



NOTE

Corallivory on small *Porites* colonies increases with coral colony size but is reduced by macroalgal associational refuge

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Received: 19 January 2022 / Accepted: 30 August 2023 / Published online: 25 September 2023
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Abstract Numerous tropical macroalgae provide associational refuge to other benthic organisms, presumably due to their physical structure and/or production of chemical metabolites. One feature determining their effectiveness as an associational refuge is likely to be the size of the organism benefitting from the refuge. Using a manipulative experiment in the back reef of Moorea, French Polynesia, we tested if the macroalga *Turbinaria ornata* provided an associational refuge from fish corallivores for small colonies of massive *Porites* spp., and how this differed with colony size (20–100 mm diameter). Tissue loss through corallivory increased with colony size but was ~72% less for *Porites* colonies associated with *T. ornata* versus colonies separated from this macroalga, while dense macroalgae beds on contemporary reefs negatively impact the recruitment, growth and survival of corals, small colonies of *Porites* appear to benefit, through reduced corallivory, by associating with the macroalga *Turbinaria*. This association may come at a cost (e.g., reduced growth) and should be the focus of future research.

Keywords Macroalgae · Corallivory · Associational refuge · Competition · *Turbinaria ornata*

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00338-023-02424-1>.

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Introduction

On many Indo-Pacific reefs, an increased frequency and magnitude of disturbances has led to decreases in coral abundance and increases in cover of macroalgae (Bruno et al. 2007; Hughes et al. 2017). Macroalgae can be strong competitors for space when interacting with corals (Hay 1986; Box & Mumby 2007; Clements et al. 2018), and the outcomes of such interactions contribute to phase shifts favoring macroalgal dominance (Brown et al. 2020). At high abundances, macroalgae can inhibit settlement of coral larvae through pre-emption of benthic space (Birrell et al. 2005), reduce coral recruitment (Bulleri et al. 2018), and depress the growth of corals (Venera-Ponton et al. 2011). These effects are mediated through indirect competitive effects such as shading (McCook et al. 2001), and direct effects such as overgrowth (Jorissen et al. 2016), chemical defense, and physical abrasion (Rasher and Hay 2010).

In addition to their negative effects, many tropical macroalgae may provide a benefit to other taxa through the provision of associational refugia from consumers due to their physical structure and/or chemical defenses (e.g., algae: Pfister and Hay 1988; Bittick et al. 2010; Loffler et al. 2015; motile invertebrates: Duffy and Hay 1994; scleractinian corals: Bulleri et al. 2013; Clements and Hay 2015). Associational refuges are created when taxa exploit attributes of another species to acquire protection from predators and disturbance, which can increase species richness (Hay 1986) and modify community structure (Stachowicz 2001). Tropical canopy-forming macroalgae, such as *Sargassum* and *Turbinaria*, create opportunities for associational refuges from fish and invertebrate herbivores that find them unpalatable (Hay 1986; Duffy and Hay 1990; 1994), or through their physical structure reducing detection and predation on taxa with which they are

associated (Bulleri et al. 2013). The relative effect of macroalgae on associated taxa is likely conditional because the direction and magnitude of the effect are dependent on environmental conditions (Bronstein 1994), or the demographic attributes (e.g., life stage, body size; Hacker and Steneck 1990) of the taxon hypothesized to benefit from the association, as well as the taxon providing the service. For corals, the presence and strength of the associational refuge provided by macroalgae may vary with colony size if, for example, their effects are attenuated when colonies are taller than the macroalgal thalli adjacent to which they are growing.

Corallivory by fishes is an important process structuring coral communities (Rice et al. 2019) and can lead to partial and full mortality of coral colonies (Roff et al. 2011). However, small coral colonies have a higher chance of dying from corallivory than larger colonies, because small colonies are less able to withstand partial mortality (Hughes and Jackson 1985; Bythell et al. 1993; Meesters et al. 1996). A reduction in the likelihood of being consumed by corallivores would therefore be especially beneficial to small corals, with such effects potentially mediated through associational refuges. While corals can exploit associational refuges with macroalgae to reduce their susceptibility to corallivory (Bulleri et al. 2013), it is unknown whether such protection varies with coral colony size (Bulleri et al. 2013; Vieira et al. 2016). Here, we describe an experiment in which colonies of massive *Porites* spp. (a combination of *P. lutea* and *P. lobata*) placed adjacent to *Turbinaria* (i.e., in the center of a 5-cm radius circle of *Turbinaria* thalli) versus in isolation, were used to test the effect of *Turbinaria* in providing an associational refuge as a function of coral colony size. Two hypotheses were tested: (1) *Turbinaria* reduces fish

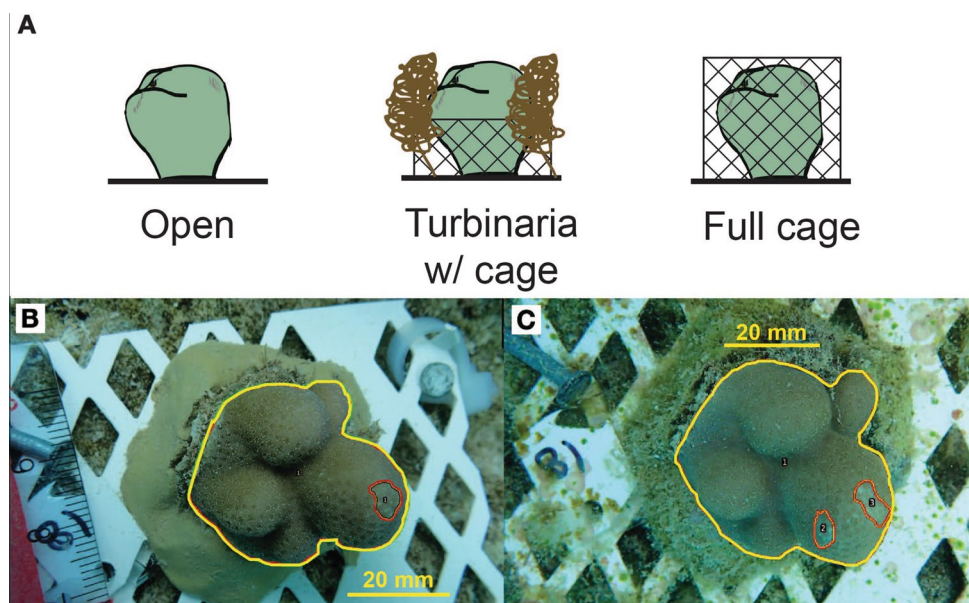
corallivory on massive *Porites* spp., and (2) this effect was dependent on coral colony size.

Materials and methods

This study was conducted during May 2019 in the back reef on the north shore of Moorea, French Polynesia (17° 28.85' N, 149° 50.36' W), where *Turbinaria* has increased in abundance over the last 15 yrs, to cover ~14% of hard substrata in 2019 (Carpenter 2020). Colonies of massive *Porites* spp. (hereafter, *Porites*) were haphazardly collected from atop dead coral bommies in the back reef at 2–3 m depth, and only colonies free of visual signs of previous corallivory were selected. Sampled colonies varied from 20 to 100 mm diameter, and this size range was selected to implement a test of colony size on the outcome of exploiting an associational refuge with macroalgae. These colonies had planar areas of 519–7,452 mm² and were likely 3–8 yrs old based on average growth rates for this genus (Pratchett et al. 2015). Colonies were fixed to 15 × 15 cm plastic bases with marine epoxy (Z-spar Splash Zone Compound, A788) and allowed to recover for 12 h in flowing seawater. *Porites* colonies were assigned to treatment groups (described below) and placed at least 2-m apart on dead portions of coral bommies at 3 m depth. Colonies attached to their plastic bases were fixed to the bommies using masonry nails. After the experiment was completed, the experimental apparatus was removed from the reef and the *Porites* colonies were reattached to the reef at the collection site.

To test the effects of *Turbinaria* on fish corallivory, cages (2 cm mesh size, Fig. 1A) were used to exclude fish corallivores from colonies of *Porites* that were placed either in

Fig. 1 A diagram of cage treatments. B, C Images of a massive *Porites* spp. with outlines drawn around colony area in yellow and damaged tissue in red (i.e., corallivory) at initial (B) and final (C) time-points



the presence of, or absence of, *Turbinaria*. Three treatments were applied: (1) an open, cageless treatment to test for corallivory unimpeded by a cage or *Turbinaria*, (2) a *Turbinaria* treatment in which semi-enclosed cages (12 cm diameter, 7.5 cm height, open top) provided access to the coral by fish corallivores through the open top, with 6 macroalgal thalli (15 cm tall) located outside of the cage, where they were unable to physically contact the coral but created an associational refuge, and (3) a full cage (12 cm diameter, 7.5 cm height, with top) that excluded corallivorous fishes (see below) without the presence of *Turbinaria*. Ten replicates (i.e., each with one *Porites* colony) were constructed for each treatment (30 corals total), and *Turbinaria* thalli for the associational refuge treatment were collected from the site in which the experiment was conducted.

Tissue damage was quantified using macro images recorded with natural lighting using an Olympus TG-3 camera, and the total area of tissue damage on each colony was compared among treatment groups using colony area as a covariate. Photographs taken at the end of the 24-day experiment (28 May) were compared to those taken at the start of the experiment (4 May) to determine the change in coral area damaged by corallivory. Photographs were taken perpendicular to each colony, calibrated with a ruler in the frame, and analyzed using Fiji software (Schindelin et al. 2012) (Fig. 1B, C). The planar area of each coral was measured by tracing the outline of the perimeter of the colony, and the area of tissue damaged with scars of corallivores (sensu Cameron and Edmunds 2014) was measured by tracing the outline of the affected areas. The origin of the damage was determined by comparing the type of damage with that created by confirmed examples of fish corallivory on colonies of *Porites* that were growing on adjacent bommies and in the cageless treatment. In the back reef of Moorea, *Chaetodon citrinellus*, *C. vagabundus* and *C. lunulatus* were the most common fish corallivores on *Porites*, with bite rates on undisturbed large colonies (100–300 cm diameter, ~10 times larger than the colonies used in this experiment) with a median of 8.5 ± 7.7 bites min^{-1} (\pm SE, $n=37$) (G. Srednick, unpublished data for 2019).

A linear model (LM) was used to test the effect of *Turbinaria* and coral colony size on the progression of tissue damage over 24 days. In this analysis, we used planar area as a measure of coral size instead of diameter because diameter does not provide adequate resolution of the 2-dimensional variation in planar area across colonies. The change in the area of damaged tissue from the initial (day 0) to final (day 24) was the response variable, and treatment (categorical) and colony size (continuous) were the predictor variables. The LM was fitted using a Gaussian distribution and the ‘stat’ base package (RStudio Team 2022) in R. Parametric assumptions were assessed by visual inspection of residual plots for normality, and the homogeneity of variances of

the model was evaluated using Levene’s test (Figure S1) using the ‘DHARMA’ package in R (Hartig 2022). Colony planar area (mm^2) was square-root transformed to satisfy parametric assumptions. All analyses were performed in the R statistical computing environment v 4.0.3 (R Core Team 2022) with the additional packages: ‘ggsignif’ (Ahlmann-Eltze and Patil 2021) and ‘tidyverse’ (Wickham et al. 2019).

Results and discussion

Our results suggest that the area of tissue damaged by fish corallivory on *Porites* increases with colony size but is reduced when colonies are associated with *Turbinaria*. In the 24-day experiment, corallivory increased with colony size ($F_{1,26}=4.68$; $p=0.04$, Fig. 2) and was greatest in fully exposed colonies (change in tissue damage: 165 ± 31 mm^2 , mean \pm SE). Corallivory was reduced by ~72% on *Porites* colonies in associated with *Turbinaria* (46 ± 41 mm^2 mean tissue damage; Treatment: $F_{2,27}=11.58$, $p<0.001$, Fig. 2). The effects of corallivory were statistically indistinguishable between *Porites* colonies associated with *Turbinaria* and with the full-cage treatments (Tukey’s HSD; $p=0.13$). Corallivory on the experimental *Porites* colonies generally increased with colony size (i.e., the slope of the linear relationship between the tissue lost to corallivory and coral colony area = 3.18, $p=0.009$; Fig. 2), with the effect being consistent among treatments (Treatment \times Area interaction: $F_{2,24}=2.03$; $p=0.15$, Fig. 2).

The present finding that small *Porites* colonies (<3000 mm^2) experienced lower rates of corallivory when associated with *Turbinaria* is consistent with a previous study (Bulleri et al. 2013). The linear relationships of corallivory

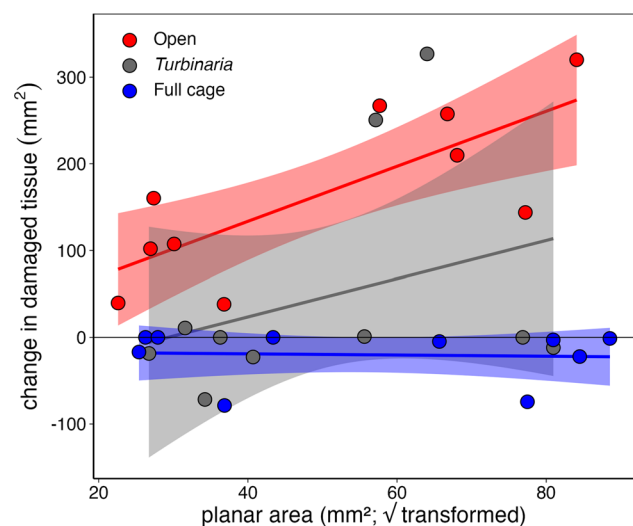


Fig. 2 Variation in corallivory among treatments, with colony planar area as covariate. $N=10$ cage treatment $^{-1}$; 30 total

on colony area indicate that a *Porites* colony 2000 mm² in area (45 on a square-root transformed scale; Fig. 2) would accrue 150 mm² of corallivory damage over 24 days when isolated from *Turbinaria*, but only 34 mm² of corallivory damage when associated with *Turbinaria*, a reduction of 77%. While this difference in corallivory between colonies placed adjacent to, versus isolated from, *Turbinaria* is consistent across the range of colony sizes examined (i.e., regression lines between colony size and corallivory for *Turbinaria* and open treatments have equal slopes), the smallest corals (i.e., ~600 mm² area) almost fully avoided the effects of corallivory when adjacent to *Turbinaria*, suggesting that small coral colonies may benefit more than larger colonies from associating with *Turbinaria*. We did not find an interaction between colony area and the presence of associational refuge that would suggest treatment-specific size dependency of corallivory. Nonetheless, the increased refuge from corallivory provided by *Turbinaria* to small, relatively young corals may partly counteract the high risks of mortality in small size classes of corals (i.e., <600 mm² area) (Hughes and Jackson 1985; Meesters et al. 1996). Consequently, the relative value of the protection afforded by close proximity to *Turbinaria* would be expected to be greatest in small versus large colonies within the size range we studied (i.e., 500–7400 mm² area).

A limitation of our experiment is the absence of a cage control treatment that would experimentally evaluate the effects of the cage alone in mediating corallivory on the corals. We rationalized the absence of cage controls by the near-complete encircling of *Turbinaria* thalli applied to the cages in the associational refuge treatment. Nevertheless, without a cage control we cannot be certain that the effects we report are a result of an associational refuge with the algae or the cage, although they demonstrate that the combination of the two confers protection from corallivory to corals. Together with examples of corals with scars of corallivory in open locations but not when crowded by algae (G Srednick, *personal observation*), our experimental evidence is consistent with the associational refuge hypothesis we posit to account for our results.

Consideration of the nuances in the outcomes of competition between taxa (e.g., coral vs. macroalgae) can have value in understanding coral community trajectories on coral reefs (Rice et al. 2019). It is possible that the protection from corallivory provided to corals by *Turbinaria* could be outweighed by their negative effects of shading and physical abrasion that can reduce coral growth rate and survival (River & Edmunds 2001; Bulleri et al. 2013; Clements et al. 2018; Clements & Hay 2023). Such effects (i.e., shading) might be greater when corals are smaller, when the benefit from associational refuge is greatest but could be alleviated as corals grow large enough to protrude out of macroalgal canopy. The aforementioned effects (i.e.,

colony size-dependent benefits from associational refuges) might be another factor of value in understanding the competitive relationships between corals and macroalgae and the factors mediating phase changes between coral-dominated and macroalgal-dominated reefs.

Acknowledgements This research was funded by the U.S. National Science Foundation (OCE 14-15268 to P.J.E.) in part through the Moorea Coral Reef LTER (OCE 16-37396). Research was completed under permits issued by the French Polynesian Government (Délégation à la Recherche) and the Haut-Commissariat de la République en Polynésie Française (Protocole d'Accueil 2019–2020). We thank the staff of the Richard B. Gump South Pacific Research Station, S. Ginther and S. Doo for field support, and two anonymous reviewers who provided comments that improved an earlier draft. This is contribution number 381 of the CSUN Marine Biology Program.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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