



Marine Invertebrate Larvae Associated with *Symbiodinium*: A Mutualism from the Start?

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Symbiodinium are dinoflagellate photosynthetic algae that associate with a diverse array of marine invertebrates, and these relationships are comprehensively documented for adult animal hosts. Conversely, comparatively little is known about the associations during larval development of animal hosts, although four different metazoan phyla (Porifera, Cnidaria, Acoelomorpha, and Mollusca) produce larvae associated with *Symbiodinium*. These phyla represent considerable diversities in larval forms, manner of symbiont acquisition, and requirements on the presence of symbionts for successful metamorphosis. Importantly, the different requirements are conveyed by specific symbiont types that are selected by the host animal larvae. Nevertheless, it remains to be determined whether these associations during larval stages already represent mutualistic interactions, as evident from the relationship of *Symbiodinium* with their adult animal hosts. For instance, molecular studies suggest that the host larval transcriptome is nearly unaltered after symbiont acquisition. Even so, a symbiosis-specific gene has been identified in *Symbiodinium* that is expressed in larval host stages, and similar genes are currently being described for host organisms. However, some reports suggest that the metabolic exchange between host larvae and *Symbiodinium* may not cover the energetic requirements of the host. Here, we review current studies to summarize what is known about the association between metazoan larvae and *Symbiodinium*. In particular, our aim was to gather in how far the mutualistic relationship present between adult animals hosts and *Symbiodinium* is already laid out at the time of symbiont acquisition by host larvae. We conclude that the mutualistic relationship between animal hosts and algal symbionts in many cases is not set up during larval development. Furthermore, symbiont identity may influence whether a mutualism can be established during host larval stages.

Keywords: symbiosis, zooxanthellae, coral reef, larval ecology, planula, veliger

INTRODUCTION

Marine invertebrates typically present indirect development and their generally planktonic larvae act as the dispersive stage. This is a particularly important adaptation, as it directly influences species distribution and abundance, and also enables geographical range expansion and recovery of populations (Strathmann et al., 2002). Many factors influence larval development and its dispersal, such as oceanographic conditions, predation avoidance by planktivorous organisms,

energy reserves, and feeding abilities (Pechenik, 1990). As a response to such wide array of scenarios, there is a significant diversity of larval forms presented by metazoan organisms (Wray and Raff, 1991). Certain larval types are planktotrophic and required to feed, thus presenting specialized organs, while others are lecithotrophic and can survive through metamorphosis while relying solely on endogenous reserves (Thorson, 1950; Pechenik, 1999).

Despite the diversity of requirements for different marine invertebrate larvae, certain larval forms not only require to feed in the plankton, but also acquire symbionts (Fitt et al., 1986; Mieog et al., 2009; Garcia Ramos and Banaszak, 2014). Many metazoan phyla, especially scleractinian corals within the Cnidaria, engage in a mutualistic symbiosis with the photosynthetic dinoflagellates in the genus *Symbiodinium* (Stat et al., 2006; Venn et al., 2008). The majority of these corals are broadcast spawners and newly-formed planula larvae, while lecithotrophic, must acquire their symbionts horizontally (Harrison and Wallace, 1990; Baird et al., 2009; Harrison, 2011). The planktonic larvae acquire different free-living *Symbiodinium* strains from the environmental pool before selecting one or more specific strains at a later stage (Belda-Baillie et al., 1999; Weis et al., 2001; Coffroth and Santos, 2005).

Further, although numerous studies are available on animal-dinoflagellate symbioses, there is still an overall paucity of knowledge on this relationship during host larval development, especially in regard to metabolite exchange and symbiosis-related differential gene expression. In fact, this paucity of information raises the question as to whether the mutualistic nature of this relationship is already present during host larval development or becomes established at a later stage. Likewise, while there is much information on the impacts of climate change and anthropogenic influence on adult and symbiotic coral reef organisms (Hoegh-Guldberg, 1999; Hughes et al., 2003; Hoegh-Guldberg et al., 2007), comparatively little is known about the impacts of these environmental changes on *Symbiodinium*-associated animal larvae. Therefore, here we aim to compile, describe, and interpret the available data on metazoan larva-*Symbiodinium* associations, with emphasis on the ecological, molecular and biochemical relationship, evolution, and impact of climate change.

MARINE INVERTEBRATE LARVAE ASSOCIATED WITH *SYMBIODINIUM*

Four different metazoan phyla produce larval forms that associate with *Symbiodinium*: Porifera, Cnidaria, Acoelomorpha, and Mollusca (Table 1). Two protist taxa are also known to associate with *Symbiodinium*, Foraminifera (Pochon and Gates, 2010), and Ciliophora (Mordret et al., 2016). Invertebrate larvae acquire symbionts in two different ways: vertically (transmitted to the offspring in parental oocytes) or horizontally by oral ingestion during larval development. Both strategies have their advantages. Vertical transmission ensures that a successful symbiont strain is supplied to the larvae (Wilkinson and Sherratt, 2001), while horizontal transmission allows for the larvae to

acquire a diversity of symbionts, some of which may be more compatible with different environmental conditions encountered after dispersal (Baird et al., 2007).

Sponges and acoelomorph worms are the two groups in which particularly little is known about their association with *Symbiodinium*, especially during larval development. Within sponges, the association with *Symbiodinium* seems to be largely restricted to the family Clionidae (Hill et al., 2011) and parenchymella larvae contain parentally-seeded symbionts (Mariani et al., 2000, 2001). In the case of acoelomorph worms, the genus *Waminoa* harbors two different symbiotic dinoflagellates, *Symbiodinium* and *Amphidinium*, which are also transmitted vertically (Barneah et al., 2007b). Other acoelomorph genera are known to associate with *Symbiodinium* (Trench and Winsor, 1987), but no information regarding their larval development has been reported.

In the case of cnidarians, while broad knowledge on their association with *Symbiodinium* is available, there are still relatively few studies on the larva-*Symbiodinium* association (Rodriguez-Lanetty et al., 2006; Voolstra et al., 2009b; Schnitzler and Weis, 2010; Wolfowicz et al., 2016). Approximately 80-90% of reef-building coral species (Scleractinia) are broadcast spawners and acquire symbionts horizontally (Harrison and Wallace, 1990; Baird et al., 2009; Harrison, 2011). On the other hand, many of the less common brooding species transmit symbionts vertically, most notably in the family Pocilloporidae (Baird et al., 2009). In the case of soft coral species (Alcyonacea), the incidence of vertical transmission seems to be higher (Benayahu et al., 1988; Achituv et al., 1992) than for scleractinians. Coral larvae are typically lecithotrophic (Morse et al., 1996) and while symbiont acquisition may improve host fitness, it does not seem to be a requirement for metamorphosis (Schwarz et al., 1999; Mieog et al., 2009). In the case of other cnidarians such as anemones and jellyfish, there is still very little information on the role of *Symbiodinium* in their larval ecology.

Among mollusks, giant clams (subfamily Tridacninae) are possibly the most conspicuous species associated with *Symbiodinium*. In this group symbiont acquisition is horizontal (Fitt and Trench, 1981) and a requirement for successful metamorphosis (Mies et al., 2017a). Differently from other metazoan hosts, symbionts are only acquired during the second larval stage (veliger), as the first larval stage is a non-feeding trochophore (Fitt et al., 1984; Heslinga et al., 1984). To date, giant clams are also the only known *Symbiodinium* hosts that during larval development do not move symbionts from the digestive tract or equivalent to endodermal tissues (Schwarz et al., 2002; Marlow and Martindale, 2007; Huang et al., 2008), as they remain in the digestive tract throughout the larval development (Fitt et al., 1986; Hirose et al., 2006). The other mollusk group associated with *Symbiodinium* is Gastropoda. The Queen Conch *Strombus gigas* is the largest among them to do so and symbiont acquisition is also horizontal and apparently required for metamorphosis (Garcia Ramos and Banaszak, 2014). While a large diversity of nudibranchs (mainly aeolids) are known to associate with *Symbiodinium*, there is a scarcity of larval experiments, possibly due to their typically restricted diet (Dionísio et al., 2013). The only exception is *Berghia stephanieae*,

TABLE 1 | Host taxa and their larval stages associated with *Symbiodinium*, also describing mode of symbiont transmission and addressing whether the presence of *Symbiodinium* in larval tissues is critical for successfully attaining metamorphosis.

| Host taxon | Mode of <i>Symbiodinium</i> transmission | Larval stages associated with <i>Symbiodinium</i> | <i>Symbiodinium</i> acquisition as a requirement for metamorphosis | References |
|--------------|--|---|--|---|
| Porifera | Vertical | Parenchymella | n/a | Mariani et al., 2000, 2001 |
| Cnidaria | | | | |
| Scyphozoa | Vertical and horizontal | Planula | No | Montgomery and Kremer, 1995; Hofmann et al., 1996; Sachs and Wilcox, 2006; Mellas et al., 2014 |
| Actiniaria | Vertical and horizontal | Planula | No ^a | Bythell et al., 1997; Schwarz et al., 2002; Hambleton et al., 2014 |
| Alcyonacea | Vertical and horizontal | Planula | No | Benayahu et al., 1988, 1992; Achituv et al., 1992; Slattery et al., 1999; Barneah et al., 2004 |
| Scleractinia | Vertical and horizontal | Planula | No | Weis et al., 2001; Marlow and Martindale, 2007; Harii et al., 2009; Mieog et al., 2009; Erwin and Szmant, 2010 |
| Acoelomorpha | Vertical | Müller's larva | n/a | Barneah et al., 2007a,b; Hikosaka-Katayama et al., 2012 |
| Mollusca | | | | |
| Gastropoda | Vertical and horizontal | Veliger | Yes ^b | Kempf, 1984; Carroll and Kempf, 1990; Banaszak et al., 2013; Garcia Ramos and Banaszak, 2014; Wecker et al., 2015 |
| Bivalvia | Horizontal | Veliger and pediveliger | Yes | Fitt and Trench, 1981; Fitt et al., 1984, 1986; Heslinga et al., 1984, 1990; Mies et al., 2012 |

^aIn the case of *Aiptasia* sp.; unknown for other anemones.

^bIn the case of the Queen Conch (*Strombus gigas*); unknown for nudibranchs. n/a, Not applicable.

a species that maintains *Symbiodinium* in dorsal extensions of the digestive diverticulum. Its lecithotrophic veliger larvae undergo metamorphosis in the absence of *Symbiodinium* (Carroll and Kempf, 1990; Kempf, 1991), but recent studies suggest that this species does not engage in a mutualistic relationship (Mies et al., 2017c). While nudibranchs usually acquire symbionts horizontally (Loh et al., 2006; Burghardt and Wägele, 2014; Ahmadian et al., 2016), a case of vertical transmission has been recently reported (Wecker et al., 2015).

SYMBIODINIUM DIVERSITY

Symbiodinium dinoflagellates may be found in two different life stages, a planktonic and free-living zoospore or a symbiotic and non-motile coccoid cyst (Freudenthal, 1962; Schoenberg and Trench, 1980; Stat et al., 2006). Thus, by presenting a free-living stage, the mutualistic association is not obligate for *Symbiodinium* (Stat et al., 2006). Species within this genus are morphologically cryptic and identification is performed through the use of molecular biology techniques (LaJeunesse et al., 2012; Arif et al., 2014). Based on ribosomal, plastid and mitochondrial phylogenies, *Symbiodinium* are divided in nine clades (A–I, Figure 1) and many subclades (Rowan and Powers, 1991; LaJeunesse, 2001; Pochon et al., 2014). Species-level diversity is still being assessed, mainly through sequencing of the internal transcribed spacer 2 (ITS2, see LaJeunesse and Trench, 2000), either by denaturing gradient gel electrophoresis (DGGE) based separation of ITS2 genomic copies (LaJeunesse and Trench, 2000; LaJeunesse, 2002; Thornhill et al., 2006) or by next-generation sequencing based elucidation of ITS2 diversity (Arif et al., 2014; Batovska et al., 2016; Hume et al., 2016; Ziegler et al., 2017). As a

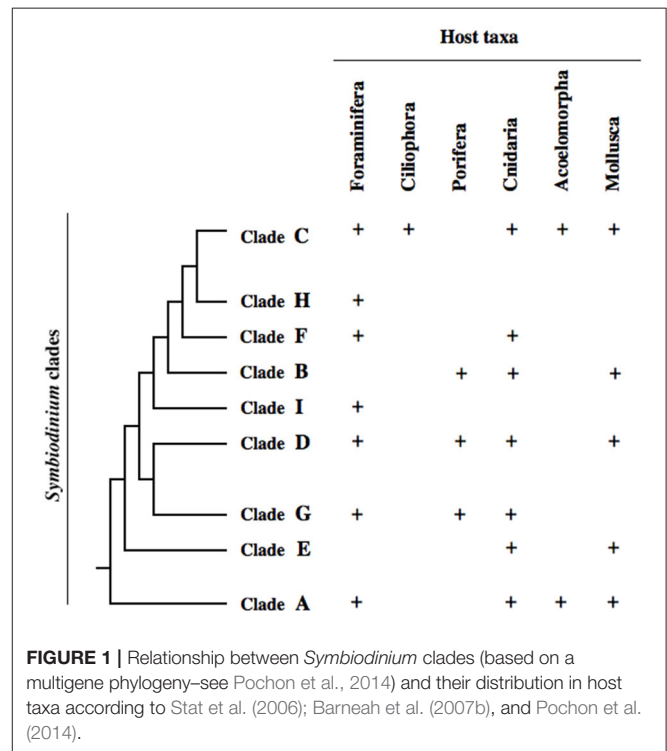


FIGURE 1 | Relationship between *Symbiodinium* clades (based on a multigene phylogeny—see Pochon et al., 2014) and their distribution in host taxa according to Stat et al. (2006); Barneah et al. (2007b), and Pochon et al. (2014).

result, many new taxa and/or strains have been described recently (LaJeunesse et al., 2012; Hume et al., 2015; Lee et al., 2015; Ziegler et al., 2017), with probably more than 100 extant species being present in the genus *Symbiodinium* (LaJeunesse, 2001).

Next-generation sequencing methods also allow to approach cryptic diversity in *Symbiodinium*-host relationships, i.e., the presence of rare, background *Symbiodinium* taxa that might be missed by genotyping methods with a lower resolution. This approach holds a dual premise: firstly, intragenomic allelic diversity of the ITS2 marker allows to resolve differences within and between individuals and species previously not possible (Batovska et al., 2016); secondly, in the case of *Symbiodinium*, deep sequencing of ITS2 diversity may uncover symbiont associations previously not detected (Arif et al., 2014; Boulotte et al., 2016). However, the contribution of low abundant *Symbiodinium* taxa to host resilience remains to be determined (Lee et al., 2016). Regardless of these considerations, the highest species diversity is found within clade C, that dominates Indo-Pacific coral reefs and is also one of the most abundant clades in the Atlantic (LaJeunesse, 2005). Host species tend to associate with a single *Symbiodinium* strain (Goulet, 2006), but multiple symbiont taxa (of different clades) may be found within a single host specimen (Rowan and Powers, 1991; Carlos et al., 2000; Baker, 2003). The type of *Symbiodinium* is a relevant factor for holobiont fitness, in both adult and larval stages (Schwarz et al., 1999; Mieog et al., 2009). While it has been reported that there is host life stage-specificity for symbiont strains, as juvenile and adult acroporid corals actively associate with different clades (Abrego et al., 2009), there is no life-stage specificity reported for larval stages yet.

SYMBIONT ACQUISITION AND LARVAL RESPONSE

Animal larvae acquire symbionts from different sources, but mainly from the water column and sediment (Adams et al., 2009; Cumbo et al., 2012; Nitschke et al., 2016). The amount of *Symbiodinium* cells acquired is highly variable among species and may vary according to environmental conditions. For acroporid corals Cumbo et al. (2012) report less than 10 symbiont cells acquired by larvae, while Harii et al. (2009) registered an average of 50–60 symbiont cells, but with high variability. Mies et al. (2017c) report about 30 cells for both giant clam and nudibranch larvae and more than 100 for coral larvae.

Animal hosts are able to select *Symbiodinium* strains through post-phagocytic recognition mechanisms involving lectin/glycan interactions (Koike et al., 2004; Wood-Charlson et al., 2006; Fransolet et al., 2012). These mechanisms are also active during larval development and reports also show that coral (Bay et al., 2011) and gastropod (Garcia Ramos and Banaszak, 2014) larvae actively select symbionts. Desired *Symbiodinium* species are kept while undesired ones suffer apoptosis (Dunn and Weis, 2009). However, there are reports that coral larvae may have no preference for different symbiont strains (Cumbo et al., 2012). In a study testing the offer of a homologous and two heterologous strains to *Fungia scutaria* larvae, there was no statistical difference in acquisition among strains, except for one of the heterologous strains that had significantly lower acquisition (Rodriguez-Lanetty et al., 2004). Interestingly, homologous strains have been shown to distribute differently in

larval tissues than heterologous strains (Rodriguez-Lanetty et al., 2006), and it has also been reported that homologous symbionts establish a more benefitting symbiosis (Trench et al., 1981; Schwarz et al., 1999; Dunn and Weis, 2009). However, Mies et al. (2017c) found no differences in survival in coral, nudibranch, and giant clam larvae associated with both homologous and heterologous *Symbiodinium* clades. Further, a recent study by Biquand et al. (2017) suggests that at least part of the specificity in the host-symbiont relationship may be determined by symbiont cell size, where *Symbiodinium* strains with a larger cell size are less likely to establish a symbiotic relationship than taxa with a smaller cell size using the laboratory model *Aiptasia* (Baumgarten et al., 2015) and corals. Nevertheless, the presence of symbionts in larval tissues (see **Figure 2**) may significantly contribute to its development. Giant clam larvae infected with *Symbiodinium* grow significantly larger than aposymbiotic larvae (Fitt et al., 1986; Mies et al., 2012) and *F. scutaria* larvae settle earlier in the presence of symbionts (Schwarz et al., 1999). However, higher growth not always suggests the establishment of symbiosis as some coral larvae have been shown to digest the symbionts (Titlyanov et al., 1998).

BIOCHEMICAL AND MOLECULAR RELATIONSHIP

The metabolite exchange between *Symbiodinium* and its adult host has been extensively documented. The host supplies the symbiont with CO₂ and other compounds for cellular synthesis such as nitrogen and phosphorus (Trench, 1979; Allemand et al., 1998; Leggat et al., 2003; Weis et al., 2008). In turn, the symbiont supplies the host with more than 90% of its metabolic requirement, in the form of organic compounds including glucose, glycerol, fatty acids, and amino acids (Muscatine, 1990; Grant et al., 1997; Papina et al., 2003; Burriesci et al., 2012). Still, very little is known about the metabolite exchange between *Symbiodinium* and metazoan larvae. To our knowledge, Kopp et al. (2016) is the only study to date confirming active metabolite exchange by showing that labeled ¹³C and ¹⁵N are translocated from symbiont to *Pocillopora damicornis* larvae. However, that same study found that these compounds contribute rather insignificantly to the larval nutrition. Other reports show that *Symbiodinium* types within clades A and C associated with coral and giant clam larvae produce a higher amount of the fatty acid DHA (docosahexaenoic acid, 22:6 ω 3–Mies et al., 2017c) and that *Symbiodinium* associated with giant clam larvae express a glycerol-synthesizing gene (Mies et al., 2017b), but in neither of those cases translocation was effectively confirmed.

One of the main issues hindering the better understanding of this relationship is the lack of molecular studies and information for *Symbiodinium*, also addressed in Leggat et al. (2011). The genomes for types within clades A, B, and F (Shoguchi et al., 2013; Lin et al., 2015; Aranda et al., 2016), transcriptomes for types within clades A–D (Bayer et al., 2012; Ladner et al., 2012; Parkinson et al., 2016) and the plastid genome for type B1 (Mungpakdee et al., 2014) and type C3 (Barbrook et al., 2014) have been sequenced in recent years, but further information,

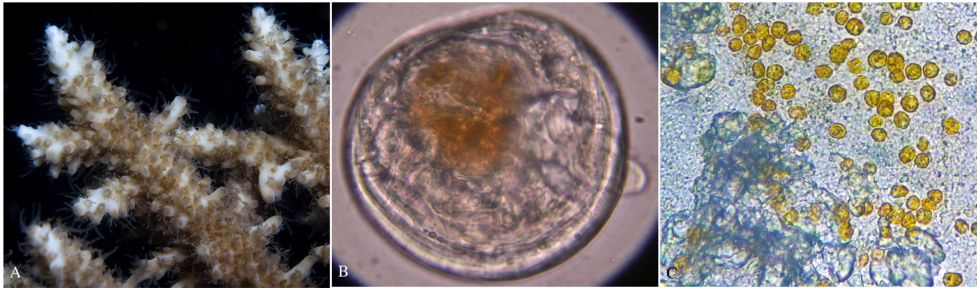


FIGURE 2 | *Symbiodinium* cells in both adult and larval host tissues. **(A)** Reef-building acroporid coral with brown coloration due to the presence of *Symbiodinium*, **(B)** *Symbiodinium* cells (orange-brownish area) in the digestive tract of a pediveliger larva of the giant clam *Tridacna crocea*, and **(C)** *Symbiodinium* cells in the gastrovascular cavity of a planula larva (squashed under a microscope) of the reef-building coral *Mussismilia hispida*.

especially on metabolic pathways, is still missing. However, a few experiments investigated differential gene expression in coral larvae with and without symbionts, all of which reported the absence of or rather small gene expression differences in the transcriptomes of symbiotic hosts when compared to the aposymbiotic state (deBoer et al., 2007; Voolstra et al., 2009b; Schnitzler and Weis, 2010). Only recently, a study by Mohamed et al. (2016) detected a transient period of differential expression involving a limited number of genes (3% of assayed transcriptome) 4 h after the exposure of *Acropora digitifera* planula larvae to a competent strain of *Symbiodinium*. While yet to be applied for larval studies, symbiosis-specific genes have been identified recently in *Aiptasia* anemones (Bucher et al., 2016; Wolfowicz et al., 2016). From the symbiont perspective, apart from the identification of protein kinases that may be involved in the establishment of symbiosis (Rosic et al., 2014), a symbiosis-specific gene was identified in *Symbiodinium* clade A, an H^+ -ATPase (Bertucci et al., 2010). This gene is the only symbiosis-specific gene that had its expression verified in *Symbiodinium* associated with invertebrate larvae (Mies et al., 2017b,c). The expression of this gene was confirmed in the veliger larvae of the giant clams *Tridacna crocea* and *T. maxima* and in the planula larvae of the hermatypic coral *Mussismilia hispida*, suggesting that symbiotic interactions are present.

EVOLUTIONARY PERSPECTIVE ON SYMBIOSIS ESTABLISHMENT

Symbiodinium is found in association with a diversity of polyphyletic hosts, which differ regarding aspects of symbiont uptake and symbiosis maintenance. Hence, the symbiosis between animal hosts and *Symbiodinium* likely formed independently on multiple occasions. The ability of *Symbiodinium* as well as other dinoflagellates to establish symbioses with such a diversity of hosts may derive from their evolutionary background as recently suggested by Aranda et al. (2016). Parasitism is common in many extant dinoflagellates (Kuperman and Matey, 1999) as well as their closest relatives, the apicomplexans (Shoguchi et al., 2013; Lin et al., 2015). It is thus possible that a putative parasitic evolutionary background

of *Symbiodinium* facilitated the infection of different hosts and their subsequent proliferation as endosymbionts. Hence, while the initial symbiosis of metazoan hosts and *Symbiodinium* may have been of parasitic nature, these symbioses evolved toward mutualistic interactions over time. Indeed, Aranda et al. (2016) recently confirmed adaptations in *Symbiodinium*, which may have facilitated the nutrient exchange with their hosts, such as an enrichment in carbon and nitrogen transporter domains. Yet, or as evidence to the derived mutualism notion, even extant metazoan-*Symbiodinium* associations are not exclusively mutualistic interactions (Stat et al., 2008; Lesser et al., 2013). Rather these interactions may exist along a continuum ranging from parasitism to mutualism depending on the identity of the host and symbiont (Sachs and Wilcox, 2006; Stat et al., 2008). Hence, the degree of mutualism between these partners may ultimately depend on the specificity of this association and the ability of the host to select for beneficial symbionts. Further, as the performance of *Symbiodinium* types depends on their host as well as environmental conditions, different hosts may select for different symbionts (Baker, 2003; Mieog et al., 2009). Thereby, the large diversity of metazoan hosts found in association with *Symbiodinium* likely contributed to the rapid divergence found in this genus (Pochon et al., 2006; Hume et al., 2016).

IMPACT OF CLIMATE CHANGE

Climate change is having a significant impact on coral reef ecosystems, particularly because of ocean acidification and the rise in seawater temperature (Hoegh-Guldberg, 1999; Hughes et al., 2003; Pandolfi et al., 2003; Hoegh-Guldberg et al., 2007). While the effects of ocean acidification have been investigated independently in marine invertebrate larvae and *Symbiodinium* (Brading et al., 2011; Nakamura et al., 2011; Waldbusser et al., 2013; Rivest and Hofmann, 2014), they yet need to be assessed on invertebrate larva-*Symbiodinium* associations. Nevertheless, it is known that the effects of ocean acidification on cultured (free-living) *Symbiodinium* is phylotype-specific, with some strains (such as A13 and A2) in fact benefitting from it and increasing their photosynthetic capacity (Brading et al., 2011). As it has also been shown that symbiont presence may mitigate the combined effects of acidification and hypoxia in non-calcifying hosts (Klein

et al., 2017), it would be interesting to verify whether the same would happen during host larval development.

In contrast, the bleaching phenomenon, defined by the loss of *Symbiodinium* cells from host tissue due to rising seawater surface temperatures has been well documented (Brown, 1997; Hoegh-Guldberg, 1999; Fitt et al., 2001). For adult and larval hosts alike, the presence of symbionts is generally regarded as positive for coral reef larvae development and fitness, but under thermal stress it may have the opposite effect. High temperatures cause the symbionts to become a source of reactive oxygen species (ROS), which leads to significantly higher larval mortality (Weis, 2008; Baird et al., 2009; Yakovleva et al., 2009; Schnitzler et al., 2012). Some of the effects of ROS include DNA damage and higher rates of antioxidant activity (Yakovleva et al., 2009; Nesa et al., 2012).

The bleaching threshold for corals and coral larvae alike is usually only 1.0–1.5°C above the prevailing maximum temperature (Edmunds et al., 2005; Mieog et al., 2009). At this time, the expression of heat-shock proteins and oxidative-stress genes becomes detectable (DeSalvo et al., 2008, 2010; Rodriguez-Lanetty et al., 2009; Meyer et al., 2011). Data by Mies et al. (2017c) show that coral and giant clam larvae from Vietnam bleach at 29°C and hardly survive past 32°C. However, the highly-tolerant larvae of *Pocillopora damicornis* (from Okinawa, Japan) have been shown to withstand a temperature of 32°C, despite losing the majority of its symbiont cells (Haryanti et al., 2015). Nevertheless, the bleaching threshold may be greatly influenced by host and symbiont physiology and genetics, and also by the oceanographic conditions *in situ* (Roik et al., 2016). The symbiont type associated with the larvae may also influence bleaching intensity, as coral and giant clam larvae associated with *Symbiodinium* types within A and C bleach at lower rates than types within clades B, D, E, and F (Mies et al., 2017c). However, further investigation is required, especially for strains in clade D, which increase the adult host temperature tolerance threshold and become dominant during bleaching events (Berkelmans and van Oppen, 2006; Jones et al., 2008; Mieog et al., 2009; Ladner et al., 2012). Taken together, the effects of climate change on larval-symbiont associations are not clear at present, but increasing seawater temperatures may lead to increased loads of ROS, which in turn may limit the association of certain symbiont types with host larvae.

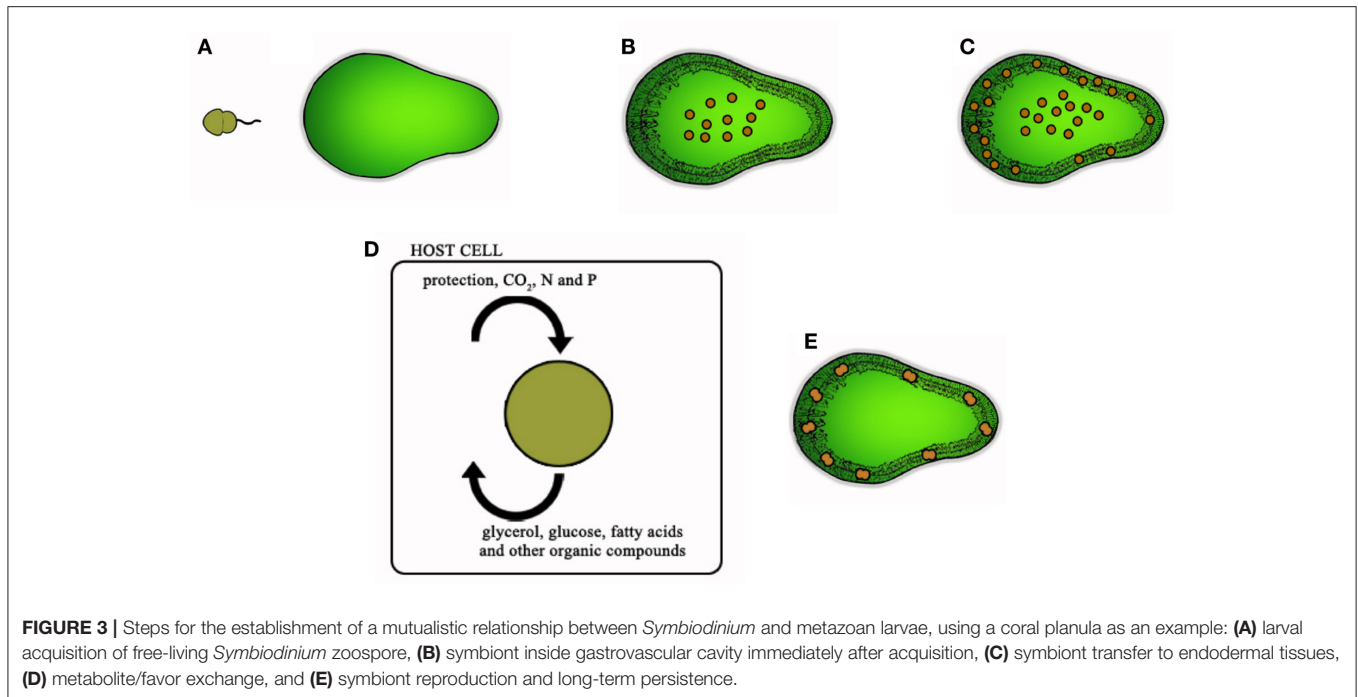
IS THERE A MUTUALISM FROM THE START?

Symbiosis is usually defined as the long-term interaction between two different organisms and mutualism is defined as a beneficial relationship for both parties. Considering the information presented in the previous sections, it remains to be determined whether a mutualistic symbiosis is in place for most metazoan larva-*Symbiodinium* associations. According to Davy et al. (2012), the establishment of symbiosis between *Symbiodinium* and its host is a complex process that involves several steps: symbiont uptake, phagocytosis by host cells (in the case of intracellular relationship), function integration, symbiont

reproduction, and long-term persistence. Therefore, for hosts in their larval development, the establishment of symbiosis would have to follow the steps in **Figure 3**, which include symbiont acquisition, transfer of symbionts from gut to endodermal tissue, metabolite exchange and symbiont reproduction and persistence.

The vast majority of experiments performed on invertebrate larva-*Symbiodinium* associations only visually observed the acquisition of symbionts and no metabolite exchange was detected, which fails to meet the criteria and events described above and shown in **Figure 3**. Especially considering reports that some larvae may digest the symbionts instead of engaging in a symbiotic relationship (Titlyanov et al., 1998; Mies et al., 2017c). The available gene expression studies are inconclusive in regard to whether the observed gene expression changes in coral larvae are specific to the symbiont exposure (deBoer et al., 2007; Voolstra et al., 2009a; Schnitzler and Weis, 2010; Mohamed et al., 2016). For instance, it is unclear if these changes are related to a mutualistic relationship or to the mere presence of a foreign algal body. Yet, the reports of higher production of fatty acids by *Symbiodinium* associated with coral and giant clam larvae (Mies et al., 2017c) and increases in larval caloric content and competence due to symbiont presence (Ben-David-Zaslow and Benayahu, 1998) suggest metabolite exchange. To date, perhaps the most compelling confirmation of a symbiosis between metazoan larvae and *Symbiodinium* may come from the expression of symbiosis-specific marker genes and the translocation of organic compounds. In this regard, the studies by Mies et al. (2017b,c) and Kopp et al. (2016) may provide critical support. These studies show the expression of a putative symbiosis-specific gene by *Symbiodinium* associated with coral (*Mussismilia hispida*) and giant clam (*Tridacna crocea* and *T. maxima*) larvae and the transfer of labeled carbon and nitrogen from symbiont to coral planulae (*Pocillopora damicornis*), respectively. However, these authors also point out that the energetic intake from this is insignificant for larvae nutrition, supporting that the initial symbiotic relationship might not be mutualistic in nature. Hence, the search for marker genes that could potentially disentangle different states in the symbiotic relationship (i.e., from an initial parasitic or commensal to a mutualistic interaction) is warranted.

Taken together, hosting *Symbiodinium* may be of no or little direct benefit to early larval animal host life stages. Yet, a mutualistic relationship is present in adult invertebrate-*Symbiodinium* associations. Thus, a gradual transition of the nature of the symbiotic association toward mutualism has to occur at one point during host development. In this context, the selection of symbionts within the host may increase the relative abundance of beneficial symbionts (Wolfowicz et al., 2016). Further, the rate of carbon translocation per symbiont may increase as the density of symbionts increases in relation to the host cells. The translocation of carbon by *Symbiodinium* requires the availability of excess carbon (Ezzat et al., 2015). In mature symbioses, it is suggested that this is achieved by the constant nitrogen limitation of symbiont growth (Falkowski et al., 1993; Pogoreutz et al., 2017). Yet, it is questionable whether algal symbionts are nitrogen-limited during early larval host stages. Nitrogen from host metabolism



is an important source for algal nutrition (Rädecker et al., 2015). However, the ratio of symbiont to host biomass is significantly higher in early larval stages than in adult hosts (Muscatine et al., 1998). Thus, significantly more host-derived nitrogen may be available to *Symbiodinium* during early larval development. While this would enable a rapid proliferation of symbionts, it would inhibit the availability of excess carbon available for translocation to the host. Hence, the onset of nitrogen limitation and subsequent initiation of carbon translocation may only occur once the density of symbionts in association with the host has passed a certain threshold. This scenario, although speculative at this point, would explain the transition toward mutualistic interactions during the maturation of the symbiosis between *Symbiodinium* and marine animal invertebrates.

CONCLUSIONS

Our review provides an analysis on the relationship between *Symbiodinium* and marine invertebrate larvae. The information compiled and discussed shows that there is significant heterogeneity in larval response to initial infection by the symbiont, even within the same host taxon. Some species may

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digest symbionts while others actively engage in metabolite exchange and certain larval forms apparently select symbiont types while others do not. Symbiont presence may be imperative for the larval development and recruitment of certain host groups, while symbiont identity and homology may improve larval fitness and contribute to thermal tolerance. However, for the majority of cases investigated, the mutualistic relationship cannot be unequivocally confirmed. Rather, from the current available data, we suggest a gradual transition from parasitism/commensalism to mutualism, both on evolutionary and larval development time scales.

AUTHOR CONTRIBUTIONS

All authors listed, have made substantial, direct and intellectual contribution to the work, and approved it for publication.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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