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SHORT RESEARCH NOTE

Effects of predators and grazers exclusion on early post-settlement coral mortality

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Abstract Mortality of newly settled individuals is a key factor in shaping adult population size and distribution of many marine invertebrates. Despite this recognized importance, few studies have addressed early post-settlement mortality rates and causes in reef-building corals. To investigate the effects of exclusion of macro-predators and grazers on mortality of *Acropora striata* (Verrill) recruits, a caging experiment was completed at Moorea, French Polynesia. More than half of the recruits died within 7 days in the field, and although the exclusion of macro-predators and grazers did not significantly reduce nor enhance mortality, it certainly altered their cause. In the presence of macro-predators and grazers, coral recruits faced significant predation-induced mortality (50.0% of dead recruits presented a heavily damaged or missing skeleton). Conversely, in the absence of macro-predators and grazers, dead recruits were mainly intact (91.7%), and most likely suffered from competition with turf algae and associated sediment trapping. These results underline complex interacting effects of predation, competition with turf algae, and sedimentation on coral early post-settlement mortality.

Keywords Post-settlement · *Acropora striata* · Recruits · Predation · Moorea, French Polynesia

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For many benthic organisms, the first days or weeks following settlement are characterized by very high rates of mortality (Gosselin & Qian, 1997). This drastic bottleneck has profound implications on population structure, dynamics, and capacity for recovery after disturbance (Gosselin & Qian, 1997; Hunt & Scheibling, 1997; Arthur et al., 2006).

Scleractinian corals are the dominant reef-building organisms in coral reefs. They are responsible for providing the structural framework to one of the most diverse ecosystems (Jones et al., 2004). As a consequence, understanding their maintenance processes is critical, particularly in the context of increasing disturbances faced by coral reefs (Hughes et al., 2003; Adjeroud et al., 2007). Despite the recognized importance of early post-settlement mortality in shaping coral populations (Connell, 1997; Smith, 1997; Miller et al., 2000), studies addressing the extent and causes of mortality during the first days or weeks after settlement are scarce (Babcock, 1985; Christiansen et al., 2009; Penin et al., 2010). This is primarily due to the very small size of newly settled coral recruits and to their preference for cryptic habitats, which make their observation difficult.

Early after settlement, the major sources of mortality are competition, sedimentation, and predation. Few studies have focused on the effects of competition on early benthic life stages of corals. However, the presence of other benthic organisms and turf algae has been shown to increase early post-settlement coral mortality (Harriott, 1983; Kuffner et al., 2006; Birrell et al., 2008; Vermeij et al., 2009). Abrasion or burial of colonies by sediments is another cited source of early post-settlement mortality (Hunte & Wittenberg, 1992; Gilmour, 2002), and sediment trapping can be an indirect reason for the detrimental effect of competition with turf algae (Birkeland, 1977; Sato, 1985). Due to their small size at settlement, predation faced by coral recruits in the first days or weeks of their benthic life is mainly incidental, linked with dislodgement by grazers (Sammarco, 1985; Sato, 1985; Christiansen et al., 2009; Penin et al., 2010). Grazing is an important ecological process in coral reefs, benefiting corals in their competitive interactions with macroalgae (Hixon, 1997; Mumby et al., 2007; Idjadi et al., 2010). Nevertheless, studies that have manipulated the abundance of grazers, like urchins or parrotfishes, show a potentially strong effect of incidental predation during grazing activity on recruitment success (Sammarco, 1985; Christiansen et al., 2009). In a recent coral recruitment study around Moorea, French Polynesia (Penin et al., 2010), we demonstrated a clear link between mortality of recruits and the abundance of grazing parrotfishes, indicating that incidental predation can be a major source of mortality during the early post-settlement period. To complement this correlative study, we used a manipulative field experiment to compare early mortality of *Acropora striata* coral recruits in the presence and absence of macro-predators and grazers, at three different depths characterized by variable grazing pressure.

The present study was conducted on the outer slope of the north coast of the island of Moorea (17°30′S, 149°50′W), in the Society Archipelago, French Polynesia. In this system, the main macro-predators of coral recruits are grazing herbivore fishes, since grazing invertebrates, particularly urchins, display very low abundance at the study site ($<0.03\ \mathrm{m}^{-2}$; Penin et al., 2010).

Eighteen settlement tiles (unglazed terracotta, 11 × 11 × 1 cm) were artificially colonized by *Acropora striata* larvae reared in the laboratory following predicted broadcast-spawning periods in 2004 (Carroll et al., 2006). Tiles were pre-conditioned in the lagoon of Moorea for 10 days prior to being placed into aquaria containing motile *A. striata* larvae, aged 14 days. Larval settlement was observed approximately 24 h after the tiles were immersed in the tanks. One week after the beginning of settlement, living recruits present on the tiles were counted, tagged and mapped before tiles were transferred to the field. At this stage, the recruits presented an established skeleton, but were still at the one-polyp stage, and about 1 mm in size. A mean of 35.1 ± 11.8 recruits (mean ± SD) were present per tile. Six tiles were positioned at each of three depths: 6, 12, and 18 m, and half of them were covered with 1.2 cm wire mesh cages to exclude macro-predators, while the remaining tiles were left exposed. The use of such a depth gradient aimed to take advantage of natural depth variation in grazers abundance occurring on the outer slopes of Moorea (Penin et al., 2010).

After 7 days in the field, tiles were photographed and re-examined to determine the abundance of live and dead recruits; dead recruits being classified as either dead-intact (i.e., intact coral skeleton with no living tissue) or as missing (i.e., removed or heavily damaged skeleton). The effects of depth and caging on the proportion of live, dead-intact and missing recruits were assessed via Chi-square tests on recruit contingencies. Percent cover of sediments and turf algae was calculated by overlaying a grid of 30 points on each tile photograph, using CPCe (Kohler & Gill, 2006). As sediments were trapped within turf algae filaments, these categories could not be distinguished.

A Mann–Whitney non-parametric test was used to test for a difference in percent cover between the two treatments (i.e., caged vs. control tiles).

Mortality of newly settled coral recruits was high (Fig. 1). On control (un-caged) tiles, 56% of the *Acropora striata* recruits died within the first week in the field, which is comparable to other regions as diverse as Australia, Caribbean, Japan, or Kenya (Connell, 1973; Babcock, 1985; Sammarco, 1985; Sato, 1985; McClanahan et al., 2005). The high mortality rate observed in this study reinforces the hypothesis that post-settlement events can have a major influence on coral population maintenance of Acroporid corals at Moorea, as suggested in previous studies (Adjeroud et al., 2007; Penin et al., 2007; Penin et al., 2010). Nevertheless, recruit mortality may have been higher on tiles than on natural substrate, due to the absence of shelters like crevices or cavities on tiles (Brock, 1979). Moreover, mean density of recruits at the beginning of the experiment was much higher than the abundance generally observed on naturally colonized tiles (35.1 recruit per tile in the present study vs. 0.4 recruits per tile in average during the main recruitment period (Adjeroud et al., 2007)), which could have led to higher per capita mortality rate due to density dependence (Vermeij & Sandin, 2008).

The proportion of live recruits was very similar between treatments (44% on control tiles and 48% on caged tiles; Fig. 1), as confirmed by comparison of contingencies of live and dead recruits between the two treatments (χ^2 test on contingencies of live and dead recruits on caged vs. control tiles: $\chi^2 = 0.0807$; $P = 0.3689$). Conversely, differences were observed in the proportions of dead-intact and missing recruits between caged and control tiles. On control tiles, 28% of recruits were missing, whereas this proportion was much lower on caged tiles (5%). On the contrary, percentage of dead-intact recruits was much higher on caged tiles (47%) than on control tiles (28%). These differences are confirmed by comparison of contingencies of alive, dead-intact, and missing recruits (Chi-square test on contingencies of live, dead-intact, and missing recruits on caged vs. control tiles: $\chi^2 = 76.589$; $P < 0.0001$).

Among dead recruits, those whose skeleton was removed or heavily damaged (i.e., “missing recruits”) most likely faced predation or dislodgement by grazers, while those whose skeleton was intact (i.e., “dead-intact recruits”) were probably killed by other factors such as sedimentation, competition, starvation, or disease (Sato, 1985; Hunte & Wittenberg, 1992), which are unlikely to provoke the total disappearance of a skeleton in only 1 week. Even in the case of competition with other organisms, remnant parts of the skeleton are generally observed.

Exclusion of macro-predators and grazers by the use of cages did not significantly reduce nor enhance mortality, but certainly altered the cause of observed rates of mortality. On caged tiles, more than 90 % of dead recruits exhibited an intact skeleton, whereas only half of the dead recruits were intact on un-caged tiles. This was most likely due to the interacting effects of predation, competition with turf algae, and sedimentation on coral recruit survival. In the absence of macro-grazers, we observed the development of turf algae, which led to sediment trapping; 82.67 ± 6.41% (mean ± SD) of the surface of caged

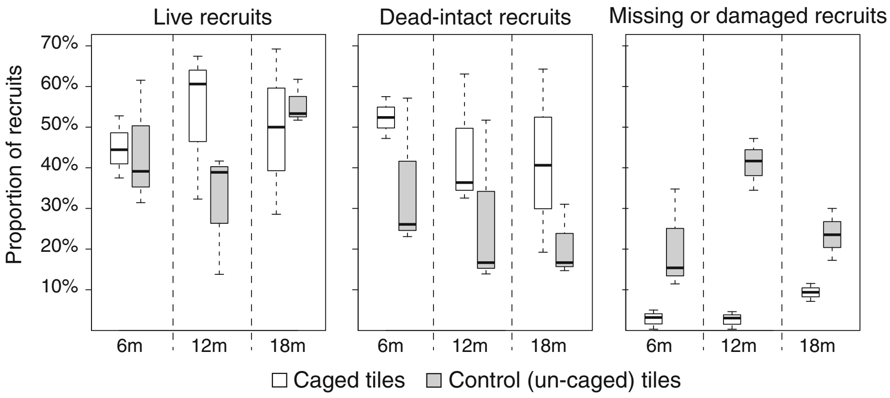

Fig. 1 Influence of predation on recruit mortality. Proportions of live *Acropora striata* recruits, dead recruits with intact skeleton, and missing or heavily damaged recruits on caged vs. control (un-caged) tiles at the 3 depths after 7 days in the field

tiles was covered by algae and sediments. In contrast, percent cover of algae and sediments were significantly lower on control tiles (24.44 ± 10.47% (mean ± SD) of the tiles surface; Mann–Whitney $P = 0.0061$; Fig. 2). Competition with turf algae and sedimentation are some of the main causes of mortality for young corals (Hunte & Wittenberg, 1992), and it is often difficult to discriminate their respective effects (Sato, 1985). Thus, eviction of macro-predators and grazers probably decreased mortality by predation (direct or incidental), but also increased mortality linked with competition and sedimentation. Conversely, on control tiles, most recruits that did not survive were missing or heavily damaged, indicating removal by predators or grazers (Fig. 3).

Contradictory effects of grazing on early post-settlement survivorship have been demonstrated in other reef systems. When grazer abundance is low, like inside cages, turf algae grows, competing with young corals, and trapping sediment, thereby increasing young coral mortality (Sato, 1985; Birrell et al., 2008), whereas, when grazer abundance is high, they limit the development of turf algae, but are also responsible for incidental predation of coral recruits (Sammarco, 1985). Grazing is an important process on coral reefs, and the presence of macro-grazers is known to be beneficial for coral resilience, tipping the scales of coral/algal interactions in the favor of corals and enhancing coral recruitment (Bellwood et al., 2004; Mumby et al., 2007; Mumby, 2009). However, results from this study, coupled with previous

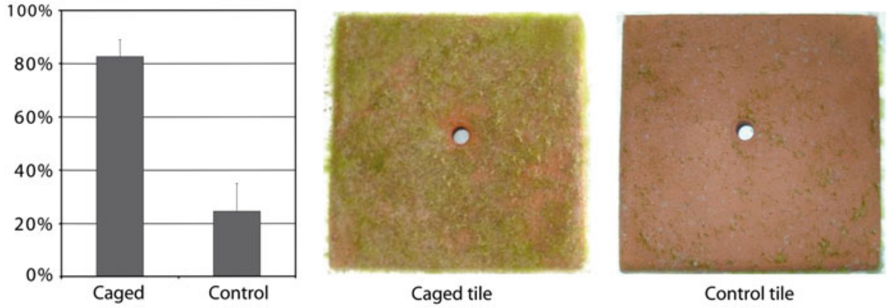

Fig. 2 Mean percent cover of sediments and algae on caged vs. control (un-caged) tiles and photograph of tiles after 7 days in the field under the caged (*left*) and control (*right*) treatments. As sediments were trapped within turf algae filaments, these categories could not be distinguished. *Error bars* represent standard deviations

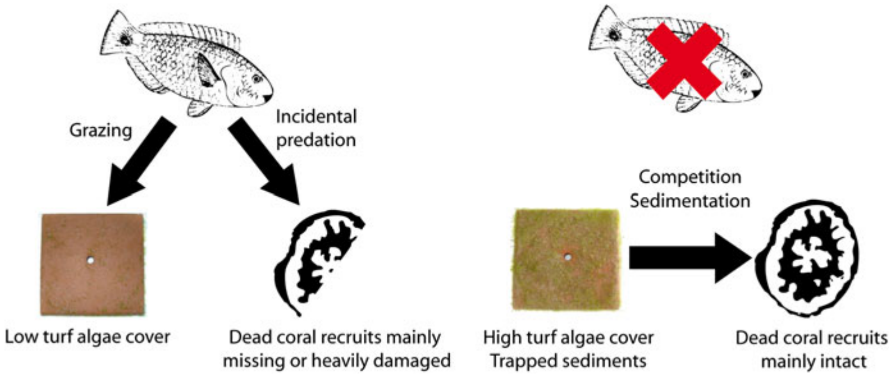

Fig. 3 Effects of macro-predators exclusion on major coral recruit mortality factor. In the presence of macro-predators and grazers, turf algal cover was low and dead recruits were mainly missing or heavily damaged whereas in the absence of macro-predators and grazers, high turf algal cover and associated sediment trapping were observed, and dead recruits were mainly intact

findings showing a direct relationship between abundance of scraping herbivorous parrotfishes and spatial variation in recruit mortality (Penin et al., 2010), suggest contradictory effects of grazers on coral recruit survivorship (Brock, 1979; Sammarco, 1985; Yap & Molina 2003). This highlights the need to further examine the "collateral damage" made by grazers to the different life cycle stages of corals, to better understand the cost/benefit ratio of grazing processes on coral reef resilience (McClanahan et al., 2005; Rotjan & Lewis 2008; Christiansen et al., 2009; Jayewardene et al., 2009). Results of the present study also suggest that if grazers were to be reduced (for example by overfishing), one may hypothesize that competition with turf algae and associated sediment trapping would become the main source of recruit mortality in this system.

The proportion of live, dead-intact, and missing recruits varied among depths on control tiles (Chi-square test on contingency of live, dead-intact, and missing recruits among depths: $\chi^2 = 20.03$; $P = 0.0005$) but not on caged tiles (Chi-square test on contingency of live, dead-intact, and missing recruits among depths: $\chi^2 = 7.936$; $P = 0.1039$). The proportion of missing recruits was higher and the proportion of live recruits was lower at 12 m compared to 6 and 18 m for control tiles, but was not significantly different among depths on caged tiles. This is most likely due to variation in predation pressure among the depth gradient, linked with variable abundance of predators and/or grazers (Penin et al., 2010). This spatial variability reinforces the hypothesis that this process may be critical in structuring coral populations, as previously demonstrated for other organisms (Steele & Forrester, 2002; Osman & Whitlatch, 2004; Almany & Webster, 2006).

This study reveals high rates of mortality of coral recruits during the first weeks of their benthic life. It also suggests that predation (including incidental dislodgement of coral recruits), competition, and sediment trapping by turf algae, can all be important sources of early mortality in corals, and that their spatial variability can play a major role in structuring populations.

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