

Spatial refugia mediate juvenile coral survival during coral–predator interactions

Clare Gallagher^{1,2}  · Christopher Doropoulos^{2,3,4}

Received: 8 March 2016 / Accepted: 4 November 2016 / Published online: 16 November 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Coral recruitment and juvenile growth are essential processes for coral population maintenance and recovery. A growing body of research has evaluated the influence of reef microstructure on coral settlement and post-settlement survival, showing that physical refugia enhance recruitment. These studies have evaluated coral recruit mortality from competition with macroalgae and indirect predation by grazing organisms, but the impact of direct predation by corallivorous piscine species on juvenile corals and how this interacts with reef microstructure is relatively unknown. This study examined whether refugia provided by micro-crevices enhance juvenile coral survival from corallivory. Juvenile corals from two different functional groups, the slow-growing massive *Porites lobata* and fast-growing branching *Pocillopora damicornis*, with average nubbin sizes of 1.4 cm × 0.3 cm and

0.5 cm × 1.0 cm (diameter × height), respectively, were attached to experimental tiles using small (1.44 cm³) and large (8.0 cm³) crevice sizes and were monitored for 29 d on a forereef in Palau. Full crevices (four sided) enhanced coral survival compared to exposed microhabitats in both coral taxa, but crevice size did not alter survival rates. Corallivores targeted recruits within crevices regardless of crevice size; dominant predators included small triggerfish (Balistidae), butterflyfish (*Chaetodon*), and wrasse (*Cheilinus*). Overall, *Pocillopora* suffered much higher rates of mortality than *Porites*. All *Pocillopora* were consumed by day 8 of the experiment, but mortality was significantly delayed in full crevices compared to exposed and partial crevice (three sided) microhabitats. In contrast, *Por. lobata* located in all microhabitats survived the entire experiment up to 29 d, with high survival in full (>90%) and partial crevices (70%), but only 28% survival in exposed microhabitats. These findings show the importance of crevices as spatial refugia from predators for juvenile corals and highlight the importance of structural complexity for juvenile coral growth and survival that enhances reef recovery.

Communicated by Biology Editor Prof. Mark J. A. Vermeij

Electronic supplementary material The online version of this article (doi:10.1007/s00338-016-1518-9) contains supplementary material, which is available to authorized users.

✉ Clare Gallagher
cgalla44@gmail.com

✉ Christopher Doropoulos
christopher.doropoulos@csiro.au

¹ Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

² Palau International Coral Reef Center, Koror 96940, Palau

³ Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

⁴ CSIRO Oceans and Atmosphere, Dutton Park, QLD 4102, Australia

Keywords Corallivory · Crevice · Microhabitat · Spatial refugia · Predation · Juvenile

Introduction

Micro-crevices and other small cryptic habitats have been examined as enhancers of survival of the early-life phases of numerous marine benthic organisms (Jackson 1977). Crevice microhabitats enhance fish recruitment by providing protective refugia for young larvae and recruits from predators (Hixon and Beets 1993; Munday et al. 1997), as

well as the recruitment of benthic invertebrate (Jackson et al. 1971; Menge and Lubchenco 1981; Walters and Wethey 1996) and algal taxa (Lubchenco 1983; Poray and Carpenter 2014; Brandl and Bellwood 2016). Crevices also serve as protective refugia for coral recruits (<1 cm maximum diameter) because the cryptic spaces protect recruits from indirect predation by grazing fish (Brock 1979; Nozawa 2008, 2012; Edmunds et al. 2014; Doropoulos et al. 2016). Since juvenile coral (1–5 cm) survival and growth are integral for reef maintenance and recovery (Bellwood et al. 2004; Hughes et al. 2007; Doropoulos et al. 2015), understanding how crevices facilitate juvenile coral survival from predation provides a deeper understanding of reef recovery mechanisms.

Corallivorous fish and invertebrates consume coral tissue, which can cause acute, instant mortality to small corals in particular (Christiansen et al. 2009; Wolf and Nugues 2013; Doropoulos et al. 2012). Corallivory can also increase a colony's susceptibility to disease and reduce fecundity and growth due to the large energetic cost of tissue repair (Meesters et al. 1994; Aeby and Santavy 2006; Cole et al. 2008; Rotjan and Lewis 2008). Penin et al. (2010) found that juvenile coral survivorship was negatively correlated with Chaetodontidae abundance, but stated the need for direct investigations on this relationship. Recent evidence from the eastern Pacific showed that juvenile *Pocillopora* corals subjected to intense predation by pufferfish compensated for reduced linear growth by growing denser and thicker skeletons with no net loss in carbonate production (Palacios et al. 2014). However, some corallivorous fish, such as scarid parrotfish, are important herbivores that benefit corals by preventing overgrowth of competitive macroalgae (Rotjan and Lewis 2008; Steneck et al. 2014; Mumby et al. 2015). Even though scarids cause indirect, non-targeted mortality to corals that is often detrimental to juvenile corals, the herbivorous activity contributes to a net positive effect on coral settlement and post-settlement survival for adult coral communities (Brock 1979; Birkeland and Neudecker 1981; Mumby 2009; Venera-Ponton et al. 2011; Doropoulos et al. 2016). Hence, the positive or negative consequences of corallivory on coral recruitment can vary depending on the identity of the corallivore and the trade-offs between targeted corallivorous predation and non-targeted predation that ultimately improves recruitment.

Cryptic spaces on experimental tiles positively influence coral settlement and early post-settlement survival (Birkeland and Neudecker 1981; Petersen et al. 2005; Nozawa 2008; Nozawa et al. 2011; Davies et al. 2013; Edmunds et al. 2014; Brandl and Bellwood 2016; Doropoulos et al. 2016). Correspondingly, coral recruit abundances positively correlate with surface irregularity on the scale of 1 cm reef rugosity (Carleton and Sammarco 1987;

Doropoulos et al. 2016). Coral settlement preference in cryptic spaces is understood to be a mechanism to avoid indirect mortality from herbivorous fish and direct mortality from corallivorous grazers (Birkeland and Neudecker 1981; Doropoulos et al. 2016). However, while crevice microhabitats certainly enhance coral recruitment, the influence of crevices on juvenile coral survival is relatively unknown. Indeed, the annual survival of juvenile *Siderastrea*, *Agaricia*, *Porites*, and *Montastrea* corals that were marked on the benthos and ranged in size from 10 to 40 mm at Conch Reef, Caribbean, did not differ among exposed, vertical, and crevice microhabitats (Edmunds et al. 2004). Similarly, a recent study from Palau that included tagged *Acropora*, *Pocillopora*, and *Porites* corals on the benthos ranging in size from 1 to 27 mm also found no differences in survival between exposed and crevice microhabitats over a 7-month period, even though the abundance of recruits was four times higher in crevices (Doropoulos et al. 2016).

Here, we use an experimental approach to assess whether crevices, both full and partial, serve as refugia from direct predation for juvenile corals. We tested the effect of two crevice sizes (1.44 and 8.0 cm³) on juvenile coral survival and whether survival differed between juvenile corals of two different functional groups: the slow-growing massive *Porites lobata* and the fast-growing branching *Pocillopora damicornis* (Darling et al. 2012).

Materials and methods

The study was conducted during June and July 2013 on the east coast of Palau, western Micronesia. Experiments were conducted at the site Short Drop Off (described in Doropoulos et al. 2014) at a depth of 7 m. The method includes two main components: an experimental assessment of juvenile coral survival, followed by observational identification of predators of the juveniles during the experiments.

Experimental assessment of juvenile coral survival: approach and analysis

Experimental crevice tiles measuring 10 × 10 cm were made from handmade molds using a mix of 2:1 of carbonate sand to cement. Two crevices sizes were chosen based on the findings of Doropoulos et al. (2016), who showed that the highest concentration of recruits on reef substratum in Palau was found in crevices with a depth of 6–11 mm and an aperture of 60–90 mm², followed by crevices with apertures that increased at 100 m² intervals. A disproportionate concentration of the smallest crevices (<50 mm² × 8 mm) lacked recruits, and larger crevices

(200, 300, and 400 mm² × 10 mm) contained recruits. Thus, we created ‘small’ crevices that measured 1.2 × 1.2 × 1.0 cm = 1.44 cm³, and ‘large’ crevices that measured 2.0 × 2.0 × 2.0 cm = 8.0 cm³.

Adult colonies of *Poc. damicornis* and *Por. lobata* (five individuals of each) were collected from the sites Beluu Lukes and East Sheltered at 2–5 m depth. Colonies of each taxon were kept in outdoor, ambient seawater flow-through aquaria after removal from the reef. Micro-nubbins of *Poc. damicornis* and *Por. lobata* were cut from adult colonies, randomized within species, and glued onto experimental crevice tiles to mimic small juvenile corals (e.g., Christiansen et al. 2009; Gibbs and Hay 2015) using monospecific treatments. Hereafter, the micro-nubbins are referred to as juvenile corals. Average juvenile coral sizes were 1.4 × 0.3 cm and 0.5 × 1.0 cm (diameter × height) for *Por. lobata* and *Poc. damicornis* nubbins, respectively ($n = 480$ individuals per coral species).

Twenty-four juveniles from one coral species were glued onto a tile replicate. These were distributed among three microhabitats: exposed, partial crevices (three closed sides and one open side), and full crevices (four closed sides). On each tile replicate, twelve individuals were located on exposed microhabitats, eight individuals in partial crevice microhabitats, and four in full crevice microhabitats (Fig. 1). Juvenile corals were maintained in aquaria for 7 d prior to transplantation onto the reef to minimize handling effects. During this time, no individuals showed any signs of stress such as bleaching (visually assessed) and no mortality was quantified.

At the forereef site, tiles were distributed between fish exclusion plots and open plots, with five replicate plots for each exclusion treatment. Plots were haphazardly placed onto a 100 m² section of reef, each separated by ≥ 1 m. Cages were used to exclude piscine corallivores from the juvenile corals, measured 40 × 26 × 10 cm, and were constructed from PVC-coated galvanized steel mesh (2.5 × 2.5 cm mesh). Open plots allowed fish access to the juvenile corals. There were five tile replicates for each treatment combination of coral species (*Pocillopora*, *Porites*) × microhabitat (exposed, partial crevice, full crevice) × crevice size (small, large) × exclusion treatment (caged, open). This resulted in an unbalanced design because there were a total of 240 individuals for exposed microhabitats compared to 160 individuals for partial crevices and 80 individuals for full crevices, for each coral species.

A step-wise approach was taken for the analysis of juvenile coral survivorship among treatments. First, corals from open treatments only were analyzed because there was no mortality of corals in the caged treatments (see “Results”). Juvenile survivorship was then visually compared among coral species and microhabitat location using

Kaplan–Meier (KM) log-rank survival curves (Kaplan and Meier 1958). The discrete stepped survivorship curves were selected because they incorporate information from each mortality event, including both uncensored and censored data. The mortality events from corallivory were uncensored data, whereas mortality events from other causes were classified as censored data. Next, statistical analyses were conducted using mixed effects Cox proportional hazard models that include tile replicates as a random effect to incorporate the pseudo-replication of multiple individuals per microhabitat within a tile (‘coxme’ package, version 2.2-3; Therneau 2012). The first analysis investigated whether survival over time was different between coral taxa. Subsequent analyses within each coral taxon compared differences in survival over time among microhabitats × crevice sizes.

Coral predator identification: approach and analysis

The experimental tiles were evaluated nine times over a 29-d period. Predation was defined as removal of the entire juvenile coral segment from its attachment place on the tile (maximum = 24 corallivore mortalities tile⁻¹). This method only accounted for excavating corallivory, not the predation caused by browsing or grazing corallivory. Mortality from causes other than corallivory was also recorded, including algal overgrowth, bleaching, and accidental human error. These non-predation outcomes were designated as ‘censored.’ Corals that remained alive for the entire length of the experiment were also noted. Any evidence of bite marks or grazing scars were noted, typically the presence of parrotfish bites on *Por. lobata* that are identifiable tooth marks occurring across the colony surface in parallel lesions (Bellwood and Choat 1990; Jayewardene et al. 2009; Traçon et al. 2013b). Evidence of eaten or withdrawn *Poc. damicornis* polyps (‘looking white’) was recorded as chronic butterflyfish grazing (Gochfeld 2004; Rotjan and Lewis 2008). This observational analysis aided the identification of corallivorous predator fish species in conjunction with video footage analysis.

To directly identify the corallivorous fish species responsible for coral predation, stationary underwater digital video cameras (GoPro HERO3 Black Edition CHDX-301 and GoPro HD HERO 960) recorded feeding activity on the open plots. Each camera was mounted onto the reef substrate and positioned approximately 1 m from an open plot. Filming occurred 13 times for an average of 106.13 ± 6.20 (SE) min.

When the open plots had few or no corals left on the tiles, cameras were positioned to film plots of caged coral, but cages were opened for filming. Any coral mortality that occurred during this filming was designated as censored, so mortality from corallivory on corals in the cage treatment

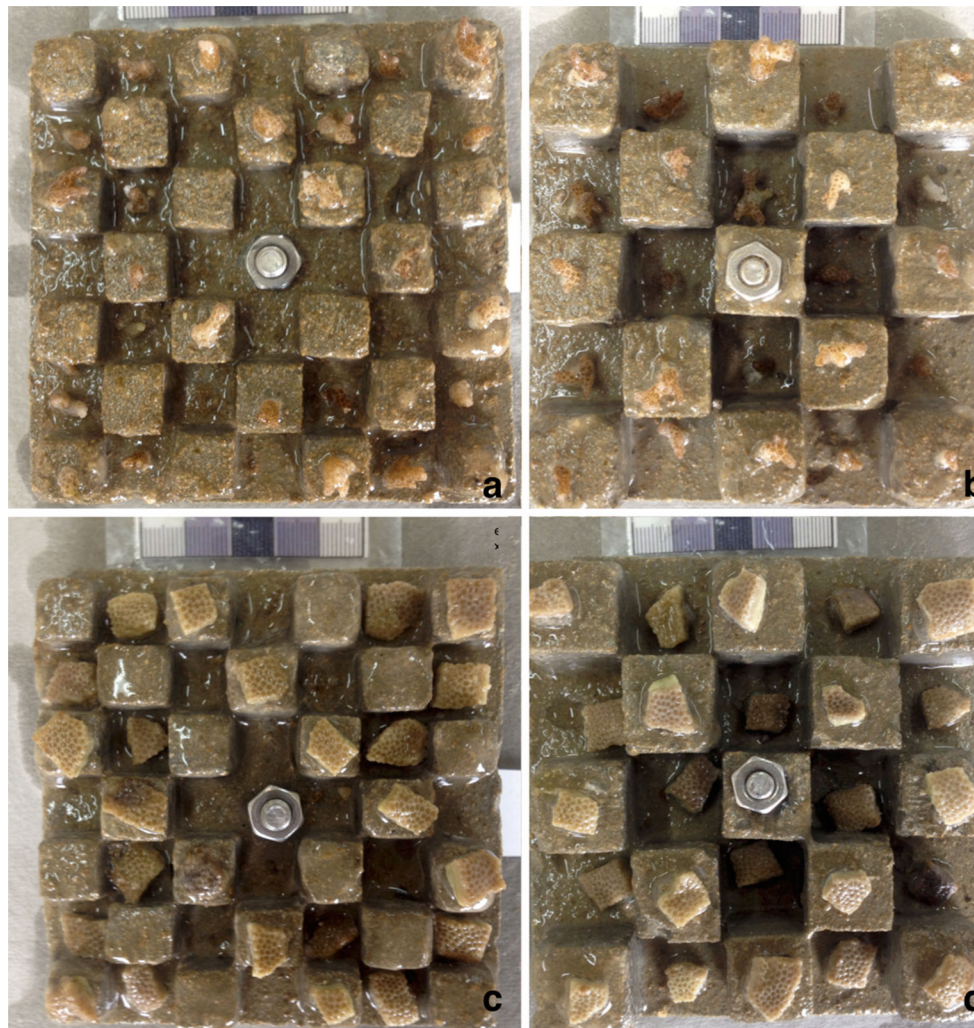


Fig. 1 Experimental tile treatments: **a** *Pocillopora damicornis* × small crevice; **b** *P. damicornis* × big crevice; **c** *Porites lobata* × small crevice; **d** *P. lobata* × big crevice. The four tile

treatments were crossed with exclusion treatment (caged or uncaged). Tiles per treatment: $n = 5$. Ruler at top center of each photo = 5 cm

was not included in the statistical analysis. This practice allowed for more video footage to identify the fish species consuming the corals, while ensuring that all plots filmed had roughly equivalent numbers of live coral as prey for the grazing fish. All video footage was viewed, and the number of bites taken by different fish species recorded. Each bite was categorized by (1) fish identity, (2) coral species bitten, (3) microhabitat location, and (4) crevice size. For the categorization of bites dependent on microhabitat location, microhabitats were only divided into two levels (exposed and crevices) because differentiation between partial and full crevices was frequently not possible. The number of bites per foray by an individual fish was used as a replicate within each video. Multiple foray events are therefore multiple data points within a video.

The number of bites (total $n = 362$) was analyzed using a generalized linear model (GLM) to account for overdispersion associated with count data. The analytical process

followed those described by Zuur et al. (2009). First, the variance-to-mean ratio was checked to confirm the presence of overdispersion. Second, two models were fit, one with Poisson and one with negative binomial distribution, and the model fits were visualized (residual vs. predicted values, normal QQ plots) and Akaike information criterion (AIC) quantified to assess the best error structure for the analysis. The models both displayed some overdispersion, but the negative binomial error structure greatly improved the model fit and reduced AIC (negative binomial = 398, Poisson = 600). Third, the variance between the models was formally tested using a likelihood ratio test (LRT) and demonstrated that the negative binomial model was clearly a better fit (LRT = 208, $P < 0.001$). Thus, the final model used a negative binomial error structure to assess differences in the number of bites among coral species (*Pocillopora*, *Porites*), microhabitats (exposed, crevice), and crevice sizes (small, large). The time of each video was

incorporated as an offset variable to account for differences in bites depending on filming time. Finally, to assess the appropriateness of the final model fit to the data, the observed and fitted counts of bites were visualized and compared for significant predictors (Electronic Supplementary Material, ESM, Figs. S1, S2) as well as the mean and SE of the observed and fitted bite rates (ESM Fig. S3). GLMs were conducted using the ‘MASS’ package (Venables and Ripley 2002) in R (R Development Core Team 2015).

Bite rates were not statistically compared among fish species due to a general lack of data points, but were plotted according to fish species to visually assess any differences. All analyses were conducted in R (version 2.15.2).

Results

Juvenile coral survivorship

In open treatments where juvenile corals were exposed to predators, rates of mortality for *Poc. damicornis* were significantly higher than for *Por. lobata* (Coxme: $\chi^2 = 30.6$, $df = 1$, $P < 0.0001$). Most *Poc. damicornis* individuals had died by 8 d apart from a single individual found in a full crevice, whereas $63 \pm 9\%$ of *Por. lobata* individuals survived the duration of the experiment up to 29 d (Fig. 2). Crevice microhabitats significantly enhanced juvenile coral survival compared to those found on exposed microhabitats, yet the effects of full and partial crevices differed between coral species (Table 1). *Pocillopora damicornis* juveniles in full crevices experienced significantly delayed mortality compared to those in partial crevices and exposed microhabitats, but there was no difference between partial crevices and exposed microhabitats (Table 1; Fig. 2). For *Por. lobata*, survival was 3.3 times higher in full crevices and 2.4 times higher in partial crevices than exposed microhabitats after 29 d (Table 1; Fig. 2). Juvenile survival was $93 \pm 5\%$ and $68 \pm 12\%$ in full and partial crevices after 29 d, compared to only $28 \pm 9\%$ of juveniles on exposed microhabitats (Fig. 2). There were no differences in bite rates between small and large crevices in either coral species (Table 1).

All individuals from both coral taxa in fish exclusion cages survived the entire experimental period. Sixteen *Pocillopora* were consumed during video recording when the cages were removed for bite analysis, but these deaths were censored in the survival analysis. It should also be noted that a total of 19 individuals died in the uncaged treatment from causes other than excavator corallivory; these events were also censored. One individual died from accidental human error, whereas the other 18 individuals

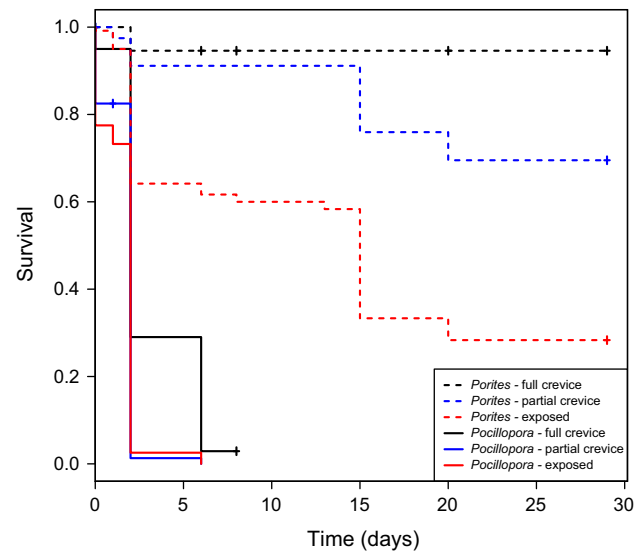


Fig. 2 Characterization of coral survival rates from corallivory for *Pocillopora damicornis* (large dashed lines) and *Porites lobata* (solid lines). Red lines exposed microhabitats, blue lines partial crevice microhabitats, and black lines full crevice microhabitats. Censoring (!) indicates death from causes other than predation or if corals were alive at the end of the experiment

that died appeared bleached. Given that partial mortality was noted prior to the death of these individuals, it is possible that chronic predation by browsing butterflyfish caused their eventual death; however, the exact reason for their mortality is unknown.

Coral predator bite rates and identification

Average bite rates were three times higher on *Poc. damicornis* than *Por. lobata* ($P < 0.001$). There were 0.058 ± 0.009 bites min^{-1} tile^{-1} on *Poc. damicornis* juveniles compared to 0.019 ± 0.004 bites min^{-1} tile^{-1} on *Por. lobata* juveniles (Fig. 3a). Moreover, bite rates on individuals on exposed microhabitats were 2.7 times higher than in crevice microhabitats ($P = 0.008$), with an average of 0.055 ± 0.008 bites min^{-1} tile^{-1} on juveniles on exposed microhabitats compared to 0.020 ± 0.004 bites min^{-1} tile^{-1} in crevice microhabitats (partial and full crevices pooled; Fig. 3b). There were no differences in bite rates between small and large crevices in both taxa (0.055 ± 0.004 vs. 0.044 ± 0.004 bites min^{-1} tile^{-1} , $P = 0.4$).

The fish species recorded preying on coral included two species of butterflyfish (*Chaetodon lunulatus*, *C. punctatofasciatus*), two species of triggerfish (*Balistapus undulatus*, *Balistoides viridescens*), and one species of wrasse (*Cheilinus fasciatus*), all of which were adults. Bite rates were highly variable among fish species; *Chaetodon lunulatus* had the highest bite rate (0.11 ± 0.02 bites min^{-1} tile^{-1}) on *Poc. damicornis* juveniles on exposed microhabitats (Fig. 4). Butterflyfish frequently bit individual juvenile

Table 1 Statistical outcomes of juvenile coral survival analyses for *Pocillopora damicornis* and *Porites lobata* using Cox mixed effects proportional hazards models

Coral species	Factor	χ^2	df	<i>P</i>	Pairwise	<i>z</i>	<i>P</i>
<i>Pocillopora damicornis</i>	Crevice size	1.08	1	0.2984			
	Microhabitat	23.94	2	<0.001	E vs. PC	0.34	0.73
					E vs. FC	4.51	<0.001
					PC vs. FC	4.01	<0.001
<i>Porites lobata</i>	Crev. × micro	0.46	2	0.7935			
	Crevice size	0.4671	1	0.4943			
	Microhabitat	100.55	2	<0.001	E vs. PC	7.07	<0.001
					E vs. FC	4.89	<0.001
					PC vs. FC	2.43	0.015
	Crev. × micro	1.789	2	0.4088			

Pairwise comparisons among survival rates are only shown for the significant main effect of microhabitat. *E* exposed microhabitat, *PC* partial crevice microhabitat, *FC* full crevice microhabitat

polyps but did not cause any obvious immediate mortality, whereas triggerfish and wrasse were recorded taking few bites, but each bite caused instantaneous mortality to individual juvenile corals. Only *Poc. damicornis* experienced acute bites from the triggerfish and wrasse (Fig. 4), whereas bite marks with parallel lesions from scarids were only observed on individuals of *Por. lobata*. *Chlorurus sordidus* (bullethead parrotfish) were observed swimming in close proximity to the tiles, but no individual was directly recorded consuming the experimental coral.

Discussion

Crevices and cryptic microhabitats are known to provide protection from predation to newly settled coral recruits (Nozawa 2008; Edmunds et al. 2014; Doropoulos et al. 2016). Fewer studies have examined whether such microhabitats provide similar protection to juvenile corals and results vary (Edmunds et al. 2004; Brandl et al. 2013). This study used an experimental approach to understand the survival of juvenile corals, which were attached to tiles containing different-sized crevices. Overall, crevice size did not influence juvenile coral survival, but both full and partial crevices improved survival or provided a longer temporal escape from predation compared to exposed microhabitats.

Most individuals of *Poc. damicornis* were rapidly consumed within 8 d following deployment, even though crevices facilitated a longer temporal escape from predation compared to partial crevices and exposed microhabitats. Thus, juveniles must reach larger size-escape thresholds on exposed surfaces to withstand direct predation pressure. In contrast, *Por. lobata* located in all microhabitats survived the entire experiment up to 29 d, with very high survival in full (>90%) and partial crevices

(70%) compared to only 28% in exposed microhabitats. Overall, crevices mediate the interaction between coral-ivorous fish and juvenile corals, increasing the survival of two common coral species. Hence, crevices and similar cryptic spaces that protect small, juvenile-sized corals from corallivorous predation optimize survival into adulthood.

Considering the morphological and life-history distinctions between *Por. lobata* and *Poc. damicornis*, it is not surprising that *Poc. damicornis* experienced such rapid and complete predation. Classified by Darling et al. (2012) as a ruderal ‘weedy’ species, *Poc. damicornis*, along with other weedy coral taxa, opportunistically colonized habitats, especially following disturbances (Doropoulos et al. 2015; Gouezo et al. 2015). Coral taxa that brood larvae often release planulae throughout the year, the planulae can settle immediately and have rapid growth, and colonies reproduce at small sizes (≥ 40 mm diameter); some species even have the ability to reproduce larvae via parthenogenesis (Ayre and Miller 2004). Such characteristics support the theory that ruderal species survive better than non-weedy species because they reproduce faster and can colonize reef space after disturbance more successfully than slow-growing species (Darling et al. 2012). Thus, even though *Poc. damicornis* experienced much more rapid predation and mortality compared to *Por. lobata*, its life-history strategy suggests that crevices could be even more influential for its survival beyond early juvenile bottlenecks.

In contrast, slow-growing broadcast spawners including *Por. lobata* are often classified as *K*-selected species because of their longevity, low turnover, and high stress tolerance, including high tolerance of predation from grazing fish (Harriott 1985; Darling et al. 2012). Interestingly, these species facilitate increased reef microstructural complexity, since crevices are found in the undersides, holes, and pits of large foliaceous massive corals, in addition to the hard limestone reef matrix. The

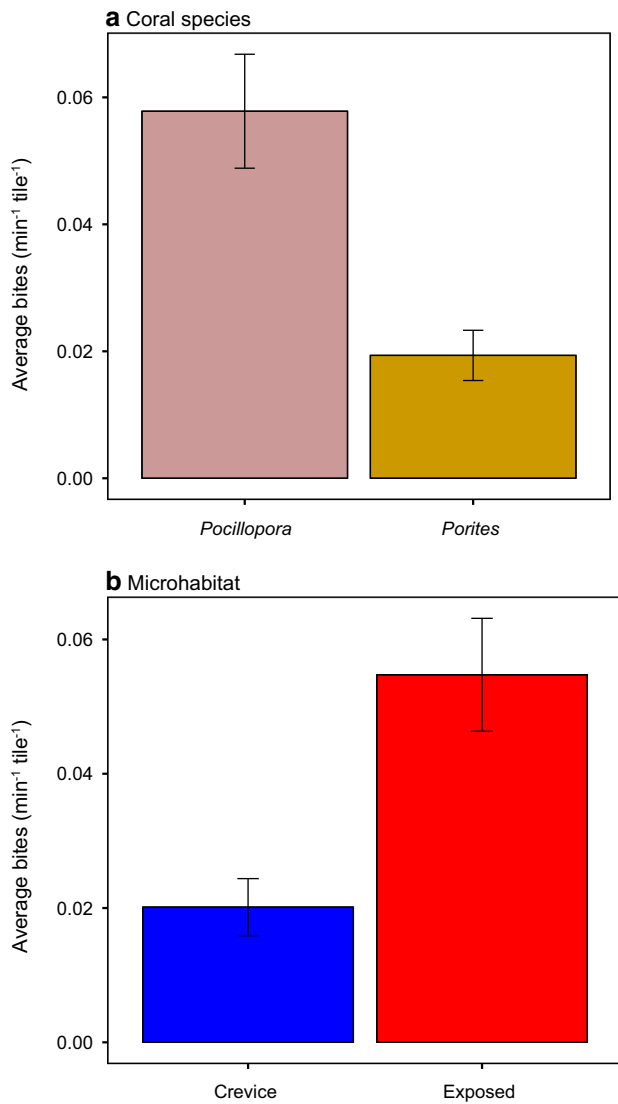


Fig. 3 Average bite rates on coral micro-nubbins (bites min⁻¹ tile⁻¹) of all fish species pooled displaying the significant predictors of **a** coral species (*Pocillopora damicornis*, *Porites lobata*) and **b** microhabitat location (crevice, exposed). Error bars are standard errors

architectural complexity of massive *Porites*, along with other massive corals, has been recognized to influence the survival of juvenile corals in the reef system by providing more ‘nooks and crannies’ for protection of coral juveniles vulnerable to corallivory (Miller et al. 2000). Conversely, the fragile branching physical structure of *Poc. damicornis*, along with other ruderal and competitive *r*-selected species, does not provide an abundance of crevices in the reef, especially after disturbances such as typhoons turn skeletons into rubble. Yet even after intense wave action, a dead but intact massive *Porites* skeleton still provides cryptic spaces for recruitment. Lenihan et al. (2011) found that the survival of *r*-selected species *Poc. verrucosa* and *Acropora retusa* was influenced by the presence of dead and partially

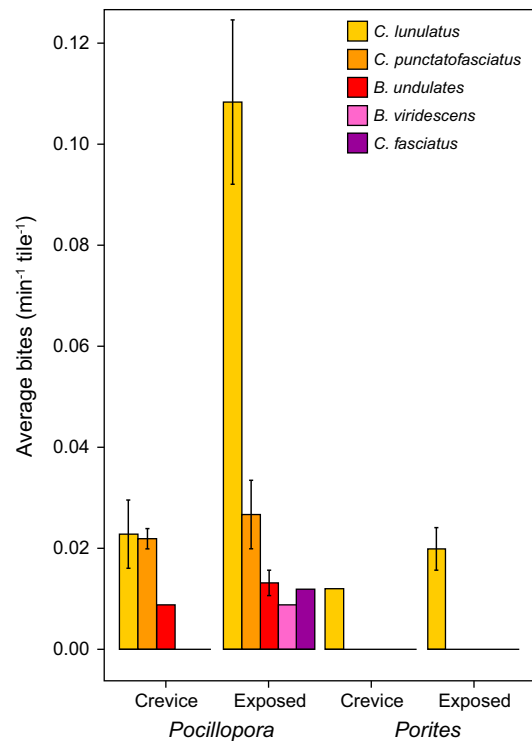


Fig. 4 Average bite rates (bites min⁻¹ tile⁻¹) by corallivorous fish species on *Pocillopora damicornis* and *Porites lobata* in crevice and exposed microhabitats. *C. lunulatus* = *Chaetodon lunulatus*, *C. punctatofasciatus* = *Chaetodon punctatofasciatus*, *B. undulates* = *Balistapus undulates*, *B. viridescens* = *Balistoides viridescens*, *C. fasciatus* = *Cheilinus fasciatus*. Error bars are standard errors. Columns without error bars are single observations

dead massive *Porites* colonies, which provided these branching corals with protection from predation and other disturbances. Specific to this study, it should be noted that the different morphologies of *Pocillopora* and *Porites* (small and upright versus wide and flat) could have influenced predation pressure results because the former could easily be excavated in one bite by a corallivore, whereas the encrusting form of the latter would require multiple corallivore bites for complete consumption.

Surprisingly, the size of the crevices in this experiment did not affect coral survival, suggesting the variation in crevice size of 1–8 cm³ is of little importance for juvenile corals to escape fish predation. There are two likely explanations for the insignificant effect of crevice size on coral survival in this experiment, related to (1) changes in effective refuge sizes throughout early coral ontogeny, and (2) the diversity of feeding morphologies in the surrounding fish community.

First, different crevice sizes can play varying roles in early phases of coral ontogeny. Coral larvae have been shown to settle preferentially in small crevices most similar to their larval width (Whalan et al. 2015). Nozawa (2012) also compared the post-settlement survival of newly settled

Echinophyllia aspera and *Favites abdita* on experimental tiles with three different crevice sizes (5, 15, and 25 mm wide, and all 4 mm deep) over a 2-yr period. Corals had higher survival rates in the smallest crevice size, suggesting that the effective refuge size for newly settled coral recruits was at the scale of millimeters that corresponds with their size at settlement (Nozawa 2012). However, the results from our study suggest that for juvenile corals that have escaped early post-settlement bottlenecks, the effective refuge size, if smaller than 8.0 cm³, is of less importance than the more important escape of having any crevice refuge at all.

Second, the identification of the corallivorous fish responsible for the coral mortality is consistent with published reports of the diets of these taxa, with *Chaetodon*, Balistidae, and *Cheilinus* all reported to consume *Poc. damicornis* and *Por. lobata* (Neudecker 1979; Bellwood 1994; Cole et al. 2008; Hoey and Bellwood 2008; Rotjan and Lewis 2008). The range in size and feeding morphology of the excavating corallivores could explain why there was no difference in coral survival between the two crevice sizes. The small crevices were still large enough for the orange-lined triggerfish, *Balistapus undulatus*, to prey on the coral, consistent with findings that *B. undulatus* is especially versatile in microhabitat use among reef zones. Bean et al. (2002) found that of five species of triggerfish examined, *B. undulatus* was the only one to indiscriminately use all substrata sampled (turf algae, rubble, massive coral, branching coral, soft coral, columnar coral, laminar, foliaceous coral, coralline algae, rock). This is also consistent with the feeding morphology of *B. undulatus*: Its jaws have high mobility achieved by a reduced autopalatine (paired deep bone on the roof the mouth) that has lost contact with its lower jaw, which implies that the mouth can access small spaces more easily than less mobile jaw structures (Konstantinidis and Johnson 2012).

In comparison, even though the larger titan triggerfish, *Balistoides viridescens*, and the red-breasted wrasse, *Cheilinus fasciatus*, only preyed on individuals on exposed surfaces, there was no discrepancy based on tile crevice sizes. These species feeding on exposed nubbins is consistent with their feeding morphology. Westneat (1994) documented that *C. fasciatus* has jaw and hyoid systems that favor force transmission over velocity of opening, which corresponds to a diet primarily of benthic invertebrates; in comparison, groups with jaw and hyoid systems that exhibit high velocity when feeding favor diets of primarily evasive prey.

Even though only a few, acute, and mortality-inducing predation events of the corallivorous excavator species *Balistapus undulatus*, *Balistoides viridescens*, and *C. fasciatus* were recorded, previous studies confirm that these species' predation behavior is characterized by acute bites

of coral tissue and skeleton (Rotjan and Lewis 2008; Gibbs and Hay 2015). Excavating corallivores consume entire small coral fragments in few bites compared to the number of bites taken by browsing corallivores. The observed behavior of the two browsing *Chaetodon* species is also consistent with reports of the diets of butterflyfish, which chronically browse individual coral polyps and never consume coral skeleton, let alone entire coral fragments (Birkeland and Neudecker 1981; Rotjan and Lewis 2008). Yet chronic polyp removal can still induce partial or complete coral mortality (Neudecker 1979). Such partial mortality was observed in this study by corals exhibiting bleaching-like symptoms and a white appearance. However, our study did not determine whether chronic polyp removal of *Poc. damicornis* ultimately caused mortality, which echoes the finding from Lenihan et al. (2011) that partial predation by *Chaetodon* on *Poc. verrucosa* and *A. retusa* was often not noticeable on the soft tissue as recent as 72 h after grazing. In contrast, Cole et al. (2011) examined chronic browsing by *Chaetodon*, finding that the amount of coral consumption, albeit at the single-polyp scale, was considerable and may pose sub-lethal effects on healthy reefs. Compiled with other stressors, chronic browsing by butterflyfish may lead to coral mortality, but this requires more detailed research.

The evidence of lesions on *Por. lobata* juveniles suggests that other fish species were responsible for some of the coral mortality. Scars observed on *Por. lobata* juveniles on exposed locations (approximately five scars by the end of the experiment; no scars were observed on juveniles in crevices) correspond to scars previously recorded from *Chlorurus sordidus* (Jayewardene et al. 2009). This evidence and the video footage of *C. sordidus* in close proximity to the experimental tiles make it highly likely that *C. sordidus* preyed on *Por. lobata*. The net effect of parrotfish corallivory and macroalgae control on juvenile corals has previously been examined, and studies have found that removing parrotfish from a reef system results in a net deficit to juvenile coral growth and survival due to elevated coral–algal competition (Bak and Engel 1979; Mumby 2006, 2009; Venera-Ponton et al. 2011). To expand on this repeated finding, albeit with variation among geographic regions, it would be useful for future studies to isolate the effects of corallivory on crevice-protected juvenile corals to focus specifically on the effects of parrotfish corallivory, isolated from the effects of chronic browsing corallivory, as also suggested by Brandl and Bellwood (2016).

There are several limitations to this study that warrant future work. First, the experiment lacked tiles with varying proportions of different crevice sizes—i.e., all tiles contained either large or small crevices. Future experiments could use tiles with varying proportions of different crevice sizes to account for the possibility that different-sized

corallivores exploit different-sized crevices relative to their body size. Isolating patterns of how corallivore body sizes are related to exploitation of different crevice sizes would elucidate more specific insights into each corallivore's functional niche within crevices. (Brandl and Bellwood 2013, 2016; Fox and Bellwood 2013). Second, predation rates on micro-nubbins that mimic juvenile corals are likely to be overestimated due to their highly aggregated distribution resulting in localized hot spots of predation, as has also been shown with *Pocillopora* on reef flats in Fiji (Gibbs and Hay 2015) and shallow reef slopes in Hawaii (Jayewardene et al. 2009). The density of juvenile corals on the experimental tiles was much higher than is found on the natural surrounding reef; tiles contained 24 juvenile corals per 0.01 m². In Palau, average juvenile coral density was 12.5 and 10 individuals m⁻², at 3 and 10 m depth, respectively (Gouezo et al. 2015). On the Great Barrier Reef, Trapon et al. (2013a) showed that juvenile corals had a mean density of 6.9 individuals m⁻². Thus, the juvenile coral density on the experimental tiles may have increased overall corallivory predation pressure, and more subtle differences in coral survival among different crevice sizes may be detected if lower densities of juvenile corals were employed on experimental tiles.

Other aspects of the experimental protocol have been examined and critiqued in the recent literature. Rocker and Brandl (2015) and Casey et al. (2015) showed that the transplantation of corals from one site to another could cause physiological changes in coral colonies, i.e., increased attractiveness in transplanted corals compared to native corals that could cause selective predation by corallivores. Ainsworth and Hoegh-Guldberg (2009) showed that acclimating corals in aquaria prior to in situ transplantation could alter the natural bacterial communities of corals, which may lead to changes in the chemical signals omitted by the corals, also possibly altering the corals' attractiveness to predators. In addition, the coral nubbins used were taken from adult colonies, which do not precisely mimic true juvenile corals; instead, they would have already been reproductively active, possibly increasing their attractiveness to corallivores. Compiled, these caveats suggest that the transplanted coral nubbins could have increased attractiveness compared to the surrounding native corals, which may account for the rapid consumption of *Poc. damicornis* nubbins, along with heightening the nubbins' susceptibility to stress and non-predator-induced death such as disease or bleaching. Yet, regardless of these caveats and suggested improvements to the experimental protocol, the conclusion about the importance of crevices to juvenile coral survival remains robust because the caveats equally affect all individuals in both microhabitats used in the study.

Overall, we found that crevice microhabitats provide an important refuge for small juvenile corals. However, even

though crevices delayed mortality compared to exposed microhabitats, intense targeted predation on branching *Pocillopora* did result in their total loss in our experimental manipulations after 8 d. In comparison, both full and partial crevices provided a microhabitat that significantly increased survival after 29 d of the massive *Porites* juvenile corals that had a more encrusting form. While we did not find any differences in juvenile coral survival between two sizes of crevices, further investigations into different crevice dimensions are still needed to fully elucidate effective refuge sizes throughout early coral ontogeny from recruits to larger juveniles. As coral reefs endure more severe anthropogenic stress into the future that result in their flattening (Bozec and Mumby 2015) and reduction in potential refugia spaces (Lenihan et al. 2011), better understanding of the ecological implications of crevices and how they relate to coral population dynamics may assist in the enhancement of reef recovery.

Acknowledgements This study was funded by grants to CG from the Department of Ecology and Evolutionary Biology and the Office of the Dean of the College, both at Princeton University, and to CD through an Australian Endeavour Award Postdoctoral Fellowship. We thank Yimnang Golbuu and all the staff of PICRC for their support, along with the Marine Spatial Ecology Lab at The University of Queensland for supporting this collaboration. Mirta Zupan provided valuable field assistance and Professor Stephen Pacala provided valuable guidance. We thank Alice Rogers for reviewing the manuscript prior to submission, and Simon Brandl, Kazuhiko Sakai, and one anonymous reviewer whose efforts greatly improved the manuscript through the review process.

References

- Aeby GS, Santavy DL (2006) Factors affecting susceptibility of the coral *Montastraea faveolata* to black-band disease. *Mar Ecol Prog Ser* 318:103–110
- Ainsworth TD, Hoegh-Guldberg O (2009) Bacterial communities closely associated with coral tissues vary under experimental and natural reef conditions and thermal stress. *Aquatic Biology* 4:289–296
- Ayre DJ, Miller KJ (2004) Where do clonal larvae go? Adult genotypic diversity conflicts with reproductive effort in the brooding coral *Pocillopora damicornis*. *Mar Ecol Prog Ser* 277:95–105
- Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar Biol* 54:341–352
- Bean K, Jones GP, Caley MJ (2002) Relationships among distribution, abundance and microhabitat specialisation in a guild of coral reef triggerfish (family Balistidae). *Mar Ecol Prog Ser* 233:263–272
- Bellwood DR (1994) A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidae) with a revision of genera. *Records of the Australian Museum (Supplement)* 20:1–86
- Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ Biol Fish* 28:189–214
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833

- Birkeland C, Neudecker S (1981) Foraging behavior of two Caribbean Chaetodontids: *Chaetodon capistratus* and *C. aculeatus*. *Copeia* 1:169–178
- Bozec YM, Mumby PJ (2015) The dynamics of architectural complexity on coral reefs under climate change. *Glob Chang Biol* 21:223–235
- Brandl SJ, Bellwood DR (2013) Individual-based analyses reveal limited functional overlap in a coral reef fish community. *J Anim Ecol* 83:661–670
- Brandl SJ, Bellwood DR (2016) Microtopographic refuges shape consumer-producer dynamics by mediating consumer functional diversity. *Oecologia* 182:203–217
- Brandl SJ, Hoey AS, Bellwood DR (2013) Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. *Coral Reefs* 33:421–430
- Brock R (1979) An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar Biol* 51:381–388
- Carleton JH, Sammarco PW (1987) Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques. *Bull Mar Sci* 40:85–98
- Casey JM, Connolly SR, Ainsworth TD (2015) Coral transplantation triggers shift in microbiome and promotion of coral disease associated potential pathogens. *Sci Rep* 5:11903
- Christiansen NA, Ward S, Harii S, Tibbetts IR (2009) Grazing by a small fish affects the early stages of a post-settlement stony coral. *Coral Reefs* 28:47–51
- Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish Fish* 9:286–307
- Cole AJ, Lawton RJ, Pratchett MS, Wilson SK (2011) Chronic coral consumption by butterflyfishes. *Coral Reefs* 30:85–93
- Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Cote IM (2012) Evaluating life-history strategies of reef corals from species traits. *Ecol Lett* 15:1378–1386
- Davies SW, Matz MV, Vize PD (2013) Ecological complexity of coral recruitment processes: effects of invertebrate herbivores on coral recruitment and growth depends upon substratum properties and coral species. *PLoS One* 8:e72830
- Doropoulos C, Ward S, Marshall A, Diaz-Pulido G, Mumby PJ (2012) Interactions among chronic and acute impacts on coral recruits: the importance of size-escape thresholds. *Ecology* 93:2131–2138
- Doropoulos C, Ward S, Roff G, González-Rivero M, Mumby PJ (2015) Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. *PLoS One* 10:e0128535
- Doropoulos C, Roff G, Zupan M, Nestor V, Isechal AL, Mumby PJ (2014) Reef-scale failure of coral settlement following typhoon disturbance and macroalgal bloom in Palau, Western Pacific. *Coral Reefs* 33:613–623
- Doropoulos C, Roff G, Bozec YM, Zupan M, Werninghausen J, Mumby PJ (2016) Characterising the ecological trade-offs throughout the early ontogeny of coral recruitment. *Ecol Monogr* 86:20–44
- Edmunds PJ, Bruno JF, Carlon DB (2004) Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. *Mar Ecol Prog Ser* 278:115–124
- Edmunds PJ, Nozawa Y, Villanueva RD (2014) Refuges modulate coral recruitment in the Caribbean and the Pacific. *J Exp Mar Bio Ecol* 454:78–84
- Fox RJ, Bellwood DR (2013) Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs* 32:13–23
- Gibbs DA, Hay ME (2015) Spatial patterns of coral survivorship: impacts of adult proximity versus other drivers of localized mortality. *PeerJ* 3:e1440
- Gochfeld DJ (2004) Predation-induced morphological and behavioral defenses in a hard coral: implications for foraging behavior of coral-feeding butterflyfishes. *Mar Ecol Prog Ser* 267:145–158
- Gouezo M, Golbuu Y, van Woerik R, Rehm L, Koshiba S, Doropoulos C (2015) Impact of two sequential typhoons on coral reef communities in Palau. *Mar Ecol Prog Ser* 540:73–85
- Harriott VH (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. *Mar Ecol Prog Ser* 21:81–88
- Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol Monogr* 63:77–101
- Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27:37–47
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniewskij N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360–365
- Jackson JBC (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am Nat* 1977:743–767
- Jackson JB, Goreau TF, Hartman WD (1971) Recent brachiopod-coraline sponge communities and their paleoecological significance. *Science* 173:623–625
- Jayewardene D, Donahue MJ, Birkeland C (2009) Effects of frequent fish predation on corals in Hawaii. *Coral Reefs* 28:499–506
- Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. *Am Stat* 53:457–481
- Konstantinidis P, Johnson GD (2012) Ontogeny of the jaw apparatus and suspensorium of the Tetraodontiformes. *Acta Zool* 93:351–366
- Lenihan HS, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Influence of corallivory, competition, and habitat structure on coral community shifts. *Ecology* 92:1959–1971
- Lubchenco J (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64:1116–1123
- Meesters EH, Noordeloos M, Bak RPM (1994) Damage and regeneration — links to growth in the reef-building coral *Montastrea annularis*. *Mar Ecol Prog Ser* 112:119–128
- Menge BA, Lubchenco J (1981) Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol Monogr* 51:429–450
- Miller SL, Weil E, Szmant AM (2000) Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* 19:115–123
- Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol Appl* 16:747–769
- Mumby PJ (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28:761–773
- Mumby PJ, Steneck RS, Adjeroud M, Arnold SN (2015) High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. *Oikos* 125:644–655
- Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Mar Ecol Prog Ser* 152:227–239
- Neudecker S (1979) Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology* 60:666–672
- Nozawa Y (2008) Micro-crevice structure enhances coral spat survivorship. *J Exp Mar Bio Ecol* 367:127–130
- Nozawa Y (2012) Effective size of refugia for coral spat survival. *J Exp Mar Bio Ecol* 413:145–149
- Nozawa Y, Tanaka K, Reimer JD (2011) Reconsideration of the surface structure of settlement plates used in coral recruitment studies. *Zool Stud* 50:53–60

- Palacios MM, Muñoz CG, Zapata FA (2014) Fish corallivory on a pocilloporid reef and experimental coral responses to predation. *Coral Reefs* 33:625–636
- Penin L, Michonneau F, Baird AH, Connolly SR, Pratchett MS, Kayal M, Adjeroud M (2010) Early post-settlement mortality and the structure of coral assemblages. *Mar Ecol Prog Ser* 408:55–64
- Petersen D, Laterveer M, Schuhmacher H (2005) Innovative substrate tiles to spatially control larval settlement in coral culture. *Mar Biol* 146:937–942
- Poray AK, Carpenter RC (2014) Distributions of coral reef macroalgae in a back reef habitat in Moorea, French Polynesia. *Coral Reefs* 33:67–76
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rocker MM, Brandl SJ (2015) Transplantation of corals into a new environment results in substantial skeletal loss in *Acropora tenuis*. *Mar Biodivers* 45:321–326
- Rotjan RD, Lewis SM (2008) Impact of coral predators on tropical reefs. *Mar Ecol Prog Ser* 367:73–91
- Steneck RS, Arnold SN, Mumby PJ (2014) Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternate attractors. *Mar Ecol Prog Ser* 506:115–127
- Therneau TM (2012) Coxme: mixed effects Cox models. R package version 2.2-3
- Trapon ML, Pratchett MS, Hoey AS (2013a) Spatial variation in abundance, size and orientation of juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef. Australia. *PLoS One* 8:e57788
- Trapon ML, Pratchett MS, Hoey AS, Baird AH (2013b) Influence of fish grazing and sedimentation on the early post-settlement survival of the tabular coral *Acropora cytherea*. *Coral Reefs* 32:1051–1059
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York
- Venera-Ponton DE, Diaz-Pulido G, McCook LJ, Rangel-Campo A (2011) Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. *Mar Ecol Prog Ser* 421:109–115
- Walters LJ, Wethey DS (1996) Settlement and early post-settlement survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. *Mar Ecol Prog Ser* 137:161–171
- Westneat MW (1994) Transmission of force and velocity in the feeding mechanisms of labrid Fishes (Teleostei, Perciformes). *Zoomorphology* 114:103–118
- Whalan S, Wahab MA, Sprungala S, Poole AJ, de Nys R (2015) Larval settlement: the role of surface topography for sessile coral reef invertebrates. *PLoS One* 10:e0117675
- Wolf AT, Nugues MM (2013) Predation on coral settlers by the corallivorous fireworm *Hermodice carunculata*. *Coral Reefs* 32:227–231
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York