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The Host-Symbiont Complex of MCE Octocorals

Introduction

Octocorals are a major component of benthic communities worldwide and are especially important in tropical regions (Fabricius 2001; Benayahu et al. 2019). Numerous tropical octocoral species are associated with photosynthetic endosymbionts of the family Symbiodiniaceae in shallow and mesophotic coral ecosystems (MCEs; 30 - 150 m; Hinderstein et al. 2010) throughout the Indo-Pacific and Caribbean regions. Despite acute disturbances causing reductions in most coral populations worldwide, octocoral populations have shown exceptional resilience compared to reef-building scleractinian corals (Lenz et al. 2015; Tsounis and Edmunds 2017). However, the effects of environmental gradients on octocorals' vital life-history traits, such as sexual reproduction and symbiosis, have received less attention than scleractinian corals, and in particular, those found in MCEs (Liberman et al. 2018; Rossi et al. 2018; van de Water et al. 2018; Benayahu et al. 2019). My dissertation features both *ex-situ* and *in-situ* experimental approaches together with field collections of genetic and reproduction activity data to address the hypothesis that environmental conditions affect essential life history traits of zooxanthellate octocorals.

Research goals

In my Ph.D., I integrate genetic, ecological, and physiological methods to examine how environmental conditions such as depth, temperature, and pH affect key life history traits of octocorals in the Gulf of Aqaba/ Eilat (GOA/E). Specifically, I have formulated the following research questions which are approached by short-term controlled experiments, long-term field surveys, and genetic identification of octocoral-algal symbiont associations.

1. How do climate change scenarios affect the timing of breeding events, planulae, and primary polyp development of a surface-brooding octocoral?
2. How does depth affect the reproductive phenology and intensity in a surface-brooding species across space and time?
3. What is the genetic diversity of Symbiodiniaceae found in mesophotic octocorals and what are the differences compared to shallow conspecifics?
4. What are the temporal changes of horizontal symbiont acquisition along depth during the early-life stages of development?

Results

In the first chapter of my Ph.D., which was published in *Marine Environmental Research* (Liberman et al. 2021), I examined the effects of simulated climate change scenarios on the reproductive phenology of an octocoral. The results have revealed that combined elevated temperature and lower pH conditions led to a change in the timing of reproduction events and altered its inter-colony synchronicity. In contrast, the reproduction under ambient conditions has co-occurred with that of the *in-situ* reef colonies and maintained its synchronicity. Similarly, the survival of planulae that were collected from colonies under experimental conditions was significantly reduced under simulated climate change conditions compared to propagules reared under ambient ones or ‘natural’ ones (e.g., reef-derived planulae, Fig 1).

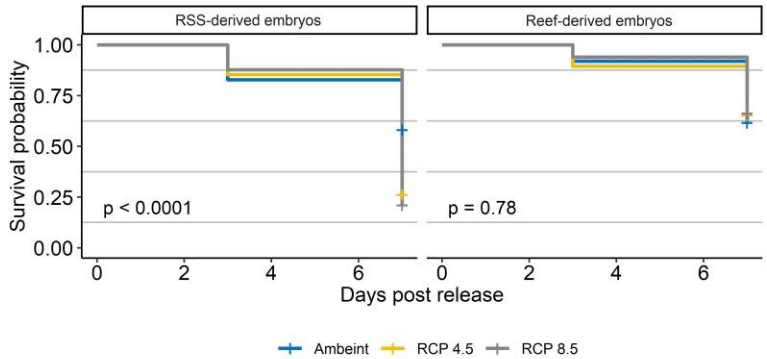

Figure 1: *Rhytisma fulvum*: Kaplan-Meier log-rank survival probability of planulae under RSS seawater conditions. Left: embryos collected from RSS colonies; right: embryos collected from reef colonies. Presented p. values are of survival probability under treatment and seawater conditions. Cross marks represent the survival probability of each treatment on day 7 after the onset of the surface-brooding events.

In my second chapter, which has been recently published in *Ecology* (Liberman et al. 2022), I examined the reproductive phenology and intensity of the octocoral *Rhytisma fulvum* over five annual breeding seasons (2016–2020) using *in-situ* observations across its entire depth range (0–45 m) (Fig. 2). The findings have revealed that the reproductive intensity of colonies found deeper than 30 m is significantly lower compared with colonies in shallower habitats (<30 m), highlighting possible constraints on coral reproduction at the deeper end of their range. In addition, the timing of reproduction events at specific depths, throughout the study period, significantly correlated with a distinct increase in seawater temperature over 1–2-day intervals (Binomial GLM). These findings suggest that temperature differences across depth lead to different timing of reproductive, imposing temporal reproductive isolation, and thus may reduce connectivity between populations across depth.

In the third chapter, which has been submitted to Frontiers in Microbiology, I used two genetic markers (ribosomal ITS2 and chloroplast 23S) to describe, for the first time, the Symbiodiniaceae associations of mesophotic octocoral species (30-70 m). The study reveals that most mesophotic octocorals host micro-algae of the genus *Cladocopium (*16 out of 20 host species), while *Symbiodinium* and *Durusdinium* are less common (3/20 and 1/20, respectively). Additionally, I used high throughput sequencing of the ITS2 to examine the algal symbiont community structure in host species that exhibit a wide depth distribution, from shallow to mesophotic depth. The results reveal that microalgae community structure is species-specific, whereas depth has a relatively smaller influence on the microalgae community found in the different octocoral hosts (Fig. 3).

In my fourth chapter, I used both high-throughput sequencing of the ITS2 and Sanger sequencing of the chloroplast non-coding region (psbA) to explore, for the first time, the dynamic of symbiont acquisition across a depth gradient and time (11-month period). Although still preliminary, my findings suggest octocoral early recruits mostly associate with similar algal symbionts across depth, however, these associations shift with time, indicating a symbiont winnowing in the initial colonization process. In addition, early recruits were found to associate with highly diverse Symbiodiniaceae genetic lineages, including cryptic ones, which have been rarely found in the GOA/E before.

Significance of research

Incorporating both experimental and *in-situ* evidence of the extent of marine species’ responses to environmental changes contribute to a better understanding of the potential consequences in an era of rapid local and global changes, all still not fully understood. The findings of lower reproduction activity in the MCEs questions whether depth can provide a long-term and viable refuge for shallow coral populations. Moreover, the study demonstrates how long-term observations of coral reproduction, alongside measurements of environmental parameters, can provide valuable insights into the ultimate cues that regulate coral reproductive phenology. Notably, the data presented in chapter two represents the most extensive dataset of coral reproductive phenology across depth, thus providing important information in a discipline that is extremely skewed towards shallow-water populations. The findings of chapter three present the first comprehensive results on MCE octocoral-algal symbionts associations, thus opening new avenues for better understanding MCEs while raising the need to preserve them. Furthermore, the results are expected to improve our understanding of octocoral adaptations to the low light conditions prevailing in the MCEs in Eilat and other biogeographical regions. The findings of my study demonstrate the importance of the GOA/E as a model ecosystem to address critical ecological and biological questions with a board global significance in an era of global change severely impacting coral reefs worldwide.

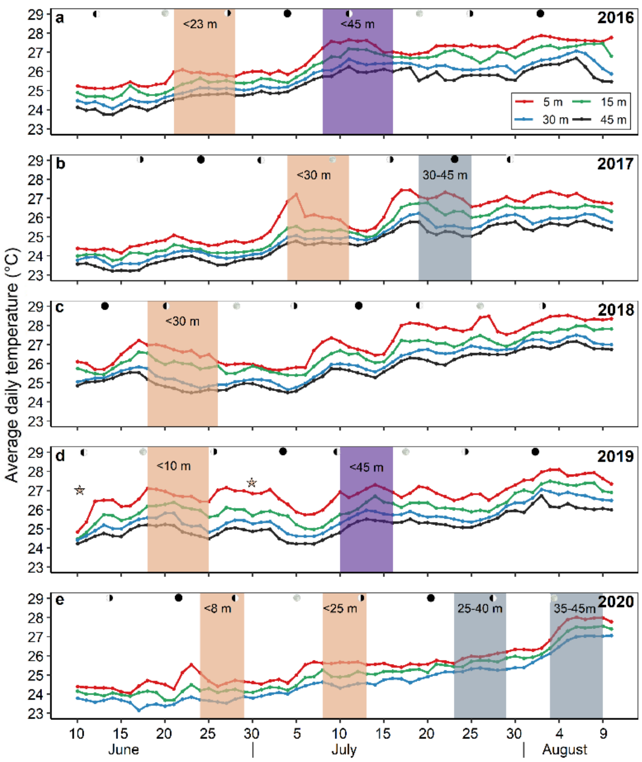

Figure 2. Surface-brooding periodicities and mean daily seawater temperatures from shallow to mesophotic depths during June–August 2016–2020. Panels (a-e) represent different years, with colored lines indicating mean daily seawater temperatures at four different depth intervals according to the legend in (a). Shaded background represents the timing of surface-brooding events with those occurring exclusively at shallow depth or MCE depicted in orange or gray, respectively, and in purple when occurring throughout the depth gradient. Lunar phases are indicated by black circles (new moon) and white circles (full moon). Asterisks in (d) represent minor surface-brooding events that occurred at shallow depth (<10 m).

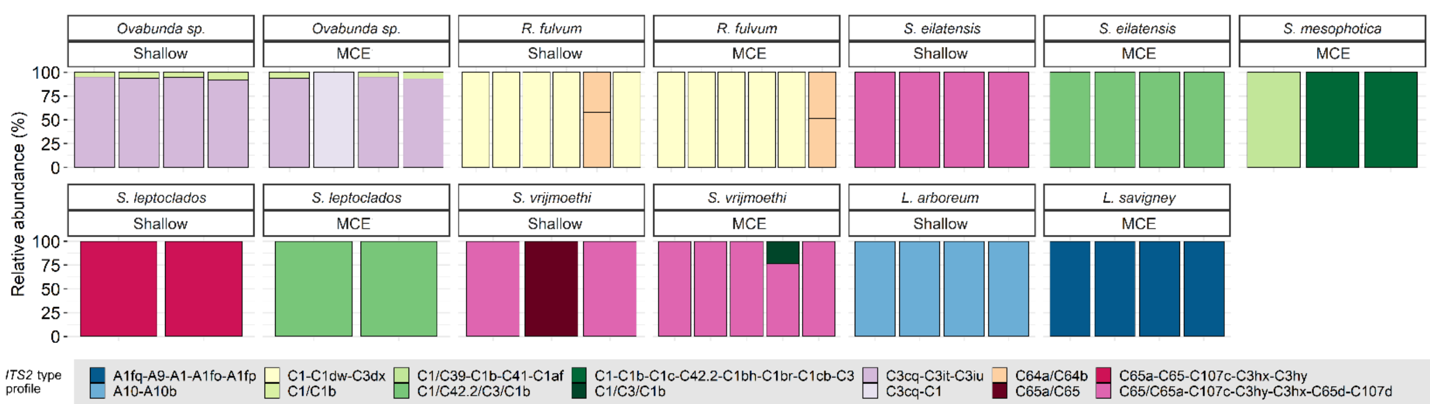

Figure 3. Normalized relative abundance of ITS2 type profiles in octocoral host species from shallow and mesophotic reefs in the Gulf of Aqaba/ Eilat. Only the >0.01% most abundant profiles are displayed. Type-profile names indicate their genus (A = *Symbiodinium* and C= *Cladocopium*), and are listed according to the abundance of the sequences found in them with '/' separating type-sequences with co-dominance in a given sample. R.=*Rhytisma* and S.= *Sinularia.*

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