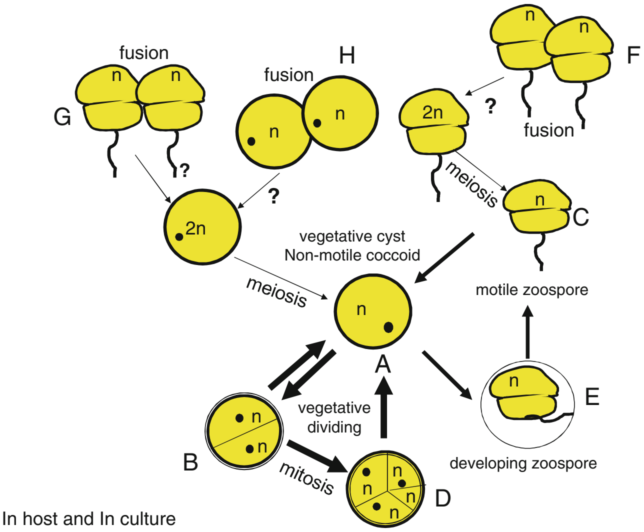

Fig. 3 Life cycle of *Symbiodinium* inside host tissue (*in hospite*) and in culture, including vegetative cyst, dividing vegetative cyst producing two daughter cells, dividing vegetative cyst producing three daughter cells, and zoospore. Different stages of cells with and/or without flagella. Fusion and meiosis of cells. n – haploid nuclear phase, 2n – diploid nuclear phase. (**a**–**c**) Observed in host and culture; (**c**) observed when zooxanthellae was released from the host; (**d**) is part of mitosis divisions; (**e**) observed in culture; and (**f**, **g**) are theoretical options (Adapted from Freudenthal 1962; Schoenberg and Trench 1980; Fitt and Trench (1983); Stat et al. (2006); and Lee John (personal comment))

(Wakefield and Kempf 2001). The symbiosome membrane and the multilayer structure are intimately associated, and also have regular-interval interconnections. As such, they represent one functional unit (Kazandjian et al. 2008).

These membranes are part of the boundary between the host and the symbionts. The transport of gases and carbon translocation occur through and in conjunction with these membranes (Wakefield et al. 2000). The dinoflagellates occupy most of the interior of macerated host cells, leaving the host cytoplasm and cell membrane as a thin outer layer. As such, the symbiotic zooxanthellae in cnidarians live within an osmotically different environment from that of free-living dinoflagellates (Goiran et al. 1997; Mayfield and Gates 2007). This spatial arrangement may support the diffusion and transport of CO_2, bicarbonate ions, and nutrients from the environment to the algae (Muscatine et al. 1998). It could be that the symbiosome membranes also protect the symbionts from being digested (Chen et al. 2005). However, it should be noted that the symbiosome does not block the effects of the host-release factor (HRF), which stimulates photosynthate release, and the photosynthesis inhibiting factor (PIF) (Grant et al. 2003, see below).

Changes in the ultrastructure take place as part of photoacclimation, e.g., increase in thylakoid number under low light as well as under eutrophication (e.g., Falkowski and Dubinsky 1981; Stambler 1998).

Morphological changes occur in the symbionts under stress conditions. These changes include shrinkage of cell contents, increased vacuolization, and disorganized and loosened thylakoids (Franklin et al. 2004). At high temperature (≥34°C), cells that become apoptotic also become smaller in size and the cytoplasmic organelles within them fuse together, forming large organelle bodies. The last apoptotic stage occurs when the cell membrane ruptures (Strychar and Sammarco 2009).

The algal cells are usually arranged in a monolayer, resulting in millions of dinoflagellates per square centimeter of coral-colony surface (Drew 1972). Since symbiont types vary in cell size (LaJeunesse 2001; LaJeunesse et al. 2005) and cell density is preliminarily a consequence of space availability (Jones and Yellowlees 1997; Stambler and Dubinsky 2005), the density varies between holobionts. The average cell-specific density (CSD) ranged from 1.11 to 2.1. While in some species, e.g., *Stylophora pistillata*, the variation in distribution of the number of algae per host cell is minimal, in others, such as the sea anemone *Condylactis gigantea,* significant variation can be found (Muscatine et al. 1998). It is higher in fed compared to starved corals (e.g., Houlbreque et al. 2004).

The zooxanthellae population in a host can include one or more genotypes in different abundances that may change under different conditions (e.g., Goulet 2006, 2007; Baker and Romanski 2007, see below). Very rare abundance can be too low for detection even by molecular methods (Baker and Romanski 2007).

Cell density in bleaching corals can be reduced to a minimum and an undetected number, but in the case of host survival, this can be the inoculum for starting a new population in the host.

4 Division and Reproduction

It has been thought that the vegetative state of algae can be either haploid or diploid (Fitt and Trench 1983); however, based on molecular genetic evidence, it is now clear that algae from the genus *Symbiodinium*, both in culture and in *hospite*, are haploid (Santos and Coffroth 2003). Although sexual reproduction has not been observed, extensive recombination in *Symbiodinium* (LaJeunesse 2001) by fusion and meiosis (Fitt and Trench 1983; Fig. 3) is probably the reason for high allelic variability for allozymes, random-amplified polymorphic, and DNA fingerprints (LaJeunesse 2001; Santos and Coffroth 2003). However, there is little evidence of genetic recombination between *Symbiodinium* types (Santos et al. 2004; Sampayo et al. 2009). For example, in the tropical Atlantic, the frequency of multiple *Symbiodinium* alleles in a single coral colony of *Favia fragum* was found to be low (Carlon and Lippe 2008).

The cell-cycle process is regulated by light–dark stimulation. Some *Symbiodinium* algae lost motility when placed in either constant light or constant dark (Yacobovitch et al. 2004; Wang et al. 2008) while other *Symbiodinium* lost their motility pattern in constant light but kept their motility rhythms in constant dark (Fitt et al. 1981; Lerch and Cook 1984; Banaszak and Trench 1995). Sequential light followed by dark (12:12 h) entrained a single cell cycle, genotype B in culture, from the G1 to the S phase, and then to the G2/M phase, within these 24 h (Fig. 2). Blue light (450 nm) mimicked regular white light, while red and infrared light had little or no effect on entraining the cell cycle. Light treatment drove cells to enter the growing/DNA synthesis stage (i.e., G1 to S to G2/M), increasing motility and photosynthetic efficiency. Inhibition of photosynthesis stops the cell proliferation process. Darkness is required for the mitotic division stage, when cells return from G2/M to G1 (Wang et al. 2008).

The G1 phase of the *Symbiodinium* sp. cell cycle was extended dramatically in the symbiotic state. The slowing down in the cell cycle was also reflected in the usual low mitotic index (MI) and the low percentage of dividing cells (3–5%) (e.g., Hoegh-Guldberg et al. 1987; Wilkerson et al. 1988; Baghdasarian and Muscatine 2000). Daily and seasonal patterns can be observed in the MI (Wilkerson et al. 1988; Dimond and Carrington 2008), which is dependent on the photoacclimation of the algae (Titlyanov et al. 2001). As a result, the doubling times, which are a few days in culture (Fitt and Trench 1983), increase even to 29 days, i.e., several weeks, inside the host (Wilkerson et al. 1988). The doubling time of the zooxanthellae in the host is about 8 days when there is no limitation of nutrients (calculation based on data from Dubinsky et al. (1990)). Nutrition of the anemone *Aiptasia pulchella* caused variation in G1 phase-duration in the cell cycle of *Symbiodinium pulchrorum* (Smith and Muscatine 1999). The recovery and the re-established symbioses after bleaching depend on the doubling time of the algae, which can be less than 5 days (Toller et al. 2001).

5 Taxonomy from Morphology to Molecular Biology, Genus to Genotype

The dinoflagellate symbionts of coelenterates mainly belong to various species of the genus *Symbiodinium* (Freudenthal 1962) but in some cases they may belong to the genus *Amphidinium* (review in Trench 1997; Karako et al. 2002; Table 1). *Symbiodinium* species differ in cell morphology, ultrastructure, circadian rhythms, growth rates, host infectability, and photoacclimation (e.g., LaJeunesse 2001).

The genus *Symbiodinium* consists of eight lineages/subgeneric “clades” (A–H), each of which includes multiple types/genotypes (e.g., Baker 2003; Coffroth and Santos 2005; Pochon et al. 2006; LaJeunesse et al. 2008). Calcification of the different types of *Symbiodinium* is based on different nuclear, mitochondrial, and chloroplast genomes. Identification is based on: (a) nuclear ribosomal genes and spacer regions: the small subunit (SSU or 18S), large subunit (LSU or 28S), and internal spacer regions (ITS1 and 2); (b) mitochondrial cytochrome b (cytb); and (c) DNA chloroplast 23S rDNA) see in Coffroth and Santos 2005; Sampayo et al. 2009).

Clone and genotype level are separated based on microsatellite alleles) see in e.g., Coffroth and Santos 2005; Pettay and Lajeunesse 2007; Carlon and Lippe 2008).

Types are a much lower level of species and, in most cases, there is no attempt to arrange them according to species. However, while the genus *Symbiodinium* includes only a few species (i.e., *Symbiodinium bermudense, Symbiodinium cariborum, Symbiodinium corculorum, Symbiodinium goreauii, Symbiodinium kawagutii, Symbiodinium meandrinae, Symbiodinium muscatinei, Symbiodinium microadriaticum, Symbiodinium pilosum, Symbiodinium pulchroru, Symbiodinium trenchii*, and *Symbiodinium californium*), it includes many tens of types (LaJeunesse 2001; LaJeunesse et al. 2005, 2008; Table 1). Only a few studies correlated between species and type (LaJeunesse 2001; Table 1).

Corals mainly associate with *Symbiodinium* clade C and, in some cases, with clades A, B, D, F, and G. Some coral colonies harbor only a single symbiont type, while others harbor two or more types simultaneously (e.g., Rowan and Knowlton 1995; Baker 2003; Goulet 2006; Mieog et al. 2007; Abrego et al. 2008; LaJeunesse et al. 2008). Clade C is the most common and diverse clade in Indo-Pacific corals (LaJeunesse 2005). Clade C dominates the Indo-Pacific host fauna and shares dominance in the Atlantic-Caribbean with

Table 1 *Symbiodinium* species and genotype

Symbiodinium species	Genotype	Host	Reference
*Symbiodinium microadriaticum**	A, A1	*Cassiopeia xamachana (*Rhizostomeae)	LaJeunesse 2001; Stat et al. 2008b
Symbiodinium microadriaticum subsp. Condylactis*	A1	*Condylactis gigantean* (Actiniaria)	LaJeunesse 2001
*Symbiodinium cariborum**	A1		LaJeunesse 2001
Symbiodinium microadriaticum subsp. Microadriaticum	A1		LaJeunesse 2001
*Symbiodinium corculorum***	A, A2	*Corculum cardissa*(Bivalvia)	LaJeunesse 2001; Stat et al. 2008b
*Symbiodinium meandrinae***	A2	*Meandrina meandrites* (Scleractinaria)	LaJeunesse 2001
*Symbiodinium pilosum***	A, A2	*Zoanthus sociatus* (Zoantharia)	LaJeunesse 2001; LaJeunesse et al. 2005; Stat et al. 2008b
Symbiodinium linucheae	A4	*Linuche unguiculata* (Coronatae)	LaJeunesse 2001
Symbiodinium microadriaticum	B	*Condylactis gigantea*	Karako-Lampert et al. 2005
*Symbiodinium pulchroru****	B1	*Aiptasia pulchella* (Actiniaria)	LaJeunesse 2001
*Symbiodinium bermudense****	B1	*Aiptasia tagetes* (Actiniaria)	LaJeunesse 2001
Symbiodinium muscatinei	B4		LaJeunesse 2001
Symbiodinium goreauii	C, C1	*Rhodactis lucida* (Corallimorph)	LaJeunesse 2001; LaJeunesse et al. 2005; Stat et al. 2008b
Symbiodinium trenchii	D		LaJeunesse et al. 2005
Symbiodinium californium	E	*Anthopleura elegantissima* (Actiniaria)	LaJeunesse 2001; LaJeunesse et al. 2005; Stat et al. 2008b
Symbiodinium varians	E		Stat et al. 2008b
Symbiodinium kawagutii	F1	*Montipora verrucosa* (Scleractinaria)	LaJeunesse 2001; LaJeunesse et al. 2005, 2008

Species marked with the same number of asterisks are probably the same species

clade B. C1 and C3, which are considered to be the ancestor core for separate types, are common in the Indo-Pacific and Atlantic-Caribbean (LaJeunesse 2005**).**

In general, but with some exceptions, clade C is the most widely distributed, and presumably has a wide temperature and salinity tolerance, dominating the tropical area (Baker 2003; Karako-Lampert et al. 2004). Some types of clade D are adapted to stress tolerance (Baker 2003). Clade B symbionts are specifically adapted to the lower light and cooler seas of higher-latitude environments in temperate areas (Rodriguez-Lanetty et al. 2001).

6 Inter- and Intrahost Transmission

The host can acquire its symbionts either from its parents or from the surrounding environment. In the case of asexual fragmentation reproduction, the symbionts are always a part of the new organisms. However, in the case of sexual reproduction, two options exist: (1) the symbionts are transferred directly from host to offspring in a process known as vertical, maternal, or closed-system transmission; (2) each generation must acquire new zooxanthellae from the surrounding seawater or, in rare cases, from a secondary host, in a process called open-system or horizontal transmission (see Karako et al. 2002; Coffroth and Santos 2005; Barneah et al. 2007a, b; Huang et al. 2008). This transmission strategy is common to most species, including coral colonies that are broadcast spawners.

Horizontal transmission is of symbionts released from different hosts that survive at the water column for short/long periods of time or via predation/infection of secondary hosts (Muller-Parker 1984; Barneah et al. 2007b). Even though *Symbiodinium* have been isolated from the water column as well as from coral sands (Loeblich and Sherley 1979; Gou et al. 2003; Coffroth et al. 2006; Hirose et al. 2008), only some of the *Symbiodinium,* specifically clade A, include free-living types, and only some of them can infect and become associated with the host (Coffroth et al. 2006). The free-living *Symbiodinium* have different characterization and their distribution changes around the world, e.g., only clade A exists in the Okinawa (Japan) sand (Hirose et al. 2008).

Generational shifts in symbiont type can occur in host broadcast spawners, whose larvae must acquire symbionts from environmental pools. However, hosts exhibiting vertical transmission (brooders) do not demonstrate this level of flexibility (LaJeunesse et al. 2004b; LaJeunesse 2005). Vertical transmission is an effective way to keep the symbiosis from one generation to another and guarantee maximum fit between the two components. However, vertical transmission may be disadvantageous: the symbionts might interfere with host developmental processes, consume limiting host nutrients, and it might be that the location of the larva development will not fit or be optimal for this symbiont genotype (Douglas 2008).

Horizontal strategy will be preferred when the vertical transmission is costly to the host. There are many types of symbionts in the environment, and control over creation of the holobiont is not by coral host alone (Genkai-Kato and Yamamura 1999).

Horizontal transmission maintains higher diversity and, by that, ensures the survival of the symbiosis, specifically under different environment conditions, similar to the advantage of sexual versus asexual reproduction (Stat et al. 2008b). In horizontal transmission, the invertebrates must be infected by *Symbiodinium* from environmental pools (Coffroth and Santos 2005), and this allows the host to become associated with *Symbiodinium* that are better adapted to local environmental conditions (van Oppen 2004; Coffroth and Santos 2005). However, a host with a horizontal acquisition system may fail to acquire symbionts (Genkai-Kato and Yamamura 1999). In the eastern Pacific, the corals *Pavona* and *Psammocora*, which rely on horizontal symbiont acquisition, harbored populations of *Symbiodinium* that were not found in the other host taxa (LaJeunesse et al. 2008).

Flexibility in the acquisition of symbionts should characterize the life history of coral species that must reacquire symbionts in each new generation (Baird et al. 2007). However, although corals obtaining their symbionts by horizontal transmission are expected to have more diverse symbionts associated with them compared to corals with vertical transmission, there are no clear statistics on that. Moreover, in acroporid corals, transmission mode does not affect symbiont diversity (van Oppen 2004). In the Great Barrier Reef (GBR), the majority of corals with a vertical strategy associated with genus-specific *Symbiodinium* type, although in some cases they associated with symbiont types similar to those found in hosts with a horizontal strategy (Stat et al. 2008a).

The different *Symbiodinium* types transfer through both horizontal and vertical transmission. *Symbiodinium* clade A transfers through a closed system in *Stylophora* in the Gulf of Eilat and in the Great Barrier Reef (Karako-Lampert et al. 2004), while *Acropora* acquires its clade A symbionts via horizontal transmission (Stat et al. 2008b). Homologous zooxanthellae of *Fungia scutaria* (Hawaii) are able to establish symbioses with larval hosts *Fungia scutaria* better than heterologous isolates, mixed with zooxanthellae from *Montipora verrucosa, Porites compressa,* and *Pocillopora damicornis* (Weis et al. 2001). This indicates a specific process occurring during infection and reorganization (Trench 1993).

The *Symbiodinium* population in coral larvae develops through vertical transmission partitioned according to coral species, while larvae develop through horizontal transmission strategy sharing a common symbiont type across the southern Great Barrier Reef environments (Stat et al. 2008a). Some vertical-transmission-strategy corals harbor one type almost exclusively: *Montipora digitata* and *Porites cylindrica* – Clsu10, and *Seriatopora hystrix* – Clsu 9. However, the pocillopordaii corals *Pocillopora damicornis* and *Stylophora pistillata* harbor different symbiont types in different colonies. In the horizontal-transmission corals *Acropora millepora, Acropora palifera*, *Favites abdita, Goniastrea favulus,* and *Lobophyllia corymbosa*, different types are found in colonies from the same species (Stat et al. 2008a).

7 Host Specificity

Symbiodinium types are found in diverse host taxon at different geographic locations, and/or under various environmental conditions. Symbiont types are not randomly distributed among cnidarians, mollusks, foraminifera, e.g., clade H is typical to foraminifera. There is no correlation between the scleractinian host taxa and phylogeny to symbiosis with microalgae (Trench 1987). Species of the same host generally harbor the same *Symbiodinium* clades but not always the same genotypes (Coffroth and Santos 2005, as review).

At the same location, different species will harbor different clades and genotypes of symbionts. For example, at the GBR, *Acropora tenuis* harbors types C1 and C2 while *Acropora millepora* harbors clade D; both coral species are broadcast spawning corals with horizontal transmission of symbionts (see Little et al. 2004). Most Hawaiian symbiont genotypes associate with a specific host genus/species and many *Symbiodinium* types from Hawaii differ from those identified in West and East Pacific hosts (LaJeunesse et al. 2004b).

The local environments influence, control, and determine specificity of the host and the *Symbiodinium* genotypes (LaJeunesse and Trench 2000; Rodriguez-Lanetty et al. 2001; Coffroth and Santos 2005, as review). Many host species are capable of symbiosis with more than one *Symbiodinium spp*.; these different symbiotic associations are typically partitioned by geographic location and physical conditions such as light and temperature (LaJeunesse 2002; LaJeunesse et al. 2004a, b). The combinations of coral species and *Symbiodinium* type change with regard to depth, irradiance, temperature gradients, latitude, and longitude.

In the eastern Pacific, colonies of *Pocillopora verrucosa*, *Pocillopora meandrina*, *Pocillopora capitata*, and *Pocillopora damicornis* host either *Symbiodinium* D1 or C1b-c. The partner combination of the holobiont appeared random and/or was patchy (LaJeunesse et al. 2008). A different pattern was found for *Porites panamensis* symbionts with clade C at the same location, where the C type was dependent on water temperature and/or depth (LaJeunesse et al. 2008). In the Gulf of Eilat, it seems that the story depends on coral species as well as location since, at the gulf, shallow-water colonies of *Stylophora pistillata* harbor clade A while deeper-water colonies harbor either clade A or C (Lampert-Karako et al. 2008). Different specificity was found for the genus *Madracis* from the southern Caribbean. This genus is dominantly associated with *Symbiodinium* clade B regardless of host species, depth, or within-colony position (Frade et al. 2008a, b). However, the specificity is of the zooxanthella genotype: type B15 occurred predominantly on the deeper reef in green and purple colonies, while type B7 was present in shallow environments in brown colonies (Frade et al. 2008a).

Changes in symbionts are more likely to occur between generations (Baird et al. 2007), under current environmental conditions. Even species that are flexible at the time of infection have strong fidelity as adults (Little et al. 2004). Juveniles of *Acropora tenuis* harbor mixed assemblages of symbionts, while adults usually host a single clade (Little et al. 2004). Larvae of *Fungia scutaria* can be infected by different symbionts from several hosts, while adult colonies usually host a single clade, although some horizontal strategies show evidence of specificity (Weis et al. 2001). In many cases, symbiont diversity is prevalent over time once established, even if environmental changes occur (Iglesias-Prieto et al. 2004; Goulet 2006, 2007), although this is not always the case (Baker and Romanski 2007; Abrego et al. 2008; Jones et al. 2008). For example, at Magnetic Island, *Acropora tenuis* juveniles initially establish symbiosis with a mix of genotype D and C1, and in less than 1 year they become dominated by genotype D; however, the adult colonies do not associate with type D (van Oppen et al. 2001). *Acropora millepora* shuffled their dominant symbiont population after bleaching from type C2 to D (Berkelmans and van Oppen 2006). The adult colonies do not harbor type D (van Oppen et al. 2001). However, the symbionts shuffled, i.e., a change occurred in the relative abundance of genetically different *Symbiodinium* types (*sensu* Baker 2003). This is one of the mechanisms that occurs in several coral species under stress conditions such as high temperature, causing bleaching (Baker 2001; Toller et al. 2001; Little et al. 2004; Baker and Romanski 2007; Jones et al. 2008; Thornhill et al. 2006). Symbiont shuffling is more likely a shifting, not a switching, in the symbiont community dominant in a colony (Jones et al. 2008).

Seriatopora hystrix (vertical transmission strategist) harbors unique symbiont types in different geographic locations within the Pacific, while *Acropora longicyathus* (horizontal transmission strategist) harbors the same types in reefs in Australia, Malaysia, and Japan (Loh et al. 2001). Horizontally transmitted associations are highly specific, despite the presence of a broad range of optional partners (Wood-Charlson et al. 2006). Only in some cases, the initial uptake of zooxanthellae by juvenile corals during natural infection is nonspecific; the association is flexible and depends on the dominant zooxanthellae (Little et al. 2004). With horizontal transmission, agglutination and phagocytosis assist in symbiont uptake by the animals (Rodriguez-Lanetty et al. 2006). Recognition between the symbionts and the coral occurs on a molecular level and depends on the identity of each partner (e.g., Belda-Baillie et al. 2002; Baker 2003; Rodriguez-Lanetty et al. 2006) to allow the phagocytosis. The specificity between *Fungia scutaria* and *Symbiodinium* sp. type C1f during the onset of symbiosis is mediated not only by recognition events before phagocytosis, but by subsequent cellular events occurring after the symbionts are incorporated into host cells (Rodriguez-Lanetty et al. 2006.(In the coral *Fungia scutaria*, the initial cell-surface cellular contact and recognition between the two partners evolve through a lectin/glycan (Wood-Charlson et al. 2006), while in the coral *Acropora millepora,* the protein Millectin, which is an ancient mannose-binding lectin, acts as a pattern recognition receptor (PRR). The Millectin can recognize carbohydrate structures on cells that are probably involved in recognition of the symbionts of the genus *Symbiodinium* (Kazandjian et al. 2008). It seems that an ancient role of C-type lectins in the innate immune response has been co-opted into the pathway that leads to the uptake of *Symbiodinium* by corals (Kazandjian et al. 2008).

Ecological dominance among clades differs between oceans (Baker 2003; LaJeunesse et al. 2003, LaJeunesse 2005). Although related as well as distant hosts harbor closely related symbionts of a similar type (Rowan and Powers 1991), high host specificity and coevolution occur. An example is the symbiotic type in *Porites*, *Montipora*, *Pocillopora*, and *Stylophora* from the Indo-Pacific and the Atlantic-Caribbean. Independent subclades of *Symbiodinium* spp. have evolved for *Porites*, a host genus common to both oceans, while each subclade has characteristic geographic distributions within each ocean (LaJeunesse 2005). Subclades within clade C that associated with different hosts indicated that host-symbiont specificity is part of the evolutionary process of development of new *Symbiodinium* species (LaJeunesse 2005).

The identification of the zooxanthellae, but not the host, on a molecular level ignores some of the specificity interaction between them. The change in the symbiont genotype associated with coral species is a long evolutionary train that differs from one location to another, from one host to another, and from one symbiont genotype to another, depending on the different environmental conditions leading to similar or different combinations.

8 The Host Factor and the Nature of Translocated Compounds

Glycerol, sugars, organic acids, amino acids, lipids, and polyunsaturated fatty acids are produced by the zooxanthellae and transferred to the host (review by Venn et al. 2008; Yellowlees et al. 2008; Stambler 2010b). The release of these photosynthetic products from isolated *Symbiodinium* cells is not triggered by changes in pH (Trench 1971).

In the host tissue, a compound described as host-release factor (HRF) stimulates the release of photosynthate from symbiotic algae (e.g., Muscatine 1967; Grant et al. 2006). The release of carbon by dinoflagellates incubated in HRF is always higher than by those incubated in seawater alone. Host-factor properties depend on the host and have different stabilities to heat (see in Biel et al. 2007). The HRF controls the amount of carbon translocated from the zooxanthellae to the host. Carbon is selectively released by the dinoflagellates to the incubation medium primarily as glycerol, with smaller amounts of glucose, organic acids, amino acids, and lipids (Fig. 4; Biel et al. 2007).

In the case of the temperate coral *Plesiastrea versipora*, the HRF, which has a low molecular weight (Mr < 1,000), stimulates the release of glycerol from its symbiotic dinoflagellate, which can then be utilized by the animal host for its own needs (Grant et al. 2006). The effect of HRF on algae is not related to changes in osmolarity (Grant et al. 2006). In this coral, HRF did not allow the glycerol to leak through the plasma membrane (Ritchie et al. 1993). However, the diversion of glycerol from the algae results in a partial decrease in the algal synthesis of triacylglycerol (TG) and starch (Grant et al. 2006).

HRF increased the ^{14}C-dihydroxyacetone phosphate pool, followed by a reduction by glycerol phosphate dehydrogenase to Gly-3-P. After glycerol-3-phosphate is saturated, Gly-3-P is shunted into a phosphatase reaction to remove the phosphate group and form glycerol (see Fig. 4; Biel et al. 2007). As a result, there is an increase in carbon fixation as glucose and starch released by dinoflagellates are incubated in HRF (Biel et al. 2007). According to Biel et al. (2007; Fig. 4), there is a connection between photosynthesis and respiration that can be seen at ultrastructural levels by the close location of chloroplasts and mitochondria (Biel et al. 2007; Fig. 1). The receptors and/or other transporters of the HRF signaling compounds are located on the algal cell membrane rather than on the host-derived symbiosome membrane (Grant et al. 2003).

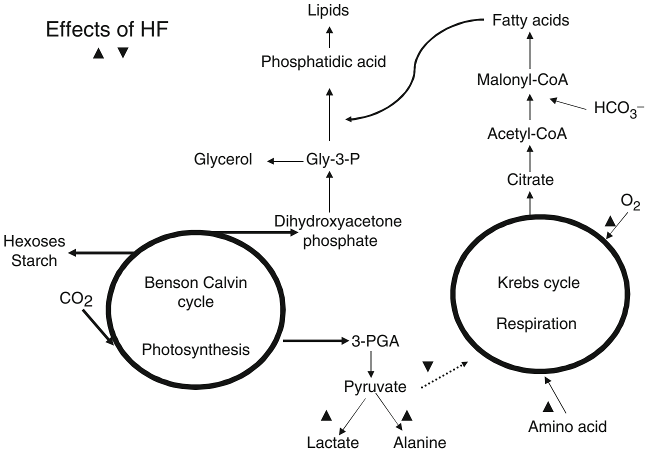

Fig. 4 Model of host-factor influence on photosynthesis and respiration of symbiotic algae. Arrow indicates increase or decrease of the biochemical reaction (Based on Biel et al. 2007)

The host factors are proteinaceous (Sutton and Hoeghguldberg 1990) and/or amino acids, including high concentrations of protein amino acids (Gates et al. 1995) and/or micromolar concentrations of the nonprotein amino acid, taurine (Wang and Douglas 1997). To better understand the host-factor mechanisms, synthetic host factor (SHF) was used. The synthetic host factor, consisting of aspartic acid, glutamic acid, M serine, histidine, glycine, arginine, taurine, alanine, tyrosine, methionine, valine, phenylalanine, isoleucine, leucine, and asparagine, at pH 8.3 and salinity of 33‰ (Gates et al. 1995; Biel et al. 2007; Stat et al. 2008b), has different effects on clades A and C from Hawaiian coral *Acrophora cytherea* (Stat et al. 2008b).

Photosynthesis inhibiting factor (PIF) is another host cell-signaling molecule, and is found in the coral *Plesiastrea versipora* (Grant et al. 2001). PIF partially inhibits photosynthetic carbon fixation in freshly isolated *Symbiodinium* from *Plesiastrea versipora* and the zoanthid *Zoanthus robustusas*, as well as algae from the coral *Montastraea annularis* in culture (Grant et al. 2006). The presence of symbiotic algae is not necessary for the production of the host signaling molecules HRF and PIF; they exist in the coral *Plesiastrea versipora* and are also expressed in naturally aposymbiotic colonies (Grant et al. 2004).

An advantage for both the algae and the corals is the removal by the algae of respiratory CO$_2$ and other metabolic breakdown products (NH$_3$, NO$_3^-$) from the host. The inorganic carbon (Ci) in the symbiosome is taken up by the *Symbiodinium* CO$_2$ concentrating mechanisms (CCMs) (Goiran et al. 1996; Leggat et al. 1999). In the chloroplast, the CCMs increase the availability of CO$_2$ to reach a high concentration that surrounds the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), and, by that, enable carbon fixation (Rowan et al. 1996; review in Yellowlees et al. 2008). Carbonic anhydrase (CA), which is required for the supply of CO$_2$ for the activation of the Rubisco and essential in the acquisition of Ci, exists in both the host and the algae (review in Yellowlees et al. 2008). The corals maintain high CA activity and, in addition, have specific transporters for the delivery of bicarbonate ions to the symbiotic algae. These characteristics provide partial pressure of CO$_2$ in the immediate surroundings of the symbiont cells that is high enough to support photosynthetic carbon fixation (Allemand et al. 1998).

The symbiotic algae have a high-affinity phosphate transporter and can store polyphosphate when phosphate is replete. Phosphate uptake is dependent on light (Jackson et al. 1989; Jackson and Yellowlees 1990). Both the host and the alga are capable of ammonium assimilation, with both possessing the enzymes glutamine synthetase (GS) and glutamate dehydrogenase (Anderson and Burris 1987; Leggat et al. 2007; Yellowlees et al. 2008; Stambler 2010b; Fig. 5). *Symbiodinium*

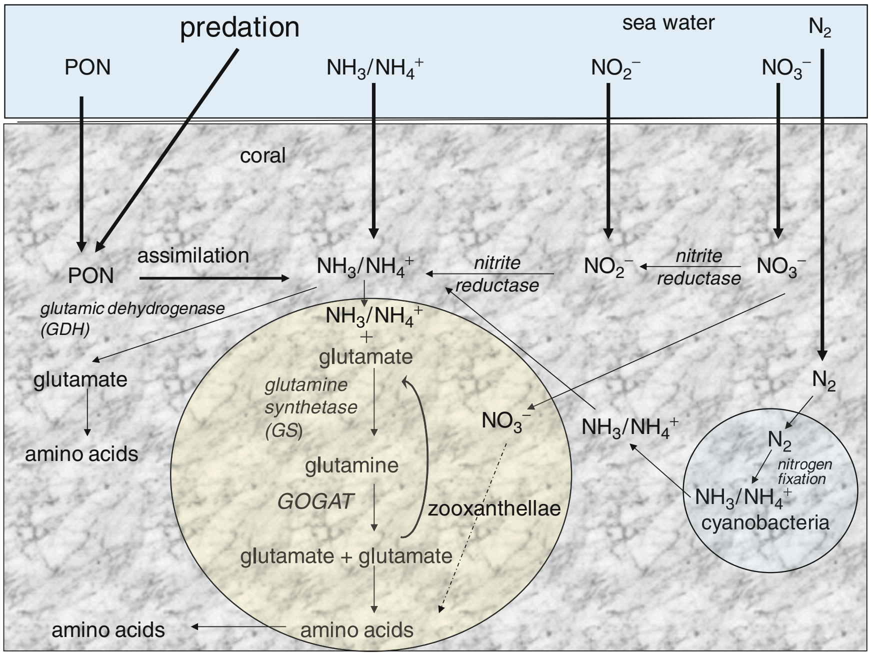

Fig. 5 Model of the nitrogen cycle in the cnidarian association (After Stambler 2010b)

are also capable of utilizing nitrate as a nitrogen source (Fagoonee et al. 1999) and for translocation to the host (Tanaka et al. 2006), presumably as amino acids. Ammonium is the preferred nitrogen source. When it is available, nitrate uptake rates decrease significantly (Grover et al. 2003).

In the Gulf of Eilat, shallow-water colonies of *Stylophora pistillata* harbor clade A (Lampert-Karako et al. 2008) and can support more than 100% of the CZAR (Falkowski et al. 1984). This is not the case for the Hawaiian coral *Acrophora cytherea*, which harbors *Symbiodinium* clade A and which releases very little carbon that can be used for host nutrition (Stat et al. 2008b).

Elevated feeding rates of the coral enhanced rates of photosynthesis normalized per unit surface area. Although this feeding does not always correspond to a higher transfer of photosynthetic products, it might change the component transferred (review in Houlbreque and Ferrier-Pages 2009).

The rate and percentage of photosynthetic carbon translocated from the zooxanthellae to the host depend on the rate of their genotype, photosynthesis rate, acclimation and adaptation, and light and nutrient availability.

9 Population Dynamics and Controls

Mechanisms of zooxanthella regulation include pre- and postmitotic processes, before or after their division (e.g., Baghdasarian and Muscatine 2000; Dimond and Carrington 2008). The premitotic process includes: (a) density-dependent, negative feedback via space or nutrient limitation (e.g., Jones and Yellowlees 1997; see in Baghdasarian and Muscatine 2000); (b) host factor leading to release of photosynthate from the symbionts (Gates et al. 1995; Baghdasarian and Muscatine 2000); and (c) host effects, mainly inhibition of symbiont cell cycle (Smith and Muscatine 1999). Postmitotic regulation includes degradation, digestion, or expulsion of symbionts alone or accompanied by the division of host cells (Titlyanov et al. 1996; Hoegh-Guldberg et al. 1987; Gates et al. 1992; Baghdasarian and Muscatine 2000; Weis 2008; Fig. 6).

Under oligotrophic conditions, zooxanthellae are nitrogen- and phosphorus-limited. They cannot multiply due to this limitation and, as a result, much of the carbon fixed in photosynthesis is translocated to the host (Falkowski et al. 1993). The result is that the growth rate of the zooxanthellae is extremely slow, with doubling times as long as 70–100 days (growth rate, $\mu = 0.007–0.001$ day^{-1}) in the common Red Sea coral *Stylophora pistillala* (Falkowski et al. 1984) compared to the much higher growth rate of zooxanthellae cultured from the coral *Acropora* sp. (0.33–0.48 day^{-1}) (Taguchi and Kinzie 2001).

The growth rate does not significantly depend on the zooxanthella genotype; however, in culture, it can be more than twice as high under high light (HL) compared to low light (LL). In the case of genotype F2 from *Meandrina meandrites*, under HL it is 0.76 day^{-1} and under LL – 0.32 day^{-1}, while in genotype A2 *Montastrea* spp., under HL – 0.46 day^{-1} and under LL – 0.22 day^{-1} (Hennige et al. 2009). It should be noted that there is increasing evidence that the growth of the zooxanthellae both in culture and in the coral host is in association with bacteria. Recently,

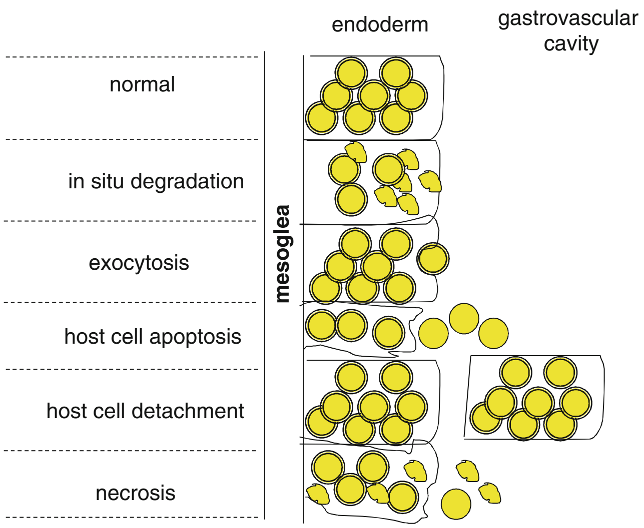

Fig. 6 Different types of cellular mechanisms of symbionts lost from host tissues. The zooxanthellae die or are killed by the host and are either expelled or digested; they undergo in situ degradation; symbiont exocytosis; host cells undergoing apoptosis or dying by necrosis release viable or degraded symbionts; symbionts lost together with host cell detachment (Adapted from Gates et al. 1992; Weis 2008)

Agostinim et al. (2009) found that Vitamin B12 is produced by the bacteria that are translocated to the zooxanthellae.

The host regulates algal density by expulsion of dividing algal cells and not by digestion (Baghdasarian and Muscatine 2000). The rate of expulsion is an opposite function of the ability of host cells to accommodate new algal cells. However, this regulation is found in some corals, e.g., *Pocillopora damicornis*, but not in others, such as *Montipora verrucosa*, *Porites compressa*, and *Fungia scutaria*. Some species have very low daily rates of algal expulsion and, in such cases, this kind of regulation is not efficient (Baghdasarian and Muscatine 2000; Fig. 7).

In cases where regulation of the algae is based on expulsion of extra algae, when the algal division rate increases due to environmental changes such as increases in light, temperature, and nutrients, leading to increase in algal division rate and is expressed in MI, there is an increased rate of expulsion of algae (Baghdasarian and Muscatine 2000). Temperatures elevated by a few degrees resulted in higher MI and expulsion rates (Baghdasarian and Muscatine 2000). In the case of temperate coral *Astrangia poculata*, while MI was independent of symbiont density, the expulsion rates were dependent. For this coral, higher MI and expulsion rates were found in summer (Dimond and Carrington 2008). Expulsion rates change according to time of day and season (Hoegh-Guldberg et al. 1987; Dimond and Carrington 2008) because of variation in the algal cell cycle with and without dependence on host nutrition.

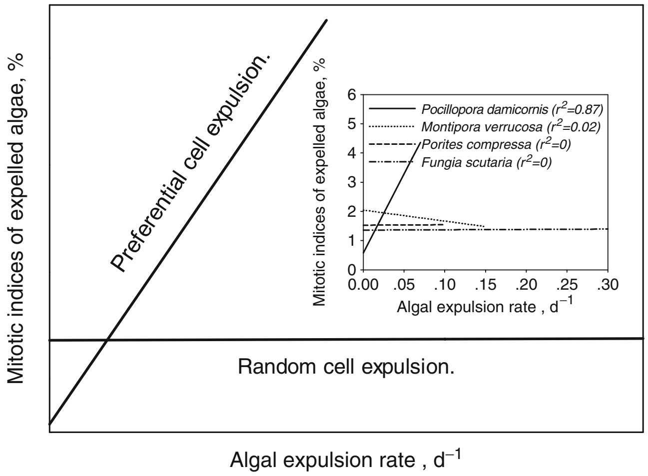

Fig. 7 Mitotic index as a function of algal expulsion rate: a. theoretical; b. in the field (Based on Baghdasarian and Muscatine 2000)

Once supplied with additional nutrients, either as inorganic compounds such as ammonium and phosphate or via zooplankton consumption by the host animal (e.g., Dubinsky et al. 1990; Falkowski et al. 1993; Dubinsky and Jokiel 1994), the zooxanthellae retain most of their photosynthetic products. The photosynthetic carbon is now utilized for the synthesis of zooxanthella biomass, accelerating their growth rates and increasing their densities up to fivefold (Dubinsky et al. 1990). Under eutrophication, there is also an increase in the number of zooxanthellae released to the surrounding water (Stimson and Kinzie 1991). Symbiont expulsion serves under eutrophication as the limiting overgrowth of the algae in the animal cells. The growth rate of the algal symbionts determines the upper limit of the standing stock and their rates of cell division (Smith and Muscatine 1999).

Under bleaching, the nitrogen uptake by corals supports zooxanthella recovery and increases their mitotic cell division (Rodrigues and Grottoli 2006).

After several days of starvation of the coral *Stylophora pistillata*, the zooxanthellae in its tissues exhibit degradation, possibly because the host used the algae as a food source (Titlyanov et al. 1996).

In the sea anemone *Anthopleura elegantissima,* no symbiosis-specific genes were involved in controlling and regulating symbiosis. Symbiosis is maintained by the varying expression of existing genes involved in vital cellular processes, including deregulation of the host cell cycle and suppression of apoptosis (Rodriguez-Lanetty et al. 2006).

There are several different types of cellular mechanisms by which zooxanthellae are lost from the host tissues: (1) in situ degradation: (a) programmed cell death (PCD) of the zooxanthellae (program always going to take place); (b) apoptosis and/or necrosis caused by biochemical and pathological processes under abnormal stimuli inducing cell death (see in Strychar et al. 2004a, b); (c) death and degradation because of stress effects, e.g., from reactive oxygen species (ROS); or (d) they are killed by the host cell (Gates et al. 1992; Weis 2008; Fig. 6). In the sea anemone *Aiptasia pulchella*, stress results in changes in lysosomal maturation and targeting of symbiosomes, resulting in symbiont digestion (Chen et al. 2005). After death, the symbionts will be digested in or expelled from the host. (2) Exocytosis, expelled freely. (3) Released inside detached host cell from the mesoglea. (4) This process releases viable or degraded symbionts with apoptotic host cells. (5) Necrosis of host causes the release of viable or degrading zooxanthellae. Loss of the zooxanthellae is into the gastrovascular cavity and, from there, to the surrounding water (Gates et al. 1992; Weis 2008; Fig. 6).

It is possible that in some cases, stress such as very high temperature causes the death of both the symbionts and the host simultaneously, while in other cases, death of the zooxanthellae or the coral will take place one after the other.

As a result of heat stress, apoptosis and necrosis occur simultaneously in both the sea anemone *Aiptasia sp*. tissues and its symbionts. Rate of apoptosis in the anemone endoderm increases within minutes of exposure to high temperature. Coincident with the timing of loss of zooxanthellae during bleaching, peak rates of apoptosis-like cell death is observed in the host. As exposure continues, apoptosis host cell number declines while necrosis cell number increases. Apoptosis and necrosis activity increases simultaneously in the zooxanthella cells dependent on temperature dose (Dunn et al. 2004). Apoptotic markers in response to heat stress in *Symbiodinium* spp. cells include: chromatin condensation, intact plasma membrane, vacuolization and vesicle formation, and cytoplasmic condensation (Dunn et al. 2004).

In the apoptosis of symbiont organisms in response to increased temperature and light, there is an increase in the activity of selective cysteine aspartate-specific proteases – caspase (Dunn et al. 2006; Richier et al. 2006; Weis 2008). During bleaching, apoptosis acts to maintain homeostasis, mitigate tissue damage, and remove dysfunctional symbionts (Dunn et al. 2004). Bleaching response might also represent a modified immune response that recognizes and removes dysfunctional symbionts (Dunn et al. 2007).

During stress leading to bleaching, although normal algae might be expelled under continuous and strong stress, usually the expulsion is of amorphous material and disorganized/digested cellular cells (Franklin et al. 2004). In the case of *Acropora hyacinthus* and *Porites solida* exposed to temperature stress as high as ≥34°C, it was not the host that was sensitive to temperature, but rather the symbionts, leading to expelled zooxanthellae characterized by irreversible ultrastructural and physiological changes symptomatic of cell degeneration and death (called apoptosis) or necrosis (Strychar and Sammarco 2009).

Holobiont corals with different clades may have developed different regulation mechanisms depending on the host, including its physiology and the environmental conditions (Rowan et al. 1997; Baghdasarian and Muscatine 2000), as well as mechanisms of the zooxanthellae themselves for expulsion from the host. Expulsion of zooxanthellae can occur under normal conditions, increased nutrition of the coral host, and under stress. Expulsion can be either during increasing symbiont density in the coral tissues (in the case of eutrophication) or during stress leading to bleaching (low density of zooxanthellae). Even though in recent years, study has focused on stress mechanisms causing bleaching and zooxanthellae loss from host tissues (the expulsion of zooxanthellae that in most cases are not viable and probably would not survive (Hill and Ralph 2007)), we should keep in mind that the release of zooxanthellae to the surrounding water is a natural control of their population number in the host, and is the only way that zooxanthellae are able to change their host. These released zooxanthellae are viable, and can infect other corals or larvae to create a new association by horizontal transmission.

10 Distribution Within Colony and Polyp

Corals harboring genetically mixed communities of *Symbiodinium* often show distribution patterns in accordance with differences in a light field across an individual colony. In *Acropora tenuis*, parts exposed to the Sun harbor type C2 while the shaded portions of the same colony harbor type C1 (van Oppen et al. 2001) *Symbiodinium* clade C is found predominately in the sides of *Montastraea* sp., while clade A is found predominately at the top of the same colonies (Rowan et al. 1997). In an individual colony of *Acropora valid*, Sun- and shade-adapted polyps were found to harbor either *Symbiodinium* clade C types alone or clades A and C simultaneously. Polyps harboring both clades A and C show higher metabolic activity of respiration and photosynthesis (Ulstrup et al. 2007).

Zooxanthellae are rare at the tip of stony corals (Fang et al. 1989). The tips that are exposed to high light have lower chlorophyll per coral unit area compared with the lower branches, which contain a higher concentration of photosynthetic pigments (Falkowski et al. 1984). In some cases, branches exposed to low light will have more zooxanthellae than those parts exposed to higher light, and/or more chlorophyll per algal cell (Titlyanov et al. 2001). Coral parts facing the dark will have no zooxanthellae (Dubinsky and Jokiel 1994; Titlyanov et al. 2001).

There is spatial heterogeneity in coral photosynthesis (Falkowski et al. 1984; Gladfelter et al. 1989; Kuhl et al. 1995; Ralph et al. 2002, 2005). Physiologically, zooxanthellae *in hospite* perform differently between Sun- and shade-adapted surfaces of individual colonies (Ralph et al. 2005), and between polyps and coenosarc tissue (Ralph et al. 2002). Polyps have lower photosynthesis available radiation (PAR) absorptivity than coenosarc tissue in *Acropora nobilis* (branching coral) and *Pavona decussata* (plate coral), whereas *Goniastrea australiensis* (massive coral) exhibits the opposite pattern. *Acropora nobilis* exhibits heterogeneity along the longitudinal axis of the branch; this can be differentiated from the effect of variations in illumination across the rugose and curved surfaces (Ralph et al. 2005). Differential bleaching responses between polyps and coenosarc tissue were found in *Pocillopora damicornis* but not in *Acropora nobilis* and *Cyphastrea serailia* (Hill et al. 2004).

11 Photosynthesis

Symbiodinium contain typical components of dinoflagellates: chlorophyll *a*, chlorophyll c_2, and carotenoids (peridinin, dinoxanthin, diadinoxanthin (DD, Dn,(diatoxanthin (Dt), and β-carotene) (e.g., Kleppel et al. 1989; Levy et al. 2006; Venn et al. 2006). The chlorophyll is part of the photosynthesis apparatus while Dn and Dt are part of the photoprotective xanthophyll (Brown et al. 2002). The zooxanthellae acclimate to photosynthesis under different light conditions. As light increases, the algal growth rate (μ), maximum photosynthesis, respiration, in vivo absorption (a*), and β carotene increase (Fig. 8). At the same time, chlorophyll *a* and *c*, peridinin concentrations, thylakoid area, the size of photosynthetic units (PSUs), and quantum yield (φ) decrease (Falkowski and Dubinsky 1981; Stambler and Dubinsky 2004; Fig. 8). The zooxanthellae photoacclimate, including, in addition to the adjustment of pigmentation, changes in the number of reaction centers in the light-harvesting photosystems (Falkowski and Dubinsky 1981; Dubinsky and Falkowski 2010). As a result of the photoacclimation of the zooxanthellae, corals can grow in shallow water exposed to sunlight and in deep water down to the photic zone (e.g., Mass et al. 2007; Stambler et al. 2008; Frade et al. 2008c). The photic zone is considered the depth from the surface to a depth of 1% of the sea subsurface light level. It should be noticed that photoinhibition is always observed in freshly isolated zooxanthellae (FIZ) (Fig. 9), but only occurs in shallow water at very high light intensity, inside the coral tissue (Hoegh-Guldberg and Jones 1999; review in Bhagooli and Hidaka 2004; Stambler and Dubinsky 2004; Levy et al. 2006; Frade et al. 2008c).

The light-saturated rate of photosynthesis (P_{max}), compensation light intensity (E_c), and light intensity of incipient saturation (E_k), all decrease with depth while the efficiency of photosynthesis (α) increases with depth (Mass et al. 2007; Hennige et al. 2008; Stambler et al. 2008). The response to light also depends on daily changes in light, for example, higher photosynthetic rates occur in the afternoon rather than the morning at the same PAR levels; however, this may vary significantly between species (Levy et al. 2004). Shallow-water coral reefs show a diurnal xanthophyll diadinoxanthin (Dn) and diatoxanthin (Dt) pattern, as well as changes in the photosynthesis parameter, such as quantum yield and photochemical efficiency (Fv/Fm). The potential of the maximum quantum yield of photochemistry in photosystem II (PSII) is determined in a dark-adapted state as the

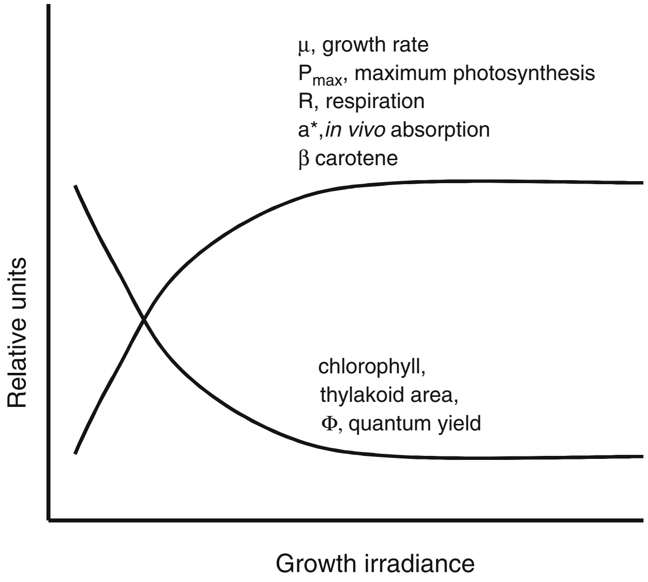

Fig. 8 Changes in chlorophyll concentration; P_{max}, maximum photosynthesis; R, respiration; a*, in vivo absorption; β carotene; thylakoid area; Φ, quantum yield; μ, growth rate as response to light intensity during growth (Based on Dubinsky et al. 1995)

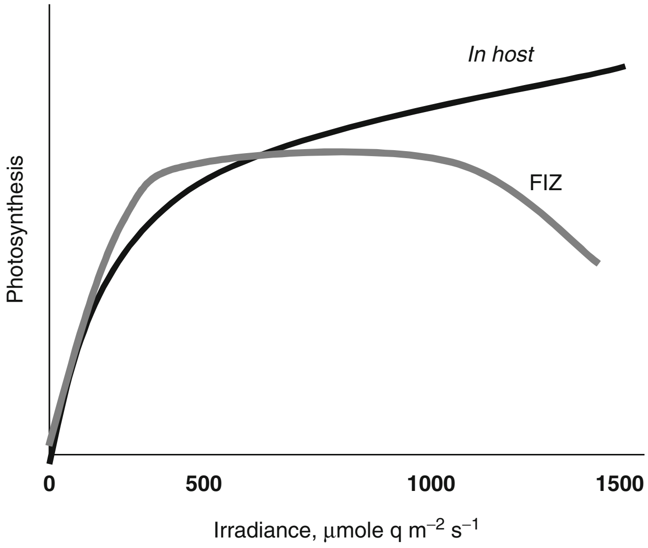

Fig. 9 Photosynthesis rate *in hospite* and in fresh isolated zooxanthellae (FIZ) as function of light intensity

ratio Fv/Fm = (Fm–F_0)/Fm, where F_0, Fm are the minimum and maximum yields of chlorophyll fluorescence, respectively, measured after a dark period (relative units). Fv, the variable fluorescent, is determined as Fv = (Fm–F_0) (Brown et al. 1999). The patterns of the xanthophyll cycling that exist in different *Symbiodinium* genotypes and the diel effective quantum yield of photosystem II, nonphotochemical quenching (NPQ) of the fluorescence, differ between corals species even when residing at the same depth (Warner and Berry-Lowe 2006).

The photosynthesis of freshly isolated zooxanthellae (FIZ) differs significantly from their photosynthesis in host tissue (Fig. 9) due to the different lights they are exposed to, their packaging in the tissue, and competition on CO_2 with the coral (Dubinsky et al. 1990; Stambler and Dubinsky 2005). Acclimation of the holobiont to different light levels involves the following coral host responses: (a) some host nonfluorescent pigments upregulate response to elevated irradiance. As a response, maximum photosynthesis per chlorophyll correlates with the concentration of an orange-absorbing nonfluorescent pigment (CP-580) in the coral *Montipora monasteriata* (Dove et al. 2008, Fig. 10); (b) under low light, changes in the shape of the colonies include flattening, and by that, they reduce the shading of the branches one of the other (e.g., Dustan 1975; Graus and Macintyre 1976; Stambler and Dubinsky 2005; Mass et al. 2007; Kaniewska et al. 2008); (c) increase in fluorescent host pigments acts as photoprotector under high light and UV; (d) changes in the skeleton of the coral host (Enriquez et al. 2005); and (e) changes in host-tissue thickness, e.g., tissue mass is smaller at the lower part of the colony (Anthony et al. 2002).

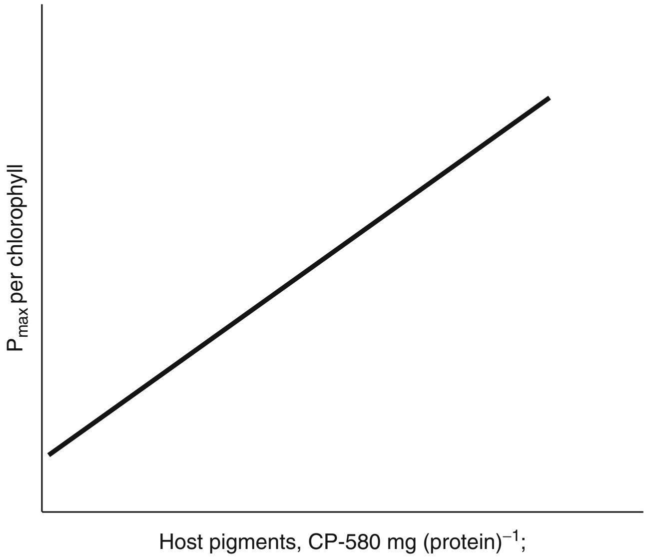

Fig. 10 Maximum photosynthesis per chlorophyll of the symbionts as a function of the host pigment concentrations (Based on Dove et al. 2008)

Stress that damages photosynthesis might lead to bleaching (Stambler and Dubinsky 2004; Stambler 2010a). Some of the damage is: (1) decrease in the efficiency of photosystem II (PSII) under high temperature, which causes a malfunction in the light reactions of photosynthesis; (2) degradation of the reaction center D1 protein, which occurs with temperature-dependent loss of PSII activity (Warner et al. 1999); (3) PSII damage that affects the impairment of the Calvin-Benson cycle and causes a decrease in carboxylation of ribulose 1,5 bisphosphate (RuBP) – Rubisco (Jones et al. 1998); (4) increase in reactive oxygen species (ROS) concentration, leading to cellular damage (Lesser 2006); and (5) damage of the thylakoid membranes, causing an increase in the rate of electron transport on the acceptor side of PSII with a simultaneous decrease in the maximum quantum yield of photochemistry in the reaction center (Tchernov et al. 2004). Combination of stress, specifically under high light and temperature, leads to chronic photoinhibition (Bhagooli and Hidaka 2004). pCO_2 enrichment of *Symbiodinium in hospite* of the coral *Acropora Formosa* caused an increase in chlorophyll *a* per cell under subsaturating light levels, thus supporting the idea that zooxanthellae are CO_2-limiting in the coral tissue. While light-enhanced dark respiration per cell increased due to an increase in the immediate products of the Calvin cycle, the dark respiration stayed the same; xanthophyll de-epoxidation increased; all of this leads to decreases in photosynthetic capacity per chlorophyll (Crawley et al. 2010). Expression of the first enzyme in the photorespiratory cycle, phosphoglycolate phosphatase (PGPase), was reduced by 50% under high CO_2 environment. This reduction in PGPase coincided with the decline in zooxanthella productivity (Crawley et al. 2010).

Physiological function of the symbionts is not always correlated with the clade level (Savage et al. 2002; LaJeunesse et al. 2003; Tchernov et al. 2004). Although photoacclimation of *Symbiodinium* genotype is variable, their light absorption per photosystem is similar (Hennige et al. 2009). In cultures and *in hospite,* most clade A *Symbiodinium* types, but not clades B, C, D, or F, show enhanced capabilities for alternative photosynthetic electron-transport pathways, including cyclic electron transport. Clade A undergoes pronounced light-induced dissociation of antenna complexes from photosystem II (PSII) reaction centers; this was not observed in other clades. As a result, clade A symbionts are resistant to high light intensities and high temperature, and, as such, survive bleaching (Lampert-Karako et al. 2008; Reynolds et al. 2008). Clades B, C, and D, found in symbioses in deeper waters than *Symbiodinium* clade A, benefit from enhanced light-harvesting capability. The *Symbiodinium* subclade B are found in shallow water, probably employing photoprotection mechanisms other than antenna translocation. *Symbiodinium* clades B and C from deeper-dwelling corals, susceptible to bleaching, can engage nonphotochemical quenching (NPQ) and varying degrees of chlororespiration (Reynolds et al. 2008).

12 Ecology: Geography, Temperature, and Host Effects

The geographical distribution of genotypically varying symbionts and their abundance is dependent on host specificity and tolerance to temperature and light variation.

Environmental gradients of light are one of the important controls of coral holobiont physiology, distribution, survival, and existence (Falkowski et al. 1990). At the GBR, in shallow water less than 3 m, *Stylophora pistillata* harbors C1, while 10 m is associated with C27 (LaJeunesse et al. 2003). The Caribbean *Montastraea spp.* hosts A and B clades in shallow waters (less than 6 m) and clade C symbionts at the deeper depths (Rowan and Knowlton 1995). The *Symbiodinium* types associated with *Montastraea* sp. and *Acropora* sp. depend on the irradiance that the colony is exposed to (Rowan et al. 1997; Ulstrup and van Oppen 2003). Different *Symbiodinium* types B show systematic patterns of distribution in different *Madracis* species over a depth and light gradient that the colony is exposed to. Brown colonies of *Madracis pharensis* from 10 m depth harbor *Symbiodinium* B7 while in deeper water (25 m), green and purple colonies of the same species are associated with type B15 (Frade et al. 2008a, b), whose larger cells are found at lower densities in the coral tissue compared to type B7. These two types show different adaptation and acclimation to light. Chlorophyll concentration per cell was higher in type B15. α, the initial slope of the photosynthesis versus irradiance curve (P versus E), i.e., the ratio of photosynthesis to light under light limitation, was higher for type B15 when normalized to algae cells (Frade et al. 2008b). In spite of this, the symbiont genotype in the *Madracis* colonies was dependent on the depths where they grow, and not on the different light microhabitats at each depth (Frade et al. 2008a).

Whether or not the distribution of coral species depends on its symbionts is not clear; however, in the eastern Pacific reefs, *Pocillopora verrucosa* with D1 type dominates shallow water while *Pavona gigantean* is associated with *Symbiodinium* C1c (Iglesias-Prieto et al. 2004). Nevertheless, juvenile corals harbored with clade C grow two to three times faster than those harbored with clade D (Little et al. 2004).

Only several host taxa are found in the western Pacific and Caribbean Oceans, which are dominated by a few prevalent generalist symbionts. In Hawaii, due to geographic isolation and low host diversity, a high proportion of coral species with vertical transmission have high symbiont diversity and specificity with no dominant generalist symbionts (LaJeunesse et al. 2004b; Fig. 11).

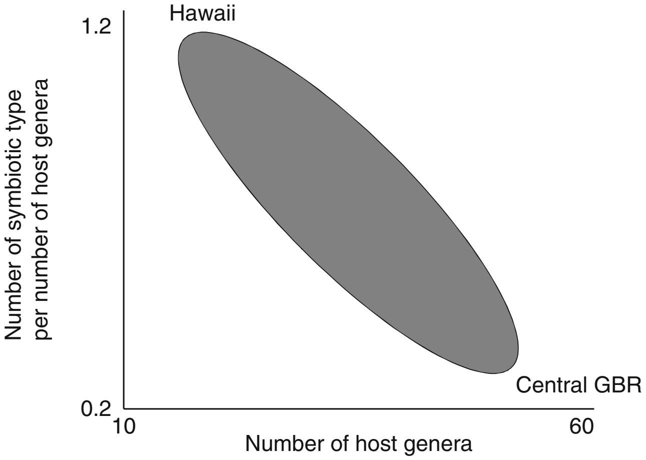

Fig. 11 The ratio between the number of symbiotic types per number of host genera and the number of host genera (Based on LaJeunesse et al. 2004b)

Corals associated with *Symbiodinium* live close to their upper thermal tolerance limits (Fitt et al. 2001). The coral *Acropora tenuis* response to bleaching is dependent on the *Symbiodinium* type with which the colony associates (Abrego et al. 2008). There are heat types within both clades C and D (Bhagooli and Hidaka 2004; Tchernov et al. 2004). For example, *Montipora digitat* with type C15 is more resistant to bleaching compared to other *Montipora* associated with other clade C types (LaJeunesse et al. 2003). *Symbiodinium* clade D (presumably D1) has been characterized as heat- or stress-tolerant based on increased frequency of this type within this clade in Caribbean and Indo-Pacific corals after bleaching events (Abrego et al. 2008; Jones et al. 2008). However, *Acropora tenuis* juveniles when hosting *Symbiodinium* type C1, demonstrate lower metabolic costs and higher physiological tolerance compared to juveniles with type D (Abrego et al. 2008). At higher eastern Pacific latitudes, *Pocillopora* spp naturally evolved and associated with type D, but not as a result of coral bleaching (Baker et al. 2004; LaJeunesse et al. 2008). It is possible that clade D includes algal types that differ in thermal tolerance (e.g., Tchernov et al. 2004). It should be noticed that phylotypes belonging to different genotypes can present similar patterns of sensitivity to elevated temperatures, but differ from their closely related sister phylotypes (Tchernov et al. 2004).

Since different *Symbiodinium* sp. have different temperature tolerances and, thus, different growth requirements (Fitt et al. 2000; Kinzie et al. 2001) over evolutionary timescales, colonies hosting thermally sensitive symbionts might become extinct by natural selection. Acquisition of less-sensitive symbiont populations (for example, clade D1 in the case of temperature increase) might result in colony survival (Buddemeier and Fautin 1993; Baker 2001; LaJeunesse et al. 2004a, b).

Zooxanthellae exposed to cold temperature stress decrease their maximum photochemical efficiency of PSII and may undergo chronic photoinhibition (Saxby et al. 2003; Thornhill et al. 2008). *Symbiodinium* type B2 associated with the temperate corals *Astrangia poculata* and *Oculina arbuscula* adapt and survive over extended periods of cold temperature stress and rapidly return to normal photosynthetic function when temperature increases (Thornhill et al. 2008).

Host-protective mechanisms against the stress of the holobiont include: the production of antioxidant enzymes (Lesser et al. 1990; Lesser 2006), mycosporine-like amino acids (MAAs) (Shick and Dunlap 2002), and fluorescent pigments (Salih et al. 2000). These protective mechanisms may be damaged under stress, for example, the fluorescent pigments are reduced at elevated temperatures (Dove 2004).

Under high light intensity, high rates of photosynthesis by the zooxanthellae generate high concentration of dissolved oxygen (Lesser 2006). These high concentrations can form reactive oxygen species (ROS). ROS causes major cellular damage, including oxidizing membranes, denaturing proteins, and damaged nucleic acids (Lesser 2006). ROS, especially the reactive nitrogen species nitric oxide (NO), may play a major role in bleaching (Bouchard and Yamasaki 2008; Weis 2008) even though both the host and the zooxanthellae have adaptations to prevent this damage. These adaptations include enzymes such as catalase, ascorbate peroxidase, and multiple isoforms of superoxide dismutase (SOD) (Richier et al. 2005, 2008; Lesser 2006; Weis 2008).

The mycosporine-like amino acids (MAAs) found in many coral dinoflagellate symbioses also originate in the endosymbionts and act as UV protectors (Shick and Dunlap 2002). For example, mycosporine-glycine, shinorine, porphyra-334, and palythine were detected in all *Symbiodinium* and their cnidarian hosts from the Mexican Caribbean (Banaszak et al. 2006). MAAs are present within the *Symbiodinium* and the host fractions (Banaszak et al. 2006). They are more concentrated in the tissues of the anthozoan host than in the zooxanthellae (Shick et al. 1995; Shick 2004; Furla et al. 2005). Under natural conditions, *Symbiodinium* clades do not influence the presence of MAAs in the symbionts from the Mexican Caribbean (Banaszak et al. 2006). This is in spite of the fact that in culture, only *Symbiodinium* clade A produces MAAs whereas other clades do not (Banaszak et al. 2006).

The thermal tolerance of *Symbiodinium* is dependent on genotype and adaptation: thermally tolerant type A1 increases light-driven O_2 consumption but not the amount of H_2O_2 produced, while sensitive type B1 increases the amount of H_2O_2 produced without an increase in light-driven O_2 consumption. In other words, the Mehler reaction, which elevates H_2O_2 production, is the response of clade B1 to temperature increase (Jones et al. 1998; Suggett et al. 2008).

Freshly isolated zooxanthellae respond to heat/light stress differently when they are *in hospite*, suggesting that the hosts play an important role in regulating the response of the holobiont (Bhagooli and Hidaka 2003). The advantage of the holobiont and its ability to survive depends on the host genotype (Baird et al. 2009) and on symbiont genotypes that change the mutualistic symbiosis interaction and efficiency under different environmental conditions. Hermatypic coral success and survival depend on the symbionts, host genomics, and the interaction between them in the local environment, with attention to the effect of the historical condition. Under continuous stress, evolutionary processes may shift the coral from a photoautotrophic to a heterotrophic situation, which already occurs under deep depths and bleaching conditions (Grottoli et al. 2006; Palardy et al. 2008; Houlbreque and Ferrier-Pages 2009). These processes may separate the symbiotic partners forever.

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