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REPORT

Associational refuges among corals mediate impacts of a crown-of-thorns starfish *Acanthaster planci* outbreak

Indirect positive interactions in communities

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Abstract Interactions among coral populations can moderate the impact of coral predator outbreaks, enhancing community resilience and recovery. This study used predator-exclusion cages and neighbour removals in a field experiment to test how indirect interactions between populations of three coral taxa, *Acropora*, *Pocillopora*, and *Porites*, influenced their survival during an outbreak of the crown-of-thorns starfish, *Acanthaster planci*, in Moorea, French Polynesia. High densities of corals enhanced survival by generating associational refuges: physical structures that impeded *Acanthaster* and protected corals, and by simple density-dependent prey dilution that reduced predation rates. *Acanthaster* showed feeding preferences, resulting in varying intensities of predation on corals, which (1) influenced the type and strength of the associational refuge among corals and (2) resulted in significant loss of the competitive dominants to the benefit of the competitive inferiors. The result was a set of indirect positive interactions (IPIs) that prevented *Acanthaster* from eradicating *Acropora* and may have enhanced *Porites*, a relatively weak competitor among corals. IPIs probably play a key role in many ecosystems, especially in coral reefs in which corals act as engineer species, to reduce impacts of perturbations and enhance community resilience. This study illustrates the importance of IPIs in community regulation with a new conceptual model.

Keywords Predation · Mortality · Habitat complexity · Indirect positive interaction · Community regulation · Resilience

Introduction

Indirect effects of species interactions are fundamental processes influencing community composition, structure, and function. They occur when the impact of a stressor on one species is influenced by another species in the system and can have positive or negative effects within the cascade of interactions. Indirect positive interactions are increasingly reported in terrestrial and aquatic systems (Callaway and Walker 1997; Stachowicz 2001; Levenbach 2008, 2009). A multitude of examples of positive indirect effects exists in the ecological literature, including case studies in

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which interspecific interactions disproportionately influence species diversity, primary production, or nutrient cycling through the modification of physical habitat (Jones et al. 1997; Altieri et al. 2007), removal of superior competitors (Paine 1974; Hacker and Gaines 1997), mitigation of stressful environmental conditions (Crain and Bertness 2006; Michalet et al. 2006), or other complexities within food webs (Grabowski et al. 2008; Schmitt et al. 2009).

An associational refuge is a form of indirect positive interaction whereby one species indirectly benefits another by reducing consumer pressure (Milchunas and Noy-Meir 2002; Bruno et al. 2003). For sessile organisms, such associations among species are usually established through a haphazard process such as passive settlement. Associational refuges can strongly influence predator–prey interactions (Bertness and Callaway 1994; Hacker and Gaines 1997; Bruno et al. 2003), a prediction tested by Levenbach (2008) who found that such refuges influence patterns of herbivory with indirect links to community dynamics. Strong top-down control of community dynamics is observed during predator outbreaks, when predator–prey interactions are intensified, prey populations are decimated, and ecosystem structure can be modified (Prugh et al. 2009). Understanding how indirect effects, including indirect positive interactions, influence the outcome of predator outbreaks may help to elucidate why certain species survive, how communities recover, and why communities are resilient.

Coral reefs have both high biodiversity and high densities of organisms, leading to intense and complex biological interactions. Scleractinian corals are ecosystem engineers that help maintain biodiversity, as growth of colonies creates physically complex habitats and modifies availability of other resources utilized by many species (Jones et al. 1997; Crain and Bertness 2006; Lenihan et al. 2008). The crown-of-thorns starfish (COTS) *Acanthaster planci* (Linnaeus, 1758) is a major coral predator on Indo-Pacific reefs (Rotjan and Lewis 2008), and outbreaks of this corallivore usually lead to mass mortality of corals and highly modified reef communities (Berumen and Pratchett 2006; Pratchett et al. 2009). However, all coral populations do not necessarily decline during an outbreak, and the effects of outbreaks can vary in time and space, especially in terms of what taxa survive and how much coral is consumed (Faure 1989; Keesing and Lucas 1992). Differences in the outcome of outbreaks appear to result in part from feeding preferences of *A. planci* (De'ath and Moran 1998; Pratchett 2007). Studies of COTS outbreaks have been for the most part observational and correlative and thus, have rarely identified specific mechanisms that can cause variation in coral community composition and structure.

This study explores the indirect effects of coral-coral interactions on the outcome of an *A. planci* outbreak and shows that associational refuges are an important factor in mitigating the impact of this otherwise catastrophic disturbance. A field experiment based on a factorial combination of predator-exclusion and coral-removals was used to test whether associational refuges provided by neighbouring corals influence the survivorship of coral colonies within an assemblage of three coral populations impacted by an outbreak of *A. planci*. The outbreak in the Society Islands of French Polynesia began in 2006 (Adjeroud et al. 2009) and impacted the study area located on the outer reef of Moorea by 2008. Results of the study were used to generalize how indirect positive interactions regulate communities, especially those in coral reef ecosystems.

Materials and methods

Study site

The study was conducted on May–August 2008 on the island of Moorea, French Polynesia (17°30′S, 149°50′W), specifically on the outer reef near Vaipahu, a site that has been monitored extensively since 1992 for coral community dynamics (e.g., Adjeroud et al. 2005, 2007; Penin et al. 2010). Coral assemblages in Moorea and elsewhere in the Indo-Pacific region are dominated by three genera, *Acropora*, *Pocillopora*, and *Porites*, that compete among each other for space and have different competitive abilities as well as susceptibility to predation by *A. planci* (Faure 1989; Adjeroud et al. 2009). *Acropora* often grows relatively fast and is usually considered a superior competitor for space among scleractinian corals (Harriott 1999; Connell et al. 2004). It is also the preferred prey for *A. planci* (De'ath and Moran 1998; Pratchett 2007). *Pocillopora* grows at moderately fast rates and can outcompete many other corals for space, except *Acropora*, and is less preferred by *A. planci* than *Acropora* (Harriott 1999). Massive *Porites* grows slowly and is susceptible to overgrowth by competitors, and is usually ranked as a weak competitor for space among corals (Cox 1986; Connell et al. 2004). *Porites* is the least preferred by *A. planci* among the three taxa (De'ath and Moran 1998; Pratchett 2007).

Experimental design

Two types of associational refuges were predicted to influence predation rates and coral responses, simple dilution and physical sheltering. We refer to these as "associational refuges". Dilution through density is caused by a relatively high abundance of surrounding corals that provide alternative prey for *A. planci*: The prey can passively divert predators from focal corals (Gurevitch et al. 2000; Milchunas and Noy-Meir 2002; Sandin and Pacala 2005).

Sheltering through physical structure is provided by neighbouring corals that impede *A. planci* from locating or reaching focal corals (Schmitt et al. 2009; and see Grabowski et al. 2008). Such physical shelter includes barriers, overhangs, or complex substrata that COTS may avoid. Variation in the rates of survival and growth for individual focal corals located within a coral community under attack by *A. planci* were tested as a function of the abundance of neighbouring corals, which influenced prey dilution, and the physical habitat structure they created, which influenced sheltering. The study also tested whether growth and survival varied among coral taxa due to feeding preference hypothesized for *A. planci* by De'ath and Moran (1998) and Pratchett (2007). The tests were performed in a relatively large field experiment using 450 randomly assigned colonies (150 for each taxon) within an area of about 500 m^2. The minimum gap between each focal coral was of 1 m. The experiment consisted of six treatments in a fully crossed factorial design, with 3 levels of predator access (caged, partial cages, or no cages) and 2 levels of coral-neighbour density (removed or not removed) (see Table 1). Focal corals consisted of the most abundant species within the three major coral taxa, *Acropora globiceps* (Dana, 1846), *Pocillopora meandrina* (Dana, 1846), and the massive *Porites* complex consisting of *P. australiensis* (Vaughan, 1918), *P. lobata* (Dana, 1846), and *P. lutea* (Milne Edwards and Haime, 1851) (Adjeroud et al. 2007; Penin et al. 2007). Each of the six predator access × coral-neighbour density treatments was applied to each of the three coral taxa. All treatments were replicated 25–31 times but some loss before or during the early stage of the experiment occurred ($n = 19$–31 per treatment). The experiment was established at the onset of the COTS outbreak during a period when densities of *A. planci* were escalating in the specific area of the experiment (Electronic Supplementary Material, ESM 1). Coral growth and mortality in each treatment replicate were measured after 100 days.

Caging treatments were designed to test for the effects of predation on coral growth and transition dynamics (i.e., proportion of corals showing growth, partial mortality, or death). Neighbour removals tested for the effect of both forms of associational refuge, dilution and physical sheltering. Predator-exclusion cages (40 cm diameter × 30 cm tall cylinders) were made of galvanized 3-cm wire mesh. Partial cages that controlled for cage artefacts were similar to full cages but did not include wire mesh along two opposing portions of the cylinder. In the neighbour-removal treatment, any coral and sessile organisms present within a distance of 10 cm from the margin of focal colonies were removed and transplanted elsewhere within the study area, thus eliminating potential associational refuges (see Fig. 1 for illustrations taken in the field). The six experimental treatments are described in detail in Table 1. The taxa of neighbouring corals were recorded but not reported here as the specific identity of these random assemblages did not influence the outcome of the experiment. The natural assemblage of neighbouring corals was dominated by the three major genera in French Polynesia (*Acropora*, *Pocillopora*, and *Porites*).

Two indices were used to quantify the relative importance of each associational refuge in terms of the survival of individual focal colonies. To quantify the dilution effect,

Table 1 Number of replicate colonies (n) and mean (±SE) of neighbouring coral density (dC) and of sheltering index (Si) per coral taxa and caging × removal treatments. Because corals are habitat-forming ecosystem engineers, the removal of neighbouring corals always lowers habitat complexity as quantified by Si

Taxa	Treatment	n	Mean dC (±SE)	Mean Si (±SE)
Acropora	Cage + removal	19	0.0 (±0.0)	4.3 (±2.1)
	Cage	23	2.5 (±0.2)	17.7 (±2.1)
	Partial cage + removal	31	0.0 (±0.0)	5.5 (±2.6)
	Partial cage	26	2.2 (±0.3)	19.7 (±2.6)
	No cage + removal	25	0.0 (±0.0)	6.2 (±2.1)
	No cage (control)	26	2.2 (±0.2)	21.0 (±2.3)
Pocillopora	Cage + removal	26	0.0 (±0.0)	−3.27 (±2.1)
	Cage	24	2.5 (±0.3)	8.5 (±3.0)
	Partial cage + removal	25	0.0 (±0.0)	−2.1 (±2.4)
	Partial cage	25	2.7 (±0.3)	10.0 (±2.2)
	No cage + removal	25	0.0 (±0.0)	2.5 (±3.0)
	No cage (control)	25	2.2 (±0.4)	14.6 (±2.4)
Porites	Cage + removal	19	0.0 (±0.0)	−2.4 (±3.0)
	Cage	29	1.4 (±0.3)	4.1 (±2.1)
	Partial cage + removal	27	0.0 (±0.0)	4.4 (±2.6)
	Partial cage	25	1.8 (±0.2)	15.6 (±2.4)
	No cage + removal	25	0.0 (±0.0)	4.6 (±2.6)
	No cage (control)	25	2.0 (±0.3)	21.0 (±3.4)

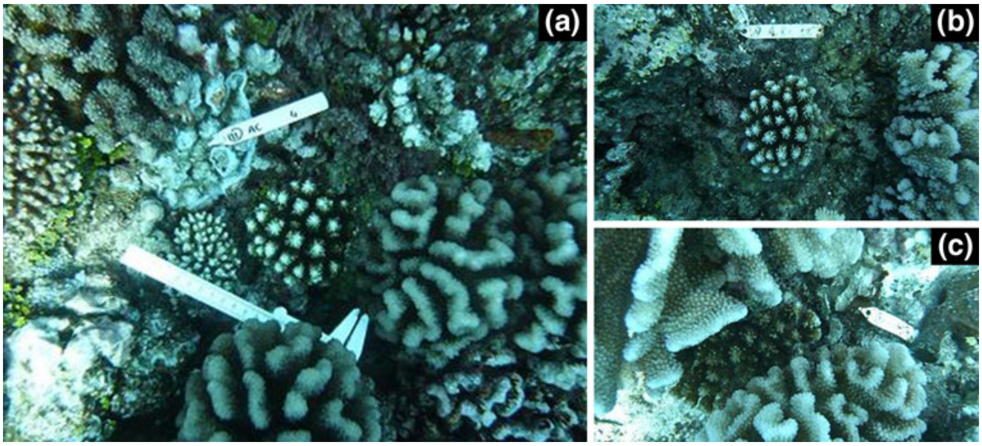

Fig. 1 Photographs taken in the field illustrating the link between the presence of surrounding corals and the two habitat characteristics neighbouring coral density (*dC*) and habitat complexity (expressed by the sheltering index *Si*). Photographs illustrate an *Acropora* colony with neighbouring corals (**a**, high *dC*, intermediate *Si*), after neighbours were removed from a 10 cm perimeter around the focal coral (**b**, low *dC*, low *Si*), and highly sheltered by neighbouring *Pocillopora* colonies that reduced detection and/or access by predators (**c**, intermediate *dC*, high *Si*)

the density of surrounding corals (*dC*) was estimated as the number of live colonies located within 5 cm of the outer edge of each focal colony. To quantify structural refuges around focal corals, a sheltering index (*Si*) was developed by calculating the difference in height between the focal colony, and two points located within a radius of 10 cm on the neighbouring substrate (i.e., live or dead corals, or seafloor). Height measurements were made vertically from the base of the focal coral, and the sheltering index was calculated as: $Si = H_{\max} + H_{opp} - h$; with $H_{\max}$ being the vertical distance to the highest neighbouring point, H_{opp} being the height of the randomly selected substrate situated as directly as possible on the opposing side of the colony in relation to $H_{\max}$, and h focal colony height. The greater the *Si*, the more a focal colony was physically sheltered by its surrounding substrates (see Fig. 1 for more detail). Mean values of *dC* and *Si* for each treatment and taxa are shown in Table 1. How values of *dC* and *Si* were linked to coral growth and transition dynamics is described below in the *Statistical analysis* section.

Treatments were maintained on a weekly basis by cleaning algae and cyanobacteria from cages, cage controls, and within neighbour-free areas around focal colonies. To account for potential caging artefacts, irradiance, mass water exchange, and sedimentation rates were measured in a subset ($n = 6$) of each treatment. Caging showed little impact on these environmental factors (see ESM 2 for details on methods and results) and was considered as having negligible effects on growth and mortality of corals within the experiment.

The experiment was established at 8–10 m water depth on the outer reef slope where coral distribution was relatively continuous, where a high density of *A. planci* was observed (see ESM 1) and where live coral cover was 38.9% ± 4.0 SE at the beginning of the experiment. This is among the highest values of live coral cover observed on outer reef slopes in French Polynesia (Adjeroud et al. 2005, 2007; Penin et al. 2007). To determine the percent cover of live coral populations and other benthic organisms, the reef was sampled at the beginning of the experiment using 10 randomly placed 1-m^2 quadrats, and the composition of the substrate was recorded beneath 81 points defined by a grid of 10-cm mesh. *A. planci* densities were quantified once a month beginning in May using four replicate 200-m^2 transects (50 × 4 m) placed haphazardly along constant depth contours within the study area. The other major macro-corallivores in the study area were butterflyfishes (Chaetodontidae) (Penin et al. 2010), but their contribution to predation on corals was not considered because the rapid decline of coral populations appeared due entirely to predation by *A. planci*.

Population responses

Corals are colonial organisms that experience colony growth and mortality but also shrinkage through partial mortality, fragmentation, and fission. Demographic responses of corals including survival, growth, and fecundity are related to colony size rather than age, and colony size is often used as a measurement of colony fitness (Hughes and Connell 1987; Hall and Hughes 1996). Colony size was measured initially and at the end of the experiment, and used to calculate colony growth, a response variable in the experiment. Colony size was estimated by calculating the surface area based on geometric formulas corresponding to the general shape of colonies (Adjeroud et al. 2007). *Pocillopora* colonies were considered spherical, and surface areas (S) were calculated using the geometric formula $S = 4 \times \pi \times \left(\frac{L+l+h}{6}\right)^2$, with ($L$) being the maximum diameter, (l) the maximum perpendicular diameter and (h) the maximum height of live colony tissue. *Acropora*, and *Porites* colonies were considered cylinders with an ellipsoidal base, and surface areas were calculated using the geometric formula $S = \frac{\pi}{4} \times L \times l \times h$.

Treatment effects on population demographics were measured by comparing colony transition dynamics (i.e., proportion of corals showing growth, partial mortality, and death) and growth rates. The transition dynamics indicated the frequency of colonies showing growth versus decline (partial mortality, and colony death) within a population. As recruitment was not considered in this study, the mean colony growth rate of a population was a direct expression of the population growth in terms of the change in total live coral cover (positive for growth, negative for decline). To minimize size-related variability in coral demographics, adult colonies were chosen within a narrow size range (maximum diameter $10 \le L \le 20$ cm), and the relative growth of colonies $\left(rG = \frac{S_{\text{final}}}{S_{\text{initial}}}\right)$ is reported. Colonies with positive growth had an $rG > 1$, while colonies that shrank had an $rG < 1$. Relative growth of dead colonies was zero as no live surface was left at the end of the experiment ($S_{\text{final}} = 0$). Population growth or decline was characterized by changes in *mean rG* values. Population decline rate (Dr) was expressed as a percent and calculated as the difference between *mean rG* and 1 (the no-surface-change threshold) multiplied by 100.

Taxa susceptibility to predation

The susceptibility to predation by *A. planci* of different coral taxa was examined within the unmanipulated controls by comparing predation frequency and intensity using transition dynamics and the *mean rG* values, respectively. To test which coral species *A. planci* preferred, Ivlev's electivity index calculated as $E_i = \frac{r_i - p_i}{r_i + p_i}$ was used. For this equation, r_i is proportion of food i consumed and p_i is proportion of food i in the environment. Here, $r_i = \frac{Dr_i}{\sum_i^n Dr_i}$ and p_i represents the contribution of species i to total live coral cover on study site at the beginning of the experiment (*A. globiceps* = 2.3%, *P. meandrina* = 13.0%, massive *Porites* spp. = 17.9%). E_i varies from -1 (avoidance) to $+1$ (important selectivity), via 0 (neutrality).

Statistical analyses

The relative growth of coral (rG) and transition dynamics (i.e., the relative abundance of colonies showing growth, partial mortality, and death) were used to quantify the demographic responses of focal corals to the experimental treatments. Under attack by COTS, the relative growth of corals was a measure of predation intensity, because it reflected the amount of coral killed by predators. Similarly, the transition dynamics was a measure of the frequency of predation on corals, as it quantified the proportion of colonies growing, shrinking, and dying within populations. To address the hypothesis that coral survivorship varied as a function of predation, presence of coral neighbours, and the taxon of the focal coral, Pearson's χ^2 test was used to compare frequencies of colonies among colony transitions (i.e., growth, partial mortality, and death). To test whether mean relative growth (*mean rG*) varied as a function of predation, presence of neighbouring corals, focal coral taxa, and their interaction, a three-way ANOVA was used in which caging, removal, and taxa were crossed fixed factors. When ANOVA was significant, Fisher's least significant differences (LSD) post hoc test was used to compare differences among individual treatments. To compare the susceptibility to predation among taxa, differences in predation frequency (measured by the transition dynamics) and intensity (quantified by the *mean rG* values) were tested for colonies in the unmanipulated control treatment (i.e., natural conditions). Predation frequency was compared using Pearson's χ^2 test on relative abundances of colonies among colony transitions. Predation intensity was tested using planned comparisons with Fisher's LSD test as a complement to a one-way ANOVA. To assess whether the two associational refuges, neighbouring coral density (quantified by dC) and physical sheltering (quantified by Si), influenced the intensity of COTS predation on focal corals, we compared *mean rG* of exposed corals (i.e., uncaged and partially caged colonies pooled, $n = 100$) in a one-way ANCOVA, in which taxon was a fixed factor, and dC and Si were random covariates. Once the influence of dC and Si on predation intensity was estimated, the relative importance of these variables in mediating the probability of predation was tested independently for each population by comparing mean values of dC and Si among colony transitions using one-way ANOVAs. These ANOVAs tested whether there were differences in neighbouring coral density and in physical sheltering among colonies showing growth, partial mortality, and death within each population. When ANOVA was significant, mean values of dC and Si were compared with Fisher's LSD post hoc test. Before ANOVAs, data were tested for normality and homoscedasticity and were $\log(x + 1)$ transformed when needed. All statistics were performed with $\alpha = 0.05$.

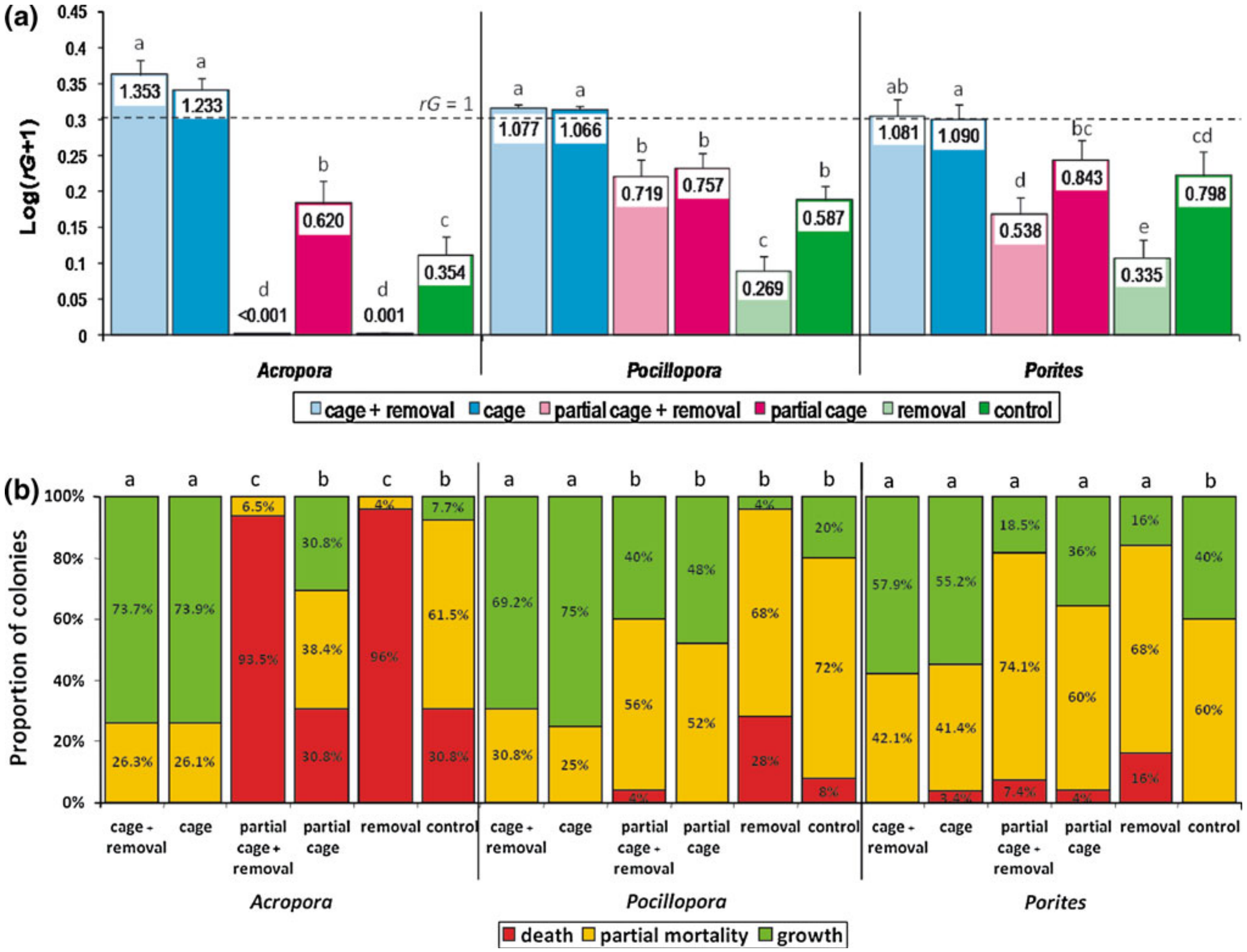

Fig. 2 Relative growth of colonies (*mean rG* +SE) after log($x + 1$) transformation (**a**) and colony transition dynamics (**b**) of taxa under different treatments ($n = 19$–31). *Horizontal dashed line* on plot (**a**) indicates the threshold of zero net growth $rG = 1$. Values on plot (**a**) indicate mean colony relative growth prior log($x + 1$) transformation, and *letters* on plots indicate statistically different groups within each taxon ($P < 0.05$). The relative growth (**a**) and the transition dynamics (**b**) are used to quantify, respectively, the intensity and the frequency of predation on corals within each treatment

Results

Acanthaster planci predation on corals

Predation by *A. planci* was intense during the study period when densities of the starfish reached 10.75 ± 2.21 SE ind.200 m^{-2} ($n = 4$, see ESM 1). The predator caused a 42.3% decline in the total live cover of all three focal coral taxa over the 100 days (average *rG* of colonies in the unmanipulated control treatment over the three taxa = 0.577 ± 0.069 SE, $n = 76$) and showed a strong preference for *Acropora* (Ivlev's electivity index, $E = 0.91$), an intermediate selectivity for *Pocillopora* ($E = 0.55$), and neutral preference relative to its abundance for *Porites* ($E = -\ 0.06$). The feeding preference of the sea star resulted in a different frequency (χ^2, $P = 0.003$) and intensity (one-way ANOVA, $F_{2,76} = 4.45$, $P = 0.015$) of predation on the three coral taxa (refer to control colonies in Fig. 2): χ^2, $P = 0.071$ between *Acropora* and *Pocillopora*, $P = 0.001$ between *Acropora* and *Porites*, $P = 0.140$ between *Pocillopora* and *Porites*; Fisher's, $P = 0.048$ between *Acropora* and *Pocillopora*, $P = 0.005$ between *Acropora* and *Porites*, $P = 0.378$ between *Pocillopora* and *Porites*. There was a relatively severe decline in live coral cover for *Acropora* ($Dr = 64.6\%$), intermediate decline for *Pocillopora* ($Dr = 41.3\%$) and relatively low decline for *Porites* ($Dr = 20.2\%$).

The survival and growth of focal corals outside of cages were heavily influenced by *A. planci* predation, especially in treatments in which neighbouring corals were removed (Fig. 2). Colonies without predation (within cages) grew whether their neighbours were removed or not while colonies exposed to predators (no cages and cage controls) declined in *mean rG*. There was a statistically significant interaction of predator-exclusion and neighbour-removal treatments (three-way ANOVA, $F_{2,450} = 12.34, P < 0.001$) because removal of surrounding corals had no effect within cages but accelerated the decline of populations when exposed to *A. planci* predation (Fig. 2). This process was particularly intense for the most preferred prey *Acropora* which was always preyed upon when neighbours were removed and whose population was driven almost to extinction (decline rate $Dr \geq 99.9\%$, vs. 64.6% when neighbouring colonies present). For the few *Acropora* that were attacked but survived, those survivors that had neighbours removed ($rG = 0.012 \pm 0.011$, $n = 3$) shrank much more than those for which neighbours were not removed ($rG = 0.458 \pm 0.060$; $n = 26$; Fisher's, $P = 0.010$). Neighbours thus had a positive effect on *Acropora* by mediating the impact of *A. planci*, resulting in lower frequency and intensity of predation on colonies.

The removal of neighbouring corals surrounding *Pocillopora* and *Porites* colonies showed results that were qualitatively similar to those observed for *Acropora*, although the responses were not all statistically significant (Fig. 2). For *Pocillopora*, colonies with neighbours removed tended to be attacked at higher rates than those that had neighbours; however, the survivors without neighbours were not significantly smaller ($rG = 0.382 \pm 0.056$; $n = 31$) than those with neighbours ($rG = 0.466 \pm 0.041$; $n = 31$; Fisher's, $P = 0.156$). The same pattern in attack frequency and relative growth was observed for *Porites* ($rG = 0.332 \pm 0.052$ vs. 0.457 ± 0.068; $n = 37$ and 30, respectively; Fisher's, $P = 0.167$).

Role of habitat characteristics in predation process

Close neighbour coral density (as quantified by *dC*) and habitat complexity (quantified by *Si*) had a significant influence on relative growth and transition dynamics of corals exposed to *A. planci* predation (Table 2). For *Acropora*, both neighbour density and physical sheltering were key for survival (Table 3). Colonies that grew and suffered partial mortality had higher levels of *dC* (higher abundance of neighbouring colonies) and *Si* (more complex habitat) compared with colonies that died (Fig. 3). As *Acropora* was the most preferred prey, the availability of alternative prey colonies was probably not sufficient to alter the predator's choice. However, physical refuges created by the presence of these neighbours apparently reduced predation frequency and intensity on *Acropora* (see Figs. 1, 2). For *Pocillopora*, the presence of neighbouring coral density had a positive effect on colony survival but habitat complexity did not (Table 3, Fig. 3). *Pocillopora* survival was thus enhanced by the availability of alternative prey in the close vicinity, resulting in an inverse density dependence of predation potentially associated with the alteration of predator's choice through dilution. *Porites* showed no significant differences among colony transitions, neither with density nor with sheltering index (Table 3).

Table 2 ANCOVA table

Source	*df*	SS	MS	*F*	*P*
Taxa (T)	2	0.938	0.469	30.582	<0.0001
dC	1	0.298	0.298	19.411	<0.0001
Si	1	0.011	0.011	0.713	0.3991
T × *dC*	2	0.169	0.085	5.519	0.0044
T × *Si*	2	0.107	0.053	3.479	0.0321
dC × *Si*	1	0.006	0.006	0.417	0.5191
T × *dC* × *Si*	2	0.107	0.053	3.488	0.0318
Residual	298	4.569	0.015		

ANCOVA table showing results of the effect of neighbouring coral density (*dC*, covariable) and sheltering index (*Si*, covariable) on the relative growth ($\log(x + 1)$ transformed data) of colonies of different coral taxa (T, fixed factor) that were exposed to predation by *A. planci*

Degrees of freedom (*df*), sum of squares (*SS*), mean square (*MS*), *F*-statistics (*F*), and *P* value (*P*)

Table 3 ANOVA table

Source	*df*	SS	MS	*F*	*P*
Acropora ($n = 108$)					
dC	2	33.474	16.737	26.212	<0.0001
Si	2	5717.665	2858.832	17.963	<0.0001
Pocillopora ($n = 100$)					
dC	2	8.873	4.437	3.779	0.0263
Si	2	74.614	37.307	0.187	0.8301
Porites ($n = 102$)					
dC	2	1.402	0.701	0.724	0.4873
Si	2	941.268	470.634	1.986	0.1427

Corresponding one-way ANOVA table for within taxa differences in *dC* and *Si* among colony transitions (growth, partial mortality, and death)

Degrees of freedom (*df*), sum of squares (*SS*), mean square (*MS*), *F*-statistics (*F*), and *P* value (*P*)

Discussion

Acanthaster planci predation on corals

Densities of *A. planci* (maximum = 53,750 ind.km^{-2}, June 2008) were among the highest reported in the literature and were much higher than the estimated maximum sustainable density for coral communities of 1,000 ind.km^{-2} (Keesing and Lucas 1992). The outbreak of the predator induced dramatic population declines that

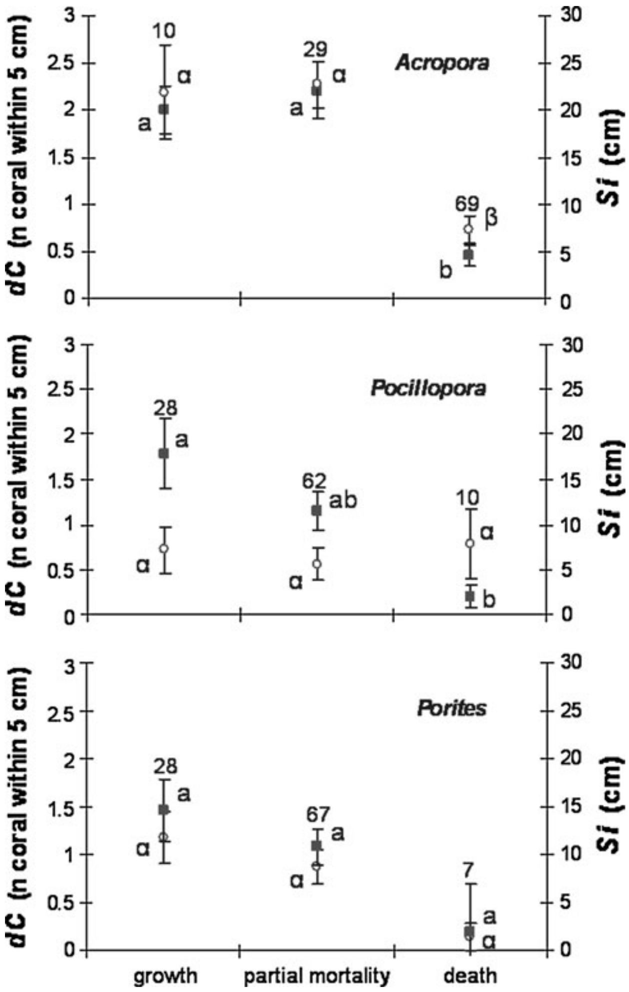

Fig. 3 Density of neighbouring corals (*dC*, *filled square*) and sheltering index (*Si*, *open circle*) of colonies exposed to predators for each colony transition (growth, partial mortality, death) (mean ±SE). Impact of *A. planci* predation increases from *left* to *right* on the *x*-axis and is null for growing colonies, intermediate for colonies showing partial mortality, and maximal for dying ones. *Numbers* on plots indicate sample sizes; *letters* on plots (**a/b** for *dC*, **α/β** for *Si*) indicate statistically different groups within populations (one-way ANOVA followed by Fisher's post hoc tests if significant, $P < 0.05$)

varied among the three focal coral taxa. Declines in coral density and live coral cover were severe for *Acropora*, intermediate for *Pocillopora*, and only moderate for *Porites*. The pattern of decline was positively related to feeding preferences of *A. planci*, as measured in aquaria (De'ath and Moran 1998; Pratchett 2007) and in the field in French Polynesia and other regions (Faure 1989; Rotjan and Lewis 2008; Pratchett et al. 2009).

The outcome of predation in terms of coral survival and growth was strongly influenced by the presence of surrounding corals, suggesting that association among neighbouring corals deterred predation by *A. planci*. However, the specific type of associational refuge varied among the three coral taxa and appeared related to the level of predation that each taxon experienced. *Porites*, the least preferred prey, experienced relatively low predation and derived no benefit from surrounding corals. However, *Porites* may benefit from associations at higher predation intensities, where positive interactions among potentially competing organisms theoretically become more important (Bertness and Callaway 1994; Hacker and Gaines 1997; Bruno et al. 2003). *Pocillopora*, the moderately preferred prey, benefited simply from the presence and increased density of surrounding corals without the provision of physical sheltering, thereby gaining an associational refuge apparently through dilution created by its neighbours. The most preferred prey, *Acropora*, escaped attacks by *A. planci* in structural refuges created by larger neighbours (i.e., potential competitors), which probably deterred detection (fewer colonies preyed upon) and access (lower proportional mortality) by COTS. Therefore, under intense predation, *Acropora* gained an advantage when it was competing with bigger corals because they provided refuge from *A. planci* (see Fig. 1).

Differences in the mechanisms by which surrounding corals provided refuge appeared to vary with the intensity of predation, a relationship that is consistent with those observed by Milchunas and Noy-Meir (2002) for terrestrial plants under varying grazing pressures. They found that associational avoidance of grazers through alteration of the grazers's choice (e.g., dilution) is usually observed in prey that are subject to moderate grazing pressure, while prey that are grazed intensely often use avoidance strategies that rely on structural or other physical refuges. A similar pattern was observed with corals preyed upon by *A. planci*, where moderately preferred prey, *Pocillopora*, escaped predation through dilution of predation pressure when surrounded by a higher density of neighbours, whereas the preferred prey, *Acropora*, only survived in structural refuges provided by bigger neighbours. Because corals are major ecosystem engineers that form reef habitat (Jones et al. 1997; Stachowicz 2001; Crain and Bertness 2006), the availability of structural or other physical refuges on reefs is often related to the density and size of resident coral colonies (see Fig. 1).

Associational refuges that generated indirect positive interactions (IPIs) among neighbouring corals in the form of structural refuges and dilution were effective in reducing consumer pressure on the most preferred taxa, *Acropora* and *Pocillopora*, during the COTS outbreak. In contrast, *Porites* the inferior competitor in this study was less preyed upon by *A. planci* than its competitors, resulting in its dominance in coral assemblages despite its relative low competitive ability. This form of regulation of superior competitors among prey populations constitutes a different type of IPI generated by predation. Predator–prey interactions are dynamic, such that their development, form, and outcome depend at least in part on their duration. As *A. planci* preys on most coral species (De'ath and Moran 1998; Pratchett 2007), its impact on a given reef is a function of the density of the predator, the duration of the outbreak, and prey preference (Keesing and Lucas 1992; Rotjan and Lewis 2008). If relatively high *A. planci* densities persist during an outbreak, predation on less preferred taxa may increase progressively, especially if preferred prey are extirpated. Sequential extirpation of prey is a common phenomenon (e.g., Kvitek et al. 1992). In contrast, if predator density declines before predators switch to less preferred prey, populations of the less preferred prey remain and may dominate the community. Such has been the case for *Porites* during a previous *A. planci* outbreak in Moorea (Faure 1989), as well as outbreaks in other regions (e.g., Rotjan and Lewis 2008; Pratchett et al. 2009). In fact, many coral communities in the Indo-Pacific are now dominated by *Porites*, implying that historical outbreaks of *A. planci* may have had an important influence on the composition of the coral communities that we observe today. Predators that act to regulate populations of superior competitors and maintain prey diversity are usually called keystone predators (Paine 1974; Hacker and Gaines 1997). However, compared with other corals, massive *Porites* shows strong resistance to a wide range of disturbances in French Polynesia and other regions (see Adjeroud et al. 2009), and *A. planci* outbreak reveals yet another disturbance for which *Porites* is resistant. IPIs may play a critical role in coral community dynamics by enhancing the survival of various species, especially in communities where competition (Connell et al. 2004) and predation (Rotjan and Lewis 2008) play major roles in regulating coral populations.

Positive versus negative interactions in community regulation

Based on a compilation of extensive data from field studies, Menge and Sutherland (1987) proposed a conceptual model of the relative importance of predation, competition, and abiotic stress in community regulation along gradients of abiotic stress and recruitment (Fig. 4). This model provided the conceptual foundation for developing ideas about positive interactions and their role in mitigating the ecological impacts of abiotic stress, competition, and predation (Bertness and Callaway 1994; Callaway and Walker 1997; Hacker and Gaines 1997; Bruno et al. 2003; Michalet et al. 2006). More recently, Crain and Bertness (2006) used Menge and Sutherland's (1987) framework as a basis for conceptualizing the relative importance of ecosystem engineers in mediating the effects of predation, competition, and abiotic stress. The major mechanism entails the creation or modification of physical habitats by the engineer species that act as structural refuges from abiotic or biotic stresses. In our study system of three engineer taxa, each possessing different susceptibilities to predation and competition (respectively, high and low for *Acropora*, low and high for *Porites*, and intermediate to both for *Pocillopora*), different types of IPIs emerged from multiple regulation pathways during a predator outbreak. The various IPIs modulated the level of predation upon each population. These results extend our understanding within the scope of the role of both ecosystem engineering and IPIs in regulation processes and illustrate the high level of complexity in ecological interactions when dealing with species playing key functional roles in communities. This study combines the elements of the prior models with the results of the present experiments, as well as the findings of published studies from other community types in a new conceptual model that describes the mechanisms through which competition, predation, and physical refuge can provide positive attributes that mediate the impact of predation, competition, and abiotic stress (Fig. 4).

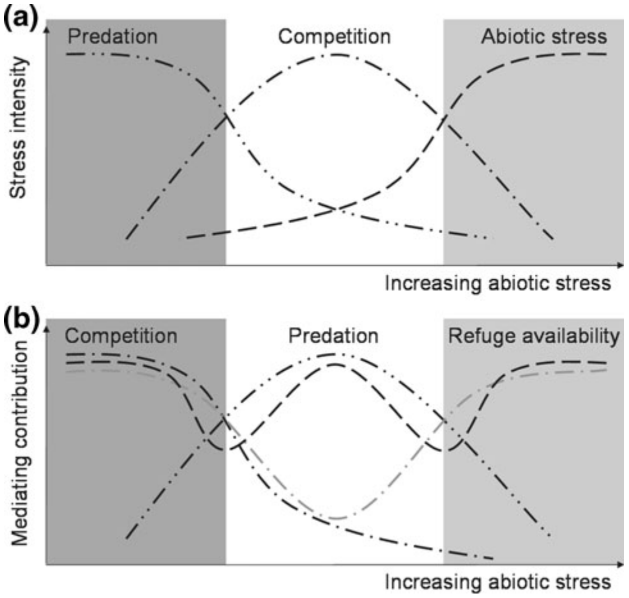

Fig. 4 **a** Conceptual model illustrating the relative importance of predation (*dashed line with two dots*), competition (*dashed line with one dot*), and abiotic stress (*dashed line*) on community regulation across a gradient of abiotic stress, adapted from Menge and Sutherland (1987). **b** A corresponding model showing the relative contribution of competition, predation, and physical refuge as processes mediating the effects of each of the Menge and Sutherland environmental stressors. *X*-axis depicts maximum predation to the *left* (mediated by competition and refuge availability), maximum competition in the *centre* (mediated by predation and refuge availability), and maximum abiotic stress on *right* (mediated by refuge availability). *Grey line* on plot **b** indicates the contribution of competing ecosystem engineers in terms of the provision of both refuge availability and the positive effects of competition. See text for more details on mechanisms and link to results from this study

A positive contribution from predation is observed within communities undergoing intense competition, specifically through the preferential regulation of superior competitor populations by predators (Paine 1974; Cox 1986; Hacker and Gaines 1997). A similar indirect positive interaction (IPI) caused by the predator was observed in this study for the less competitive taxon *Porites* that was less impacted by *A. planci* than the better competitors *Acropora* and *Pocillopora*. As competition is a relatively slow process that regulates populations on longer time scales than predation (Gurevitch et al. 2000; Chesson and Kuang 2008), and as corals are sessile organisms that grow slowly and live a long time, predators can substantially interfere with competitive interactions among corals, and through their choice of prey, can favour inferior competitors (Cox 1986; Faure 1989; Pratchett et al. 2009). Positive effects from competition occur during intense predation events through associational refuges among competitors, such as the dilution effect that lowers predation probability on focal organisms in an inversely density-dependent way (Gurevitch et al. 2000; Milchunas and Noy-Meir 2002; Sandin and Pacala 2005). A similar IPI was observed for *Pocillopora* in the present experiment because competing corals were alternative prey for predators, thus lowering predation probability on colonies. The positive influence of structural refuges generally increases with intensity of predation (Grabowski et al. 2008; Levenbach 2008, 2009), competition (Crain and Bertness 2006), and abiotic stress (Michalet et al. 2006; Altieri et al. 2007). However, the function of refuges differs with the type and intensity of stress (Bertness and Callaway 1994; Callaway and Walker 1997; Milchunas and Noy-Meir 2002). In Moorea, *Acropora* colonies escaped intense predation within structural refuges provided by surrounding colonies because the competitors engineered complex habitat, which probably precluded detection and access by predators (Grabowski et al. 2008; Schmitt et al. 2009). Because corals perform multiple ecological functions in reef communities, including engineering habitat, competing for resources, and providing prey for predators, they help regulate community dynamics through multiple types of interactions, the form and function of which are influenced by environmental gradients. The composite role of ecosystem engineers probably contributes to the high level of complexity of species interactions observed in many ecosystems.

The IPI model is generally valid for sessile communities undergoing sporadic or intense perturbations because predation, competition, and abiotic stress are key processes in community regulation in many ecosystems. However, testing the ubiquity of this model quantitatively in various systems would be difficult, as it presents asymmetric distortions in multiple dimensions because regulatory processes are highly influenced by many intrinsic and extrinsic factors (Menge and Sutherland 1987). Such factors include density, species characteristics, ecological functions, habitat features, and effectiveness of refuges, spatial and temporal scales, and the duration, intensity, and history of external stresses (e.g., Gurevitch et al. 2000; Milchunas and Noy-Meir 2002; Bruno et al. 2003). IPIs may play a key role in community resilience and recovery because they prevent predators from eradicating prey populations, prevent competitive exclusion of relative weak species, provide refuges from abiotic stress and thus, enhance resistance and plasticity of natural ecosystems under intense stresses.

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