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Growth and survival dynamics of mesophotic coral juveniles in shallow reefs

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ABSTRACT: As many degrading shallow reefs suffer from recruitment failure, mesophotic coral ecosystems have been suggested as a potential source of coral propagules promoting the recolonization of these reefs. However, whether mesophotic coral populations can repopulate shallower reefs is currently debatable. Here, we compared the response of corals settled on mesophotic (50 m) tiles and transplanted to the shallow reef (10 m), at a Nature Reserve and an unprotected site in the northern Gulf of Eilat/Aqaba, Red Sea. Mortality was substantially higher for the transplanted corals, as compared with their shallow counterparts living on the tiles, with over half of the transplanted juveniles dying 1 yr post-transplantation. Transplanted corals exhibited a 24 % higher survivorship at the MPA site. We further explored the survival and growth rates of the 4 most common transplanted coral genera (*Cyphastrea*, *Porites*, *Psammocora*, and *Stylophora*). An inverse relationship between survival and growth was evident among the transplanted coral genera; *Porites* and *Stylophora* demonstrated similar net growth rates to those of their shallow-water counterparts but lower post-transplantation survivorship, while *Cyphastrea* and *Psammocora* showed the opposite trend. Although this study demonstrates the reduced plasticity of mesophotic coral juveniles to cope with shallow-water conditions, it nonetheless offers some potential to facilitate shallow-reef recovery.

KEY WORDS: Mesophotic coral ecosystems · MCEs · Coral juveniles · Transplantation · Acclimatization · Red Sea

1. INTRODUCTION

Frequent and prolonged climate change disturbances are among the primary concerns for the future of shallow coral-reef ecosystems, suggesting that the adaptive capacities of reef organisms might not be able to keep up with the current pace of these disturbances (Edmunds et al. 2014, Torda et al. 2017). As part of the search for reliable and appropriate resources to promote the recolonization of degrading shallow-water reefs, increased interest has been focused in the past decade on deeper habitats, i.e. mesophotic coral ecosystems (MCEs; 30–160 m depth), which have been hypothesized to function as deep-reef refuges from climate change impacts (Bongaerts et al. 2010, Eyal et al. 2019a). One aspect of the hypothesis relies on the provision of propagules originating from MCEs to assist in the replenishment of impacted shallower reefs (Bongaerts et al. 2010). However, despite the potential flow of coral propagules to shallow-water reefs, it is not cer-

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tain whether they would be able to successfully mature under their new environmental conditions.

In comparison with shallow juvenile corals, recent studies have shown mesophotic juveniles to possess greater survivorship capabilities (Goodbody-Gringley et al. 2018, Kramer et al. 2019), presumably due to more predictable and favorable environmental and/or biological conditions (e.g. lower wave exposure, reduced grazing, etc.). MCE communities are nonetheless not entirely immune to environmental or biological changes, as recent evidence has indicated that MCEs may experience intermediate disturbances (Pinheiro et al. 2019). Yet, the frequency and intensity of the disturbances is lower than in shallow reefs (Eyal et al. 2019a). In the event of an increase in environmental fluctuations at MCEs, significant negative impacts are expected for the coral populations inhabiting these depths, especially for species specialized to living in these deeper habitats (Pinheiro et al. 2019). The seeding potential is therefore mainly limited to coral species that exhibit a wide depth distribution, i.e. 'depth-generalists' (Bongaerts et al. 2010). A key challenge, however, is identifying mesophotic corals that may 'win' or 'lose' (sensu Loya et al. 2001) under shallow-water conditions. To date, depth-related acclimatization studies have mainly focused on adult coral fragments (Einbinder et al. 2016, Tamir et al. 2020), yet more relevantly, no study has investigated the ability of mesophotic juveniles to cope with the environmental conditions of shallow-reef habitats. Given that some small coral colonies may be more phenotypically plastic than adults (Loya et al. 2001, Torda et al. 2017), it is important to assess how juveniles originating from MCEs might tolerate shallow-reef conditions.

Here, we examined the ability of mesophotic juvenile corals from the northern Gulf of Eilat/Aqaba (GoE/A), at 50 m depth, to acclimatize and develop at 10 m depth conditions during a 3 yr transplant experiment. Through analyses of images taken at different time intervals, we sought to: (1) determine the prolonged impact of *in situ* shallow-water conditions on mesophotic juvenile corals, and (2) distinguish those genera that could successfully undergo transplantation to shallow habitats, and thus potentially assist in their recolonization. We thus provide assessment regarding the capacity of mesophotic coral juveniles to acclimate to shallow-water environments, and evaluate their ability to survive and grow under such conditions.

2. MATERIALS AND METHODS

The transplantation experiments were conducted at 2 sites in the GoE/A that differed in their protection status (Fig. 1): (1) The Coral Nature Reserve (NR) and (2) an oil jetty (OJ), which is exposed to anthropogenic disturbances. Identical terracotta settlement tiles (20 × 20 × 1 cm; 16 tiles site^{-1} depth^{-1}), placed on monitoring racks and oriented at a 45° angle, were deployed at shallow (10 m) and mesophotic (50 m) depths in July 2011. The transplantation experiment began in February 2017 with 3 settlement racks at each site: a shallow control, a mesophotic control,

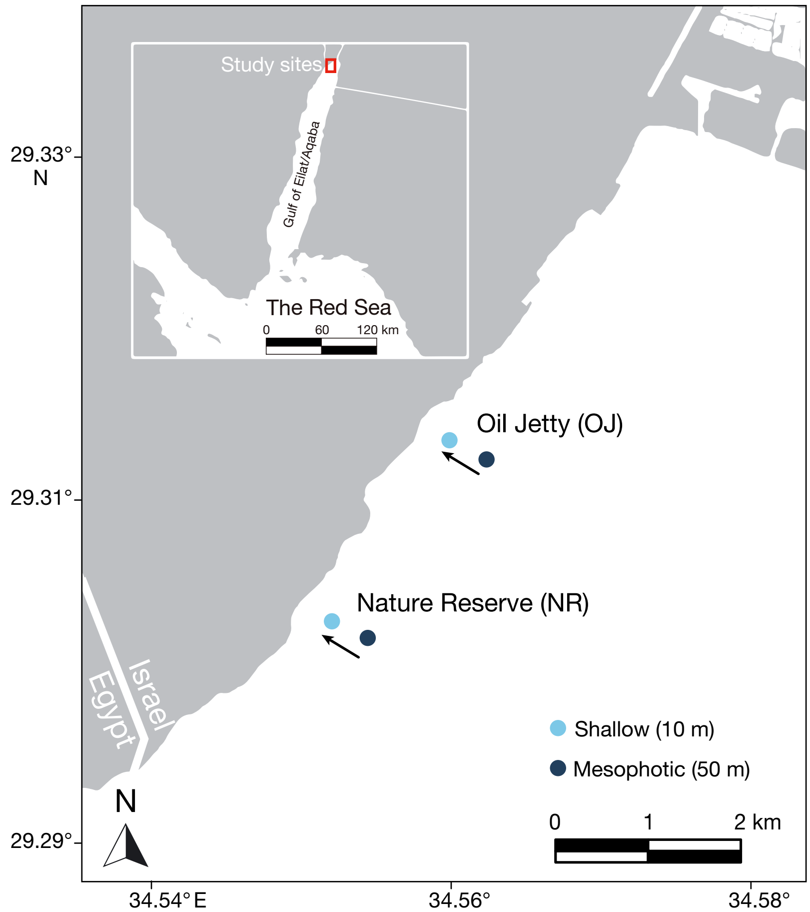


Fig. 1. Study sites in the northern Gulf of Eilat/Aqaba, Red Sea. Arrows denote the transplantation direction

and a mesophotic rack transitioned upwards to the shallow-reef sites. At the time of transplantation, both the light levels and water temperature at the shallow sites were at their annual lowest values, according to the National Monitoring Program (NMP) of the GoE/A (NMP 2017–2020; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m682p237_supp.pdf). Unfortunately, 3 mo post-transplantation, the mesophotic control tiles were vandalized. Nevertheless, realizing the limitations of our experiment, we continued monitoring the transplanted mesophotic-to-shallow tiles. We preferred to analyze the results with reference to the coral genera, due to the uncertainty in making species-specific identification in the coral early-life stages. Due to statistical considerations, for genus-specific analysis, only depth-generalists exhibiting >5 individuals per depth were selected: *Cyphastrea*, *Porites*, *Psammocora*, and *Stylophora*.

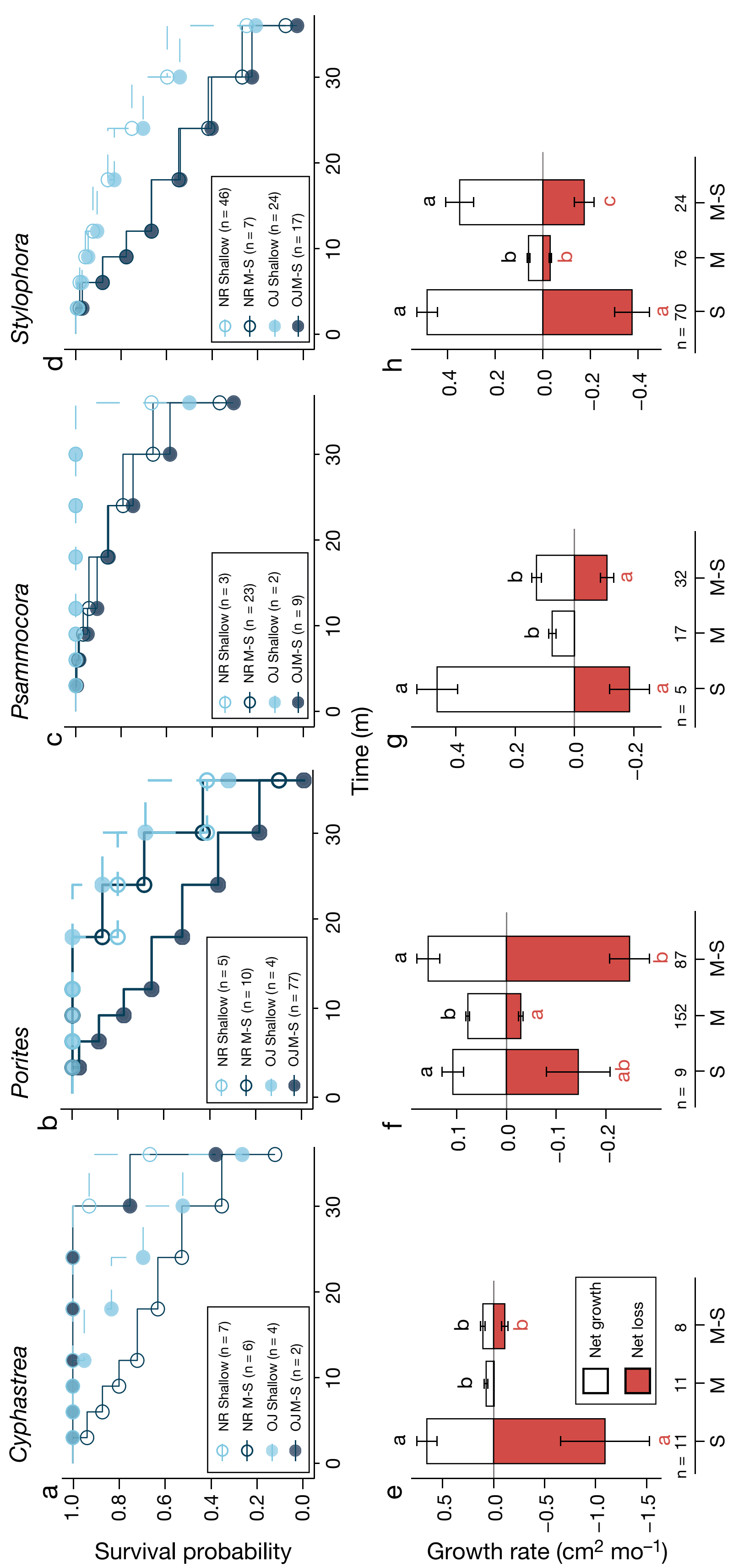
All transplanted mesophotic juveniles had previously settled on the upper surfaces of the tiles, but were turned face-down in the shallow sites to mimic the settlement pattern of shallow corals on cryptic surfaces (Kramer et al. 2019). Censuses were carried out at recurrent intervals of 3 mo during the first year, followed by 4 intervals of 6 mo during the second and third years, ending in February 2020. At each census, repeated photographs were taken of each tile (both surfaces) using a digital camera (Sony DSC-RX100M4), using the same distance and perpendicular to the tile surface. A coral juvenile was defined as occupying a horizontal planar area of <20 cm^2 (~5 cm diameter) and detectable to the eye (>1 cm^2), representing corals that had not succumbed to post-settlement mortality. Each detected coral was marked on the images for consistent follow-through.

Survivorship was compared between the shallow and the transplanted coral juveniles, and growth rates of the transplanted mesophotic juveniles were compared with both the shallow juveniles on the racks (this study) and recent size observations on resident mesophotic coral juveniles (Kramer et al. 2019). Survivorship was expressed as the percentage of juveniles detected alive after a given time. Growth rate (cm^2 mo^{-1}) was estimated as a change in the horizontal planar area over time using area measurements in Adobe Photoshop CS6, and were divided into 2 types: (1) net growth rate, defined as an overall positive growth rate (i.e. an increase in live tissue areas) and (2) net loss rate, defined as the negative growth rate (colonies experiencing partial tissue mortality resulting in a marked decrease in size). Corals that were observed only once were excluded from the growth analysis.

All statistical analyses were performed using R v.4.1.0 (R Core Team 2021). We analyzed the differences in the survival patterns of juveniles from shallow and transplanted mesophotic tiles between sites, using a non-parametric pairwise comparison survival analysis, based on the Kaplan-Meier estimator (Kaplan & Meier 1958), conducted with the package 'survival' (Therneau 2021). Survivorship and growth were modeled as a function of the depth of origin, site, and genera, using mixed-effects permutational analysis (MEPA; 1000 permutations; package 'predictmeans'; Luo et al. 2021), with tiles and time included as random effects. Post hoc comparisons for significant variables were done using permutational *t*-tests.

3. RESULTS AND DISCUSSION

Our findings imply that the ability of mesophotic juvenile corals to survive and grow under *in situ* shallow-water conditions is taxon-dependent and its extent may vary among sites. At the end of 36 mo, 228 of 334 coral juveniles originating from all depths were either dead or missing (Table S1). Regardless of site, transplanted coral juveniles exhibited significantly lower survivorship than their shallow counterparts (Mantel-Cox, $p < 0.01$), with transplanted juveniles attributing 68% of the total mortality (156/228); while approximately 22% of the original transplanted coral assemblage survived (46/202). Overall differences between sites existed in *Cyphastrea* (17% higher survivorship in OJ; permutational *t*-test, $p < 0.01$; Fig. 2a) and *Porites* (18% higher survivorship in NR; permutational *t*-test, $p < 0.01$; Fig. 2b). The juvenile corals exhibited a constant proportion of individuals dying over time (Fig. 2a–d; Fig. S2), as typically expected from corals in their early life stages (Trapon et al. 2013), yet the timing and magnitude of mortality was shown to be genus-dependent (MEPA, $p < 0.001$), indicating a differential susceptibility to shallow-water conditions among mesophotic genera. Thus, mesophotic *Stylophora* and *Porites* juveniles expressed a lower tolerance to shallow-water conditions than *Psammocora* juveniles (Mantel-Cox, $p < 0.001$; Fig. 2a–d). Furthermore, mesophotic *Stylophora* juveniles appear to be as sensitive to shallow-water conditions as their adult counterparts (Einbinder et al. 2016, Tamir et al. 2020). These results taken together with the lower abundance of *Stylophora* in mesophotic habitats (Kramer et al. 2020) suggest that their recruitment to the shallow



reefs from MCEs is low, and supports the hypothesis that the directionality of larval supply in the GoE/A may be more prominent from shallow to deeper waters (Shlesinger & Loya 2021).

These findings should be interpreted with caution since we do not know the exact depth-origin of the parental coral colonies (i.e. propagules may have arrived from shallower/deeper depths) or their reproductive mode. Nevertheless, we assume that the juveniles at each depth have already undergone selection processes that could affect their mesophotic-to-shallow water transition. For example, the acquisition of symbiotic communities from the environment of broadcast spawning corals, whose larvae typically disperse more widely, may represent a strategy to ensure that juveniles settling under a range of environmental conditions acquire photosymbionts that are locally adapted (Torda et al. 2017).

Typically, corals found in MCEs exhibit photophysiological mechanisms which enable them to utilize more light for photosynthesis. Although some mesophotic corals have at their disposal strategies to cope with changes in light, such as regulating symbiotic cell density or changing the type of symbiont (Martinez et al. 2020), a significant increase in light irradiance (up to 4-fold higher during mid-summer; Tamir et al. 2019) and expansion of spectral range can lead to severe light stress and impede survival under prolonged acute exposure. Elevated

Fig. 2. (a–d) Kaplan-Meier survival curves of 4 depth-generalist coral genera for shallow (light-blue; dashed lines) and mesophotic-to-shallow transplants (M-S; dark-blue; solid lines), from the 2 study sites (filled dots = nature reserve, NR; open dots = oil jetty, OJ). (e–h) Mean net growth (white bars) and net loss (red bars) rates (cm^2 mo^{-1}) throughout the study period (S: shallow; M: mesophotic [from Kramer et al. 2019]; M-S: mesophotic-to-shallow). Error bars are ±SE. Letters indicate significant groups within a growth type ($p < 0.05$)

temperatures are also considered a major threat to coral fitness (Leggat et al. 2019). According to the NMP, temperatures between depths were similar between February to April but were significantly higher in the shallows in mid-summer (up to 2°C; Fig. S1). Correspondingly, survivorship substantially decreased with the rise in water temperature, which may have been enough to induce bleaching in some mesophotic genera. As such, our findings suggest that sub-lethal effects caused by the combination of heat and light stresses have decreased survivorship over time. However, despite these stress factors, 22% of the transplanted juveniles did survive and could thus potentially produce propagules upon becoming reproductively mature.

Generally, survivorship of transplanted corals was significantly lower at the OJ site compared with the NR site (31.83 ± 1.51% [SE] and 55.56 ± 1.93%, respectively; MEPA, $p < 0.001$), suggesting that protected shallow reefs promote better adaptability for mesophotic coral juveniles. Historically, the OJ site is less suitable for the establishment of coral communities since it was exposed to severe anthropogenic disturbances during the 1970s to early 2000s (e.g. oil leakage, phosphate enrichment, and port contamination; Loya 2004), and continues to be threated mostly by incoming oil tankers and recreational activities in the present day. Unfortunately, the impact of local stressors coupled with the negative effects of increased heat and irradiance have amplified stress for the mesophotic juveniles during their first summer months in the GoE/A high-latitude reefs (Fig. S1).

Similar to earlier growth rate reports (Groves et al. 2018), our findings showed that individuals inhabiting mesophotic depths exhibited lower growth rates than their local shallow counterparts (MEPA, $p < 0.001$; Fig. 2e–h). Among the transplanted corals, however, only *Stylophora* and *Porites* exhibited similar growth rates to those of their shallower counterparts (permutational *t*-tests, $p > 0.05$); whereas *Cyphastrea* and *Psammocora* growth rates were depressed under the shallow conditions (permutational *t*-tests, $p < 0.01$). Our long-term study provides further evidence to the light-induced calcification postulation as demonstrated by the mesophotic *Stylophora* and *Porites*, resulting in faster growth rates; while other mesophotic coral taxa possess physiological limitations that prevent the induction of light-enhanced calcification (Eyal et al. 2019b). Since growth rates were highly variable between and within depths, we conclude that growth rate alone may be an inadequate indicator of the successful acclimatization of mesophotic corals to shallow reefs. Although this study has limitations with regard to differences in the growth period, these are unlikely to change the patterns observed between shallow and mesophotic depths. While some of the mesophotic genera transplanted to shallow waters exhibited higher survivorship than others, their growth rates were lower than their local shallower counterparts, whereas the converse occurred in other genera (Fig. 2). Hence, a potential trade-off occurs in transplanted corals between tolerating the new environment and growth. There are both costs and benefits to faster growth that influence the overall fitness of individuals within a coral population. (Birkeland 2015). For instance, natural selection favoring rapid growth by branching species, such as *Stylophora* in this study, was observed in earlier studies monitoring the recolonization of the shallow reefs, eventually increasing the probability of surviving to sexual maturity at a younger age, while species with lower recruitment success are characterized by the traits of late maturity and increased longevity (Loya 2004, Birkeland 2015). Therefore, despite the low survival percentage of the different mesophotic coral juveniles, their differential survival strategies may optimize their fitness and enable growth to maturity.

While the success of early life stages ultimately defines the future state of the coral community, we reinforce recent studies describing partial acclimatization responses by mesophotic corals, suggesting that the transition to shallow waters is complex even at varying time scales (Martinez et al. 2020, Malik et al. 2021, Shlesinger & Loya 2021). Nevertheless, despite representing a low percentage, the coral individuals that managed to survive the initial light shock and increased water temperature may continue to grow into adulthood and facilitate recovery in their new shallow habitat. Future coral acclimatization research should target aspects not covered in the present study, such as microbial and microalgae symbiont acquisitions by corals, physiological responses, and skeletal modifications.

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