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ARTICLE

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Friend of the dead: Zoanthids enhance the persistence of dead coral reef framework under high consumer pressure

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Abstract

Consumers can play critical roles in ecosystem resilience by modifying community resistance and recovery rates. In coral reefs, grazers can increase reef resilience by controlling algae and maintaining open space for coral recruitment, but can also erode the reef framework critical for coral recovery. Here we examine the context-dependent effects of herbivores on reef persistence in Caribbean Panamá. Using a series of lab and field experiments, we found that the erosional effects of the herbivorous reef urchin (*Echinometra viridis*) were 2 orders of magnitude greater on dead corals than live corals, and surveys across multiple similarly overfished reefs revealed a positive relationship between urchin densities and percent cover of bare dead coral with urchin densities exceeding 150 m^{-2} in some reefs. However, we observed that a mat-forming zoanthid (*Zoanthus pulchellus*), found exclusively on dead corals, had an inverse spatial relationship with urchins. Through a series of field experiments, we found that zoanthid overgrowth repelled urchins, increased dead coral persistence, and decreased erosion of dead corals making up the reef framework by more than 50% over a 22-month period. Our findings reveal that zoanthids can provide associational refuge to dead corals by enhancing their persistence under high urchin grazing pressure. We suggest that secondary space-holders, such as zoanthids, may play increasingly important functional roles in degraded reef systems by shielding coral skeletons from external bioeroders. Moreover, the Stress Gradient Hypothesis, which predicts that the importance of positive interactions such as associational refuges increases with consumer pressure, extends to dead foundation species such as coral skeletons crucial for ecosystem recovery.

KEYWORDS

associational effects, associational refuge, bioerosion, consumer, facilitation, foundation species, indirect effect, positive interaction, urchin

INTRODUCTION

Consumers are increasingly recognized for providing pivotal functions that promote ecosystem recovery, especially those characterized by foundation species (Dayton, 1972). For example, consumers can pollinate and facilitate primary producers by aiding in dispersal and establishment following disturbance (Brodie & Aslan, 2012), and key herbivores have been associated with reversing phase shifts (e.g., fleshy algae to coral reefs) and increasing native plant diversity (Edmunds & Carpenter, 2001; Ratajczak et al., 2022). However, consumer effects on foundation species' recovery can switch from positive to negative at high densities (Altieri et al., 2012; Mapstone et al., 2007; Silliman et al., 2013). For example, while low densities of corallivorous crown-of-thorns sea stars can increase coral diversity by consuming competitively dominant corals (De'ath & Moran, 1998), at high densities, these echinoderms can decimate reefs with detrimental effects on associated communities (Leray et al., 2012). Thus, factors that amplify consumer densities can initiate a switch to negative consumer effects on ecosystem recovery by pushing consumption to unsustainable levels (Silliman et al., 2013).

As consumer pressure increases, ecological theory predicts positive interactions that ameliorate negative consumer effects should become more important (Bertness & Callaway, 1994; He et al., 2013). Such positive interactions include "associational refuges," in which a species facilitates a beneficiary species by decreasing its susceptibility to predation/parasitism by a third species (Hay, 1986; Underwood et al., 2014). Examples often involve foundation species as beneficiaries, such as when spiny cacti protect neighboring plants from cattle grazing (Rebollo et al., 2002) and when noxious seaweeds deter herbivores from grazing palatable seaweed neighbors (Hay, 1986). Tests for associational refuges have only considered live organisms as beneficiaries; however, it has been suggested that dead foundation species that provide stable substratum, nutrient resources, and habitat for conspecifics and associated communities are also vulnerable to consumers that may directly or indirectly enhance their degradation rates, and so may also benefit from associational refuges (Saldaña, Angelini, et al., 2024).

Dead corals are the foundation of living reefs. They represent an important aspect of reef resilience as substratum for coral settlement and growth (Hughes et al., 2010; Kuffner & Toth, 2016; Wulff, 1984; Yadav et al., 2016) and habitat for associated species (Adam et al., 2014; Nelson et al., 2016; Stella et al., 2022). These include consumers, such as urchins and fishes, that consume algae and maintain bare space for coral settlement (Hughes et al., 2010; Mumby & Steneck, 2008; Schmitt et al., 2019). Yet, excessive grazing by herbivores can also erode the reef substratum and reduce the complexity and integrity of the dead coral framework (Glynn & Colgan, 1992; Molina-Hernández et al., 2022). Excessive grazing may be triggered by the overfishing of predatory species such as triggerfish, hogfish, and lobsters that results in top-down release of herbivores, such as sea urchins (Graham et al., 2017; McClanahan & Shafir, 1990; O'Leary & McClanahan, 2010). The negative erosive effects of high densities of herbivores can outweigh their positive effects on reef substrates (Mapstone et al., 2007) and drive the erosion and "flattening" of reefs—a major threat to the ecological trajectories of reefs that threatens the very geological foundation of these systems (Alvarez-Filip et al., 2009; Kuffner & Toth, 2016; Molina-Hernández et al., 2022). Thus, species that dampen the erosive impacts of consumers could play an important role in reef persistence.

Reef bioerosion is now a well-recognized threat facing coral reefs (Bruno et al., 2019; Kuffner & Toth, 2016; Perry et al., 2014), but the potential for secondary space-holder species to mediate consumer-induced bioerosion is rarely considered, likely because they are generally considered as coral competitors. Bare space is limited in tropical coral reefs, and sessile species (e.g., macroalgae, benthic invertebrates) can sometimes overgrow live corals and prevent colonization by coral recruits by occupying reef space (Birrell et al., 2008; Cruz et al., 2016; Ladd et al., 2019; Loh & Pawlik, 2014). Phase shifts from coral to macroalgae dominance have been heavily studied, and more recently, increases in the dominance of benthic invertebrates such as sponges, octocorals, and zoanthids have been documented throughout many coral reefs. Yet, our understanding of the causes and ecological effects of these increases on coral reefs is still very limited (Bell et al., 2022).

Secondary space-holders that compete with corals for reef space can also have positive effects on coral dynamics, especially when abiotic or biotic stressors (e.g., consumer pressure) increase within systems. For example, cryptic sponges can bind coral rubble together and stabilize reef substrate following disturbance (Biggs, 2013; Wulff, 1984; Wulff & Buss, 1979), and some seaweeds that compete with corals also protect corals from high densities of coralivorous sea stars by providing associational refuge as chemically defended neighbors (Clements & Hay, 2015). As corals continue to decline due to global change stressors, positive interactions among sessile species frequently assumed to compete with corals may play increasingly facilitative roles in degraded reefs under high levels of abiotic or biotic stress.

Along the Caribbean coast of Panama, overfishing has decimated predator populations (i.e., triggerfish, hogfish, and lobsters) and presumably released the reef urchin, *Echinometra viridis*, from top-down control (Sangil & Guzman, 2016), which along with habitat change (Cramer et al., 2018, 2020), has led to densities that can exceed 150 m^{-2} (Figure 1; see *Results*). Although lesser studied than the long-spined sea urchin, *Diadema antillarum*, high *E. viridis* densities (>40 m^2) have been reported elsewhere in the Caribbean such as in Puerto Rico, Belize, Jamaica, and San Blas, Panama (Brown-Saracino et al., 2007; Griffin et al., 2003; Lessios, 1988; Sammarco, 1982) and this urchin now represents a dominant grazer throughout many Caribbean reefs (Sangil & Guzman, 2016). Although *E. viridis* can prevent algal growth (Kuempel & Altieri, 2017; Sangil & Guzman, 2016), it is a known bioeroder and at high densities may threaten the integrity of reef structures (Brown-Saracino et al., 2007; Griffin et al., 2003).

Here, we investigate relationships between benthic cover and urchin distributions, the consumptive effects of urchins on both live and dead corals, and the potential for an abundant zoanthid to ameliorate these consumptive effects. We found that (1) urchin densities increase as the percent cover of dead coral on reefs increases and that (2) dead corals exhibit higher susceptibility to per capita urchin-induced erosive effects than live corals. In addition, based on our observation of the inverse relationship between urchins and the mat-forming zoanthid, *Zoanthus pulchellus*, we conducted two field experiments that revealed (3) urchins avoid zoanthid-covered dead coral and (4) zoanthids increase the persistence and decrease the erosion rates of dead coral. We found that zoanthid overgrowth provides an associational refuge to dead corals by deterring urchin activity and regulating their negative consumptive effects on the reef framework.

METHODS

Study system

Bahía Almirante is a semi-enclosed bay with a tidal amplitude of ~0.5 m (Guzmán, 2003) in the Bocas del Toro archipelago outside of the hurricane belt on the Caribbean coast of Panamá (Figure 2a) that has experienced widespread ecological degradation as a result of anthropogenic stressors (Cramer, 2013; Seemann et al., 2014, 2018). Agriculture, rapid development fueled by tourism, and global change have driven nutrient pollution, sedimentation, and hypoxia events within the bay, and overfishing has depleted predator populations (Altieri et al., 2017; Cramer, 2013; Guzman & Tewfik, 2004). Yet, amidst this context of human disturbance, many fringing and patch coral reefs have persisted at shallow depths (1–3 m). Live coral cover is relatively high on these reefs, and the composition primarily consists of weedy corals representative of many modern Caribbean reefs (Alvarez-Filip et al., 2011; Kuffner & Toth, 2016) including the branching finger coral *Porites* spp., thin lettuce leaf coral *Agaricia tenuifolia*, and the hydrocoral *Millepora alcicornis* (Dunn et al., 2017; Seemann et al., 2014). Dead corals, which are also abundant on these reefs, are commonly colonized by mats of the zoanthid *Z. pulchellus* at these depths (see *Results*; Figure 1a), and fleshy algal growth is less common as a result of grazing by small-bodied herbivores such as the striped parrotfish (*Scarus iseri*) and *E. viridis* (Kuempel & Altieri, 2017). The latter exhibits diurnal feeding in our Bocas del Toro study system (Figure 1), in contrast to its cryptic/nocturnal behavior at lower abundances where still under top-down control (McClanahan, 1999).

Habitat and urchin surveys

We surveyed benthic habitat and urchin populations on 10 shallow reefs from July to September 2019 to identify dominant space-holders and quantify relationships between habitats and urchin densities (Figure 2a, details in Appendix S1). At each site, divers laid 14 0.6 × 0.6 m gridded quadrats (25 points) every 2 m along a haphazardly placed 30 m transect (1–2 m depth) parallel to shore. The primary substrate (live coral, dead coral, or sand/grass) under each point within the quadrat was recorded. Dead corals in this system often retain morphological traits of their live counterparts (Figure 1b,c), such as corallite shape and colony structures, and in these cases, we identified dead corals to genus. We also recorded epibionts growing on the primary substratum under each point, and, if applicable, grouped these categories as zoanthid, *Halimeda* algae, sponge, fleshy macroalgae, cyanobacteria, or "other." Dead coral with sparse turf algae <3 mm and dead coral encrusted by calcareous algae were categorized as "bare" as this generally represents open substratum for settlement of sessile organisms. We counted *E. viridis* (hereafter referred to as "urchin") individuals within quadrats at all sites.

Relationships between urchin densities and substrate percent cover at the quadrat scale do not necessarily reveal fine-scale habitat associations of urchins, and we hypothesized that urchins were not randomly distributed spatially among substrate types. Therefore, at three of

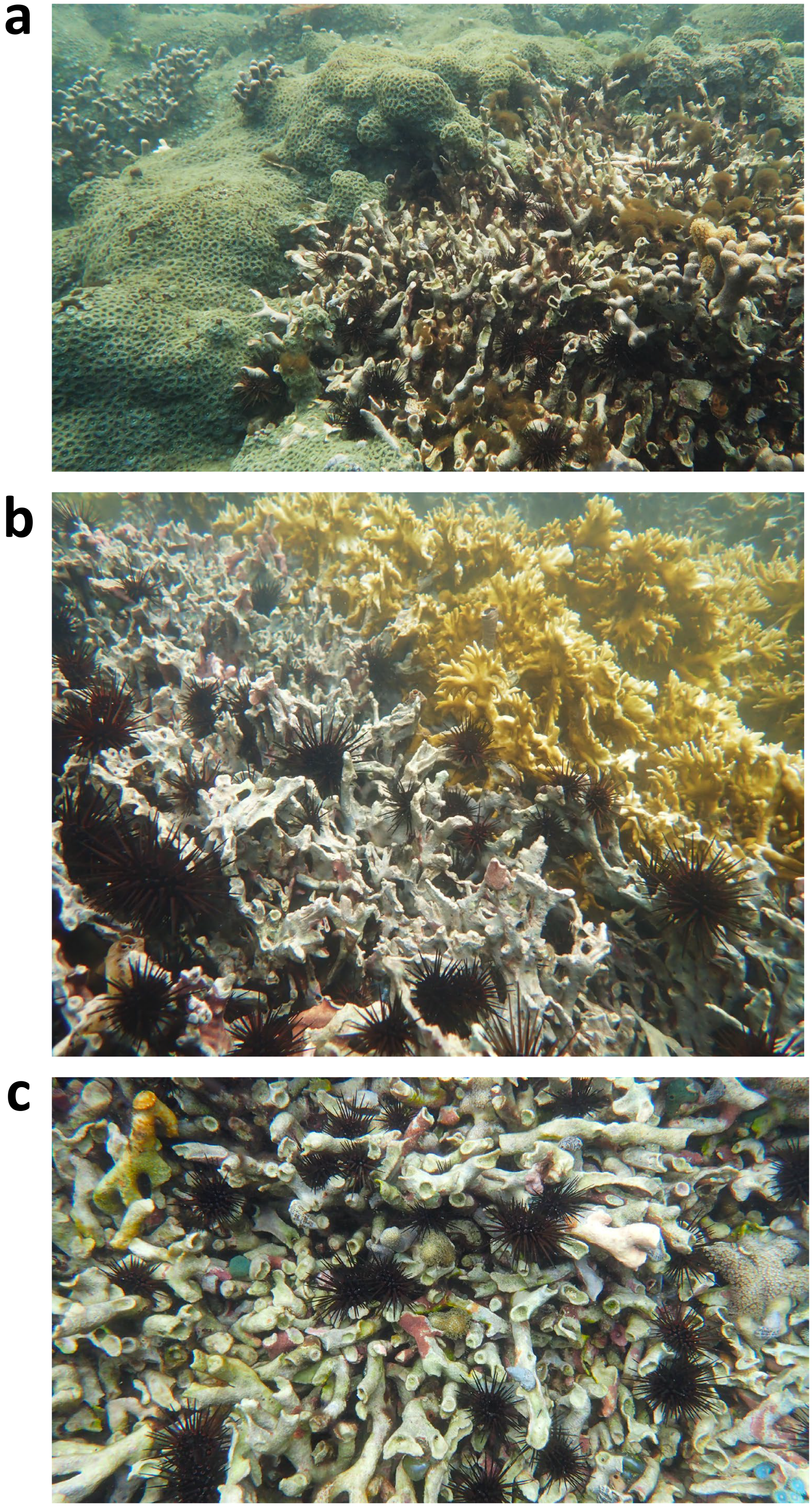

FIGURE 1 Photographs showing (a) zoanthid mat adjacent to bare dead coral littered with *Echinometra viridis*, (b) dead *Millepora* adjacent to live *Millepora*, with *E. viridis* highly abundant on the dead coral and nearly absent on the live coral. (c) *E. viridis* scattered on dead *Porites*. Images (b) and (c) demonstrate that the dead coral skeleton is clearly distinguishable to genus. Photo credit: Patrick H. Saldaña.

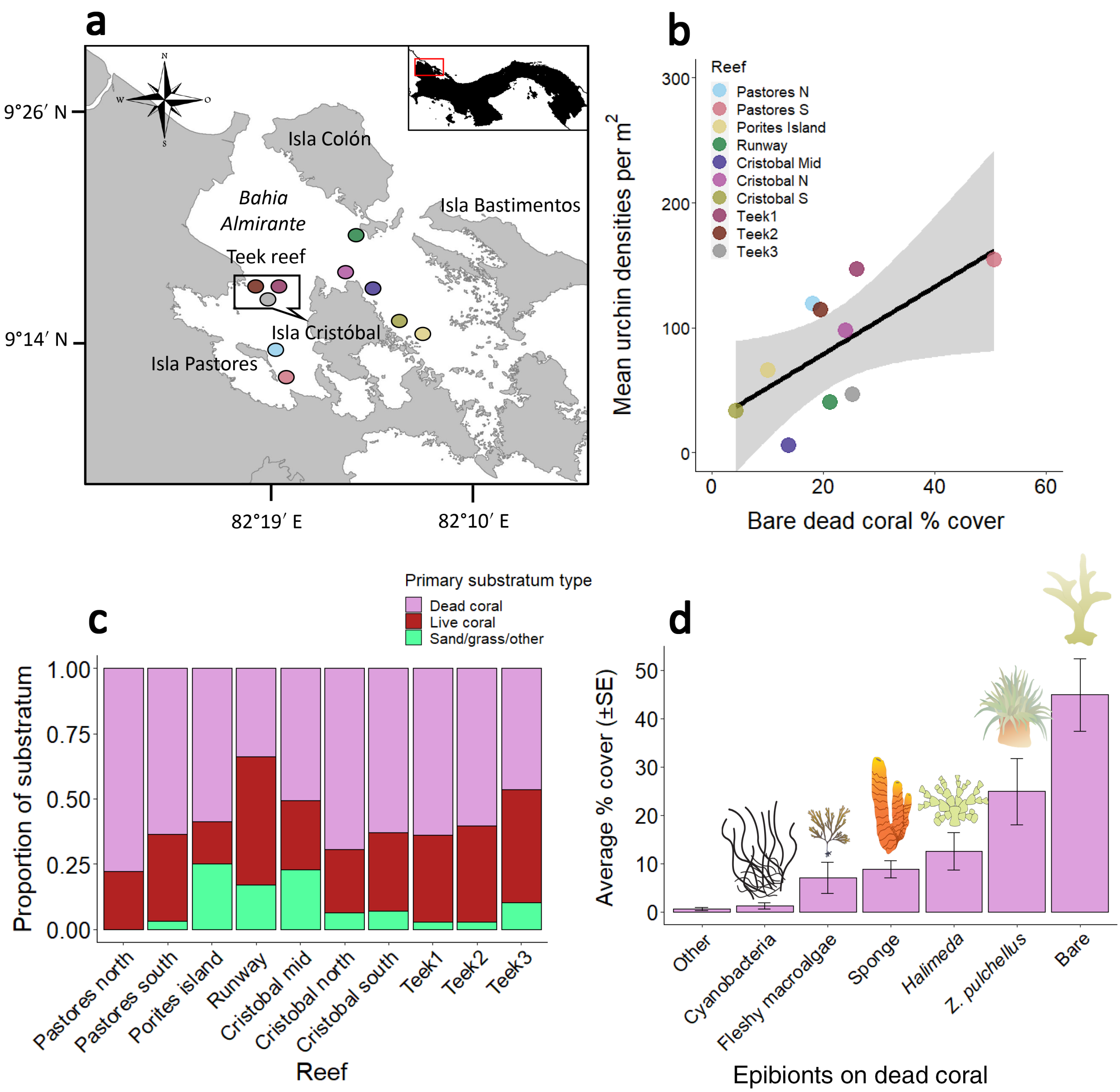

FIGURE 2 (a) Map of Bocas del Toro study region on the Caribbean coast of Panamá. (b) Mean urchin densities increased across sites as a function of bare dead coral percent cover. Colored dots represent a given surveyed reef in (a) and (b). (c) Primary substrate proportions across sites. (d) Mean percent cover (±SE) of epibionts occupying dead coral substratum.

the 10 surveyed sites (Runway, Teek1, and Teek2), we conducted surveys of urchin-substrate associations within quadrats (details in Appendix S1). Divers picked up urchins individually from within quadrats and recorded whether the substrate from which the urchin was removed was zoanthid, live coral, bare dead coral, or "other" (sponge, fleshy algae, etc.). These benthic classifications were the four most common in habitat surveys (see *Results*).

Data analysis

We used linear models to test our hypothesis that urchin densities would increase with increasing bare dead coral cover across sites. To account for correlations among the three dominant substrate types (live coral, bare dead coral, and zoanthid; see *Results*), we modeled urchin densities as a function of those predictor variable residuals. We used generalized linear models (GLMs) with an aggregated binomial distribution to test our hypothesis that urchins preferentially associate with bare dead coral in the field by comparing observed proportions of urchins among substrate types relative to the proportions expected based on the percent cover of the substrate types. We ran Pareto-smoothed importance sampling leave-one-out cross-validation (PSIS-LOO) to select models which best described the data and to calculate model weights (Vehtari et al., 2017). All statistical analyses were conducted using a Bayesian framework in R version 4.1.2 with the bayesian “brms” package (Bürkner, 2017; details in Appendix S1).

Experiment I: Differences in urchin consumptive effects among corals

Experimental setup

We conducted a laboratory experiment in outdoor flow-through seawater tanks (~1 m^{-2}) with sand filters from August to November 2019 to compare urchin consumptive effects on coral colonies that differed by coral species and coral status. Three coral species commonly observed in our surveys (*Porites furcata*, *Agaricia tenuifolia*, and *Millepora alcicornis*; hereafter referred to by genus) were crossed with three statuses (live, cleaned dead, or dead coral collected in situ), and two urchin treatments (zero or three urchins) in a fully factorial design for a total of 18 treatment combinations. An additional 19th treatment included only three urchins (urchin control treatment) to account for residual urchin feces deposition in the absence of coral. Dead corals representative of the “bare dead coral” categorization in field surveys with typical grazed turf <3 mm and endolithic algae (hereafter referred to as “dead coral”), and live corals were collected from the field and placed in the experiment directly. Cleaned dead corals were collected as live corals, and then left in the sun to dry for 5–7 days and brushed so that only skeletal material remained. The experiment took place in mesocosms constructed from inverted 4-L water bottles with an open top, that were strung from the surface of the tank and held lone treatment combinations for each 5-day trial. Each mesocosm contained a false bottom made of 7-mm mesh and had a vial at the base to capture material (i.e., urchin feces) that fell through the mesh (Appendix S2: Figures S1 and S2). We conducted nine trials, each with one replicate of each of the 19 treatment combinations. New coral colonies (~10 cm diameter) and new urchins were used for each replicate and trial.

We quantified three responses to examine the variation in bioerosional effects of urchins on corals. First, we quantified mass change of the coral colonies over the trial period to estimate the material removed by urchins. Before and after trials, we buoyantly weighed live corals and dead corals (Jokiel & Maragos, 1978) and obtained dry weights (DW) of cleaned dead corals. All buoyant weights (BW) were converted to a standard DW value for analysis to estimate changes in coral skeletal mass (Jokiel & Maragos, 1978). Second, in the treatments with urchins we recorded urchins as either present or absent on corals at three time points daily (morning, afternoon, and evening) during trials 2–9 to document their interaction with corals. Third, we quantified the deposited fecal material in sample vials at the end of each trial to estimate $CaCO_3$ deposited by urchins, which represented a proxy for their direct consumption of coral skeletons. We removed urchin spines from samples, transferred them to a muffle furnace (500°C) for 6 h to combust organic material, and determined inorganic fraction masses. We then dissolved the $CaCO_3$ from the inorganic material with HCl (10%), dried the samples at 60°C for 48 h, determined the non-$CaCO_3$ mass, subtracted that value from inorganic masses to calculate each sample’s $CaCO_3$ mass (in grams), and then divided by the number of hours per trial to determine standardized $CaCO_3$ deposition rates.

Data analysis

We used GLMs with a gamma distribution to examine differences among treatments in coral colony weight changes and $CaCO_3$ deposition rates among treatments (details in Appendix S2). Coral species, coral status, and urchin treatment were treated as fixed factors, and trial number as a random factor. Among the treatments with urchins, we also quantified proportions of urchins occupying coral colonies throughout the trial using an aggregated binomial distribution (“success” = present on coral, “failure” = not present on coral) with a logit link. Coral status and species were treated as fixed factors, “hours since start” as a covariate, and mesocosm replicate as a random variable to account for repeated sampling.

Experiment II: Urchin movement in response to zoanthids

Experimental setup

We conducted a field experiment October–November 2019 (two 4-day trials) to examine how zoanthids affect urchin use of dead coral habitat (~2 m depth) at Teek1 reef on Isla Cristobal (Figure 2a). Enclosure cages

(27 × 11 × 8 cm, 1.3-cm mesh size) were deployed on concrete bases in a sand patch adjacent to a largely dead reef with zoanthid cover. The experiment crossed two habitat treatments with two urchin density treatments in a fully factorial design. Each enclosure was visually divided crosswise into four equally sized sections. The two habitat treatments consisted of (1) 100% bare dead coral in which all four sections of the enclosures were covered with bare dead *Porites* and (2) a zoanthid-covered habitat treatment, in which section 1 was covered with bare dead *Porites* and sections 2–4 were covered with zoanthid-covered dead *Porites* (Appendix S3: Figure S1). Each enclosure initially received either 6 or 12 urchins for the low- and high-density treatments, respectively. These represented the average and high ranges of surveyed urchin densities within quadrats at this site (Appendix S3; see *Results*). Divers then recorded urchin locations within each enclosure's sections at 0900, 1300, and 1700 for four consecutive days. We conducted three replicates of each treatment combination in trial 1, and five replicates in trial 2 for a total of eight replicates per each habitat and urchin density treatment.

Data analysis

We compared urchin proportions in sections 2–4 of plots across treatments to test whether zoanthids repelled urchins by fitting and comparing GLMs with an aggregated binomial distribution. We included urchin density, habitat type, and a habitat × density interaction as fixed factors; trial as a random effect; plot ID as a random effect to account for repeated sampling; and hours since trial start as a covariate.

Experiment III: Zoanthid effects on urchin-induced bioerosion

Experimental setup

To test whether zoanthids provide refuge to dead corals from urchin-induced erosion, we deployed a fully factorial caging experiment on the reef at the Isla Cristobal experimental site in November 2019 with 30 × 30 cm plots that crossed two levels of zoanthid coverage with four levels of urchin grazing. The two levels of zoanthid coverage included (1) a no-zoanthid plot in which a bare dead *Porites* fragment was cable tied to the center of the plot, and (2) a zoanthid plot in which the dead *Porites* fragment at the center was covered by zoanthids (Appendix S4: Figure S1). The four levels of urchin grazing included (1) an *open plot* which was a mesh base that provided an anchor point for the coral fragment while also allowing urchin access, (2) an *urchin exclosure* which was a fully caged plot to exclude urchins, (3) an *urchin enclosure* which was a fully caged plot with six urchins placed inside, or (4) a *partial exclosure* with half of each cage side removed to serve as a procedural control. There were 10 replicates per treatment combination. The base of all plots was made from plastic extruded mesh (1.3-cm mesh size), and the exclosure, enclosure, and partial cages measured 30 × 30 × 15 cm ($L \times W \times H$). In addition to the center fragment which compared the direct effects of zoanthid overgrowth on erosion of dead coral by urchins, we also secured a bare dead fragment in each plot's corner to quantify whether zoanthid cover in the center of the plot would affect erosion on a nearby uncovered fragment. All experimental coral fragments were buoyantly weighed and deployed November 13–14, 2019 at the start of the experiment, with plots spaced parallel to shore in a blocked design (one replicate per treatment in each spatial block with >1 m between plots). In a preliminary experiment, zoanthid cover increased fragment BW by 3.7%, and so we applied a correction factor to each zoanthid-covered fragment weight (Appendix S4). After 22 months in September 2021, we returned to the study site and recorded whether deployed fragments were present/absent within plots (hereafter, "persistence"), and then collected remaining fragments to measure erosion rates using BW analysis. Due to the COVID-19 pandemic, the experiment was not maintained as consistently as planned, and we acknowledge that urchins may have recruited into urchin exclosure plots. Thus, we interpret these treatments as representing a reduced urchin grazing effect rather than an absence of urchin grazing. We excluded two damaged plots from analysis, as well as nine replicates from the zoanthid treatment for which we could not determine whether multiple coral fragments within the zoanthid mat were due to the focal fragment breaking apart or being joined by drift fragments.

Data analysis

We compared how treatments affected center and corner fragment persistence by fitting GLMs with a Bernoulli distribution (0 = fragment present, 1 = fragment absent) and a logit link. We included block as a random effect, and urchin grazing and zoanthid coverage treatments as predictor variables. We had low fragment persistence in some urchin grazing treatments and so could not include urchin grazing as a predictor variable for the change in fragment weights response variable (i.e., erosion rates).

For those analyses, we used linear models with only zoanthid coverage as a predictor variable.

RESULTS

Habitat and urchin surveys

Live and dead coral represented on average 31 ± 3.1% (mean ± SE) and 59 ± 3.9% of the total primary substratum across sites, respectively (Figure 2c). Of the live coral, composition across sites averaged 59 ± 8.4% *Porites*, 36 ± 8.5% *Millepora*, and 5 ± 2.8% *Agaricia*. Zoanthids were the most common epibiont of dead coral, covering 25 ± 6.8% of dead coral habitat (Figure 2d), which equated to an average of 16 ± 4.3% coverage of the entire bottom (Appendix S1: Table S1). We found that zoanthids functionally had exclusive occupancy of dead coral as substratum; out of 553 quadrat points with zoanthids, there were only two points that overlay another primary substratum/epibiont (one live sponge and one live *Porites*). Urchin densities were positively correlated with bare dead coral cover across sites (Figure 1b; Appendix S1: Tables S2 and S3). The densities of urchins located on dead coral substrate (Runway: 57 m^{-2}, Teek1: 204 m^{-2}, Teek2: 438 m^{-2}) and on zoanthid-covered dead coral (Runway: 0 m^{-2}, Teek1: 2 m^{-2}, Teek2: 51 m^{-2}) varied relative to the average urchin densities per square meter examined in the surveyed quadrats (Runway: 16 m^{-2}, Teek1: 56 m^{-2}, Teek2: 114 m^{-2}), but urchin occupancy of bare dead coral was always higher than expected given its percent cover at the quadrat scale (Appendix S1: Tables S4–S6). Zoanthid cover was minimal at Runway reef (1%), but relatively high at Teek1 (35%) and at Teek2 (34%) where model-estimated proportions of urchins on zoanthids within quadrats were lower than expected at 0.15 (95% CI = 0.12 to 0.20) and 0.01 (95% CI = 0.00 to 0.03), respectively, given zoanthid percent cover (Appendix S1: Tables S4–S6).

Experiment I: Differences in urchin consumptive effects among corals

Deposition rates of $CaCO_3$ indicative of urchin bioerosion differed among coral species and statuses (live vs. cleaned dead vs. dead) in response to urchins (Figure 3a) as the model including the interactions between urchin presence × status and urchin presence × species received a majority (64%) of LOO model weight (Appendix S2: Table S1). Among "urchin present" treatments, the highest deposition rates occurred in dead colonies (0.3 ± 0.05 g day^{-1}; mean ± SE) relative to cleaned dead and live colonies and were higher in "urchin present" than in the "urchin absent" treatments for all coral species (Figure 3a). Among the dead colonies with urchins, $CaCO_3$ deposition was higher for *Agaricia* (0.44 ± 0.11 g day^{-1}) and *Porites* (0.34 ± 0.06 g day^{-1}) than *Millepora* (0.1 ± 0.02 g day^{-1}). $CaCO_3$ deposition was negligible in live coral treatments with urchins (pooled live colonies, 0.04 ± 0.01 g day^{-1}), and urchin-only treatments (<0.01 g day^{-1}).

Erosion rates, measured as mass lost from coral colonies, revealed a pattern similar to $CaCO_3$ deposition. Urchins eroded dead and cleaned dead colonies, but not live ones (Figure 3b). The model that included urchin presence and an interaction of coral status × species received 78% of LOO model weight (Appendix S2: Table S4). Erosion rates were higher in "urchin present" treatments than "urchin absent" treatments for both dead and cleaned dead colonies, but there were no differences between the two urchin treatments for live corals as 95% CIs overlapped zero for all three species. Within "urchin present" treatments, erosion rates were higher for dead (0.33 ± 0.05 g day^{-1}) than cleaned dead corals (0.09 ± 0.03 g day^{-1}) for all species, and dead *Millepora* experienced less erosion than dead *Porites* and *Agaricia* (Figure 3b).

Urchins were more often located on dead coral fragments than live or cleaned dead fragments (Appendix S2: Figure S3). The model that included coral status and time as predictors received the strongest support from model selection (57% of LOO weight; Appendix S2: Table S7), with the proportion of urchins located on corals generally decreasing over the course of the 5-day trials. Rates of urchin association with coral fragments did not vary substantially among coral species (Appendix S2: Table S7).

Experiment II: Urchin movement in response to zoanthids

Urchins avoided zoanthid-covered coral fragments in enclosure plots and aggregated in the dead coral section and surrounding mesh when zoanthids were present (Figure 4a). Model selection assigned the most weight to the habitat + urchin density + time model (61% LOO weight; Appendix S3: Table S4). The proportion of urchins in plot sections with zoanthid-covered dead coral fragments (sections 2–4) was lower (low urchin density, mean = 0.17, 95% CI = 0.12 to 0.24; high urchin density, mean = 0.11, 95% CI = 0.07 to 0.15) than on those same plot sections when zoanthids were absent (low urchin density, mean = 0.54, 95% CI = 0.45 to 0.63; high urchin density, mean = 0.44, 95% CI = 0.36 to 0.52). Urchins generally decreased on

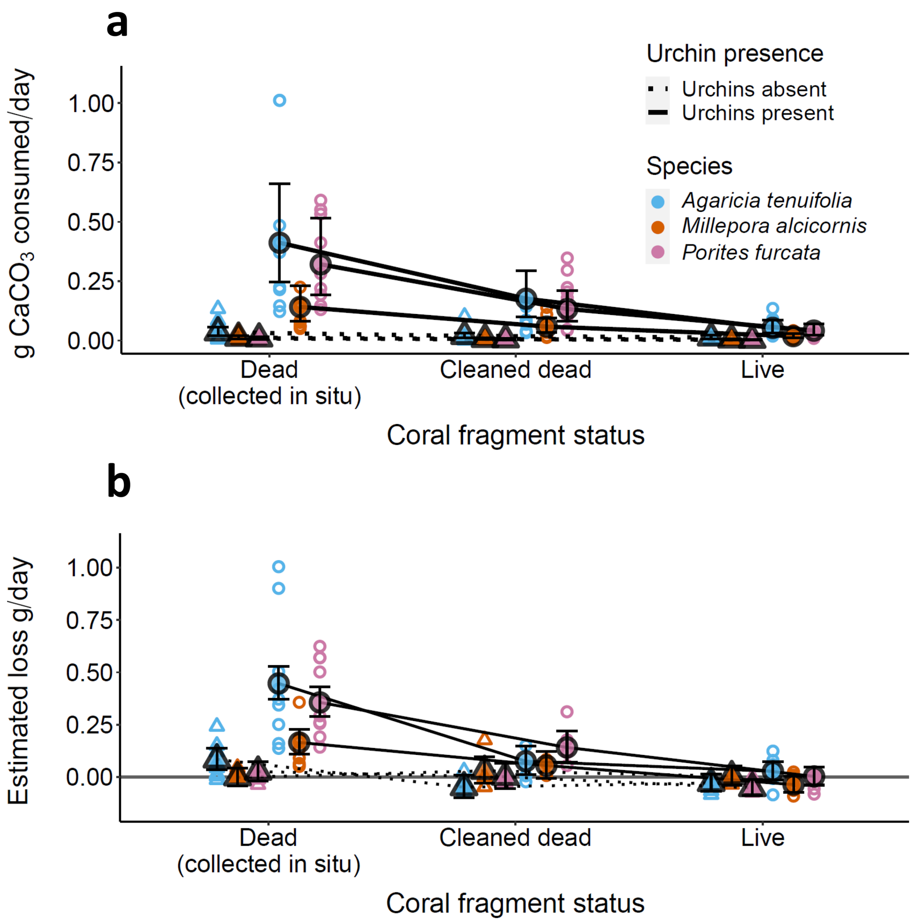

FIGURE 3 (a) Calcium carbonate deposited in mesocosms across coral and urchin treatments. (b) Loss in coral dry weight (per day) as estimated from coral buoyantly weighed and measured at the start and end of the experiment. Both measures revealed greater bioerosion in the presence of urchins and that urchins generally targeted dead colonies more relative to live or cleaned dead colonies, but the magnitude of these differences varied by coral species. Circles and triangles represent treatments with and without urchins, respectively. Open symbols represent raw data for replicate coral colonies, filled symbols are predicted model means, and black vertical bars are 95% CIs.

sections 2–4 of plots and increased on section 1 (and surrounding mesh) over the duration of the experiment (Appendix S3: Table S4).

Experiment III: Zoanthid effects on urchin-induced bioerosion

Zoanthids increased persistence rates and decreased erosion rates of dead coral fragments (Figure 4b,c). Notably, 92% of zoanthid-covered fragments (37/40) persisted to the end of the 22-month experiment, but only 28% of bare dead coral fragments (34/120) persisted (Figure 4b). The best fit model for center fragments included zoanthid coverage treatment and urchin treatment as predictor variables (81% of LOO weight; Appendix S4: Tables S5–S7). Zoanthid-covered fragments had higher persistence than bare dead coral, and urchin exclosure plots had the highest persistence of center coral fragments relative to other urchin treatments (Figure 4b, ii). Similarly, the probability of corner fragments, which were bare dead coral in all plots, persisting in urchin exclosure plots was significantly higher than for all other urchin treatments and model selection assigned the most weight (75%) to the model including urchin treatment as a factor (Appendix S4: Tables S1 and S3). Of the center fragments that persisted to the end of the experiment, erosion rates were more than 50% lower when fragments were covered by zoanthids (mean = −5.04, 95% CI = −8.94 to −1.10; Appendix S4: Table S14) than when fragments were bare (Figure 4c). We had much less analytical power for comparison of erosion in corner fragments, as fewer of these fragments persisted to the end of the experiment, and we did not detect an effect of zoanthid coverage of the center fragment on bare corner fragment erosion rates (parameter value overlapped zero; mean = −5.72, 95% CI = −12.03 to 0.62; Appendix S4: Table S11).

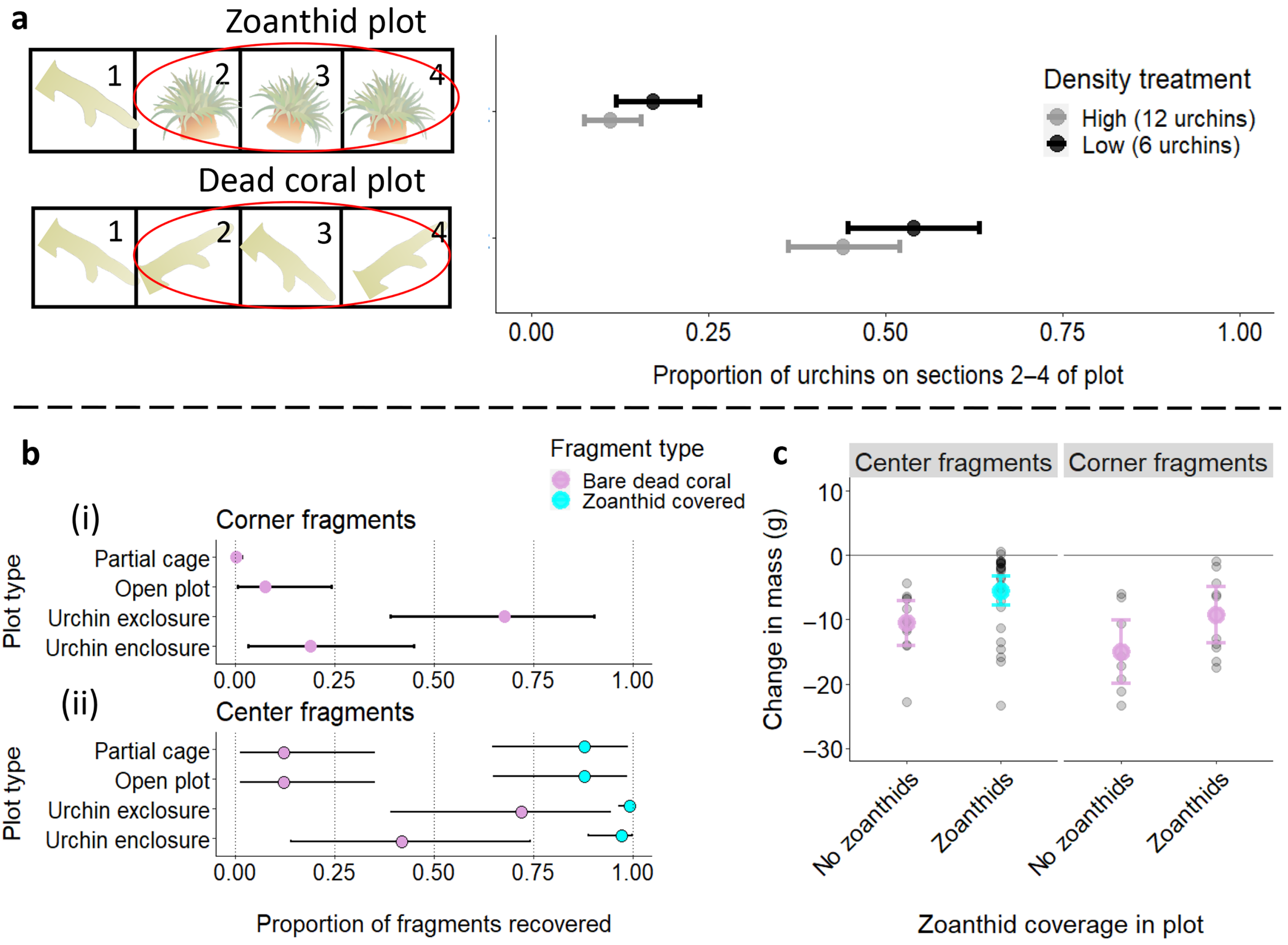

FIGURE 4 Results of experiments testing the importance of zoanthids as an associational refuge for dead coral. (a) In the urchin movement experiment, urchins avoided zoanthid-covered plot sections. Dots represent model-fitted mean proportions of urchins on sections 2–4 of the enclosure plots (zoanthid or dead coral), and bars represent 95% CIs. Illustrations next to *y*-axis titles represent visualizations of treatments, with red circles indicating the plot section from which urchin proportions were used as response variables. In the 22-month fragment erosion experiment, zoanthids (b) increased persistence and (c) decreased the erosion of dead corals. (b) Blue and purple dots represent predicted proportions of (i) corner and (ii) center fragments persisting in plots that manipulated urchin access. Black horizontal lines represent 95% CIs of the fitted estimates. Panels suggest higher persistence for zoanthid-covered fragments, as well as for bare dead fragments from urchin exclosure plots, relative to other plot types. (c) Large colored points represent fitted posterior mean changes in mass of recovered fragments and lines represent 95% posterior CIs. Small gray points represent individual replicates. Zoanthid-covered fragments (blue) experienced less erosional mass loss, on average, than bare dead fragments (purple).

DISCUSSION

We found that a common zoanthid provides associational refuge to dead corals in degraded reefs that are otherwise susceptible to bioerosion by high densities of the reef urchin, *E. viridis*. Reef urchins preferentially associate with dead corals, accumulate in high densities within dead coral patches, and rapidly erode dead coral colonies. These consumptive effects are general across multiple coral species but are consistently limited to dead coral rather than live coral. This urchin-induced erosion that threatens the persistence of the reef framework can be held in check by the abundant mat-forming zoanthid that exclusively colonizes and offers associational refuge to dead corals by protecting them from excessive urchin grazing pressure (Figure 5). Our findings suggest that overgrowth by some species typically considered nuisance opportunists, such as zoanthids, may be part of important feedbacks underlying reef persistence in which strong consumptive effects increase the importance of associational refuges, and that these dynamics depend on whether coral reefs are alive or dead.

The strong relationship we observed between urchin densities and bare dead coral cover within an overfished system suggests that bottom-up processes at least partly

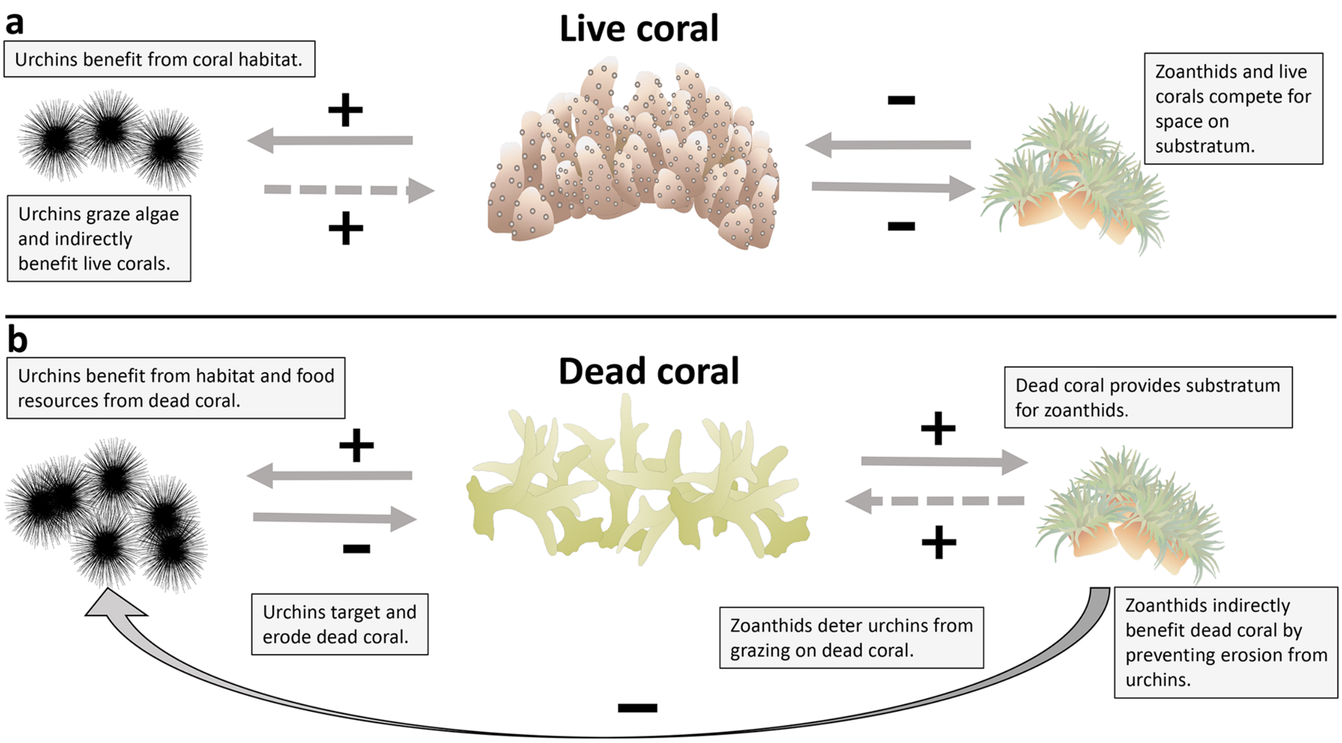

FIGURE 5 Conceptual figure of interactions among corals, zoanthids, and urchins: (a) interactions involving live corals; (b) interactions involving dead corals. The figure illustrates how the interactions that corals have with urchins and zoanthids can shift between negative and positive as a function of whether coral is alive or dead: urchins have positive indirect effects on live corals, but direct negative effects on dead corals, whereas zoanthids compete with live corals but indirectly benefit dead corals by inhibiting urchin grazing. Solid arrows represent direct effects and dashed arrows represent indirect effects. Plus and minus signs represent positive and negative effects.

control urchin distributions. It is likely that where urchins are under strong top-down control, the ratio of live to dead coral cover would explain less variation in urchin densities among reefs, as observed in other regions with less fishing pressure (McClanahan & Muthiga, 2020; Shulman, 2020). In a system such as ours, we suggest that predator depletion (Seemann et al., 2014) creates a context for bottom-up effects of coral status and composition to mediate urchin distributions and their associated consumptive effects. Paleontological data support this perspective, having revealed that increases in the abundance of *Echinometra* spp. were associated with transitions in habitat characteristics including the prevalence of coral rubble (Cramer et al., 2020).

Spikes in urchin densities have followed coral mortality events in other regions, likely due to increased food resources growing over dead corals (Glynn & Colgan, 1992), and four key results here indicate that this may drive high urchin densities on dead coral patches in Bocas del Toro. First, urchins appeared to target algae growth on dead coral, rather than the dead coral per se, as evidenced from higher urchin occupation of dead coral collected in situ than cleaned dead coral in mesocosms (Appendix S2: Figure S3). Second, urchin proportions on dead coral generally decreased over time (Appendix S2: Figure S3), which may have been due to algae depletion. Third, higher urchin feces deposition in dead coral than cleaned dead coral or live coral treatments in laboratory trials indicates higher feeding rates (Figure 3a). Fourth, in field surveys, urchin densities increased with dead coral cover but exhibited no relationship with live coral cover, and a strikingly disproportionate higher number of urchins occupied dead coral while far fewer occupied live coral than expected given the substratum composition (Appendix S1: Figure S1, Tables S4–S6). This is more likely explained by differences in food resources than structural complexity given that rugosity is higher in live coral than dead coral (Saldaña, unpublished data), and urchins in this system may prioritize trophic resources over complexity in habitat selection (Dunn et al., 2017).

Results from our 22-month fragment erosion field experiment indicate that the urchin bioerosive effects on dead coral we detected in the lab scale up to the reef environment. Urchin exclosure plots had the highest rates of fragment persistence (Figure 4b), indicating that urchin access increased coral degradation. We suggest a synergistic effect of increasing dead coral cover on these experimentally derived reef erosion rates since our surveys revealed more urchins per unit area on dead coral than live coral, and because laboratory experiments found per capita erosional effects of urchins were higher on dead coral than live coral.

Critically, our study revealed that zoanthids provide associational refuge and increase the persistence of dead corals under this high consumer pressure. The otherwise high densities of urchins associated with dead corals decreased where zoanthids carpeted the substratum (Appendix S1: Tables S4–S6), and zoanthids repelled urchins in our movement experiment (Figure 4a). We did not specifically test the mechanism causing this behavioral response, but zoanthids can sting urchins and direct their movement in temperate reefs (Levenbach, 2008), and some tropical zoanthids produce noxious allelochemicals as defense mechanisms that could repel urchins (Lonzetti et al., 2022). Yet, we observed urchins grazing on exposed dead coral closely surrounded by zoanthids, and given that corner fragments adjacent to zoanthids in our caging experiment experienced similar persistence and erosion rates to corner fragments not adjacent to zoanthids, in this system, zoanthids may simply physically block urchin access to dead coral or have a limited halo of allelopathic effects.

Although dead corals appear to trigger increased consumer pressure, they provide hard substrate required for zoanthid growth. We suggest that this represents a stabilizing feedback in which an associational refuge provided by zoanthids disrupts eroding urchin fronts (Figure 5). Although associational refuges are not traditionally considered with respect to dead organisms, dead foundation species such as corals often continue to support ecosystem function and biodiversity and are ecologically active components of the community (Saldaña, Angelini, et al., 2024). Since "flattening" of reef frameworks is a primary threat in the Caribbean (Alvarez-Filip et al., 2009), we suggest that the overgrowth of dead corals by some sessile space-holders provides an unrecognized important protective function for reef structural integrity. Given that sponges are recognized for their structural function in which they promote resilience by binding dead reef material (Wulff & Buss, 1979), the role of other non-scleractinian space-holders on reef recovery processes deserves further study.

The importance of zoanthids as an associational refuge appears to vary among dead coral species because we found lower bioerosion rates (i.e., $CaCO_3$ deposition and fragment erosion) for dead *Millepora* than for *Porites* and *Agaricia* in our laboratory experiment (Figure 3). We hypothesize several ways the lower impacts of urchin grazing on *Millepora* may indicate the importance of species traits in mediating consumer impacts. First, the highly branched morphology of this coral (Dunn et al., 2017) could limit urchin accessibility to some of its surfaces. Second, dead coral skeletal densities can influence their susceptibility to erosion (Molina-Hernández et al., 2022), and the mineral structure of *Millepora* skeleton may be more resistant to grazing than other corals. Third, *Millepora* skeletons may support algal assemblages that fail to stimulate urchin consumption to the degree of other coral species (Dunn et al., 2017). Although several studies have now compared the relative effects of nutrient loading (bottom-up) and herbivory (top-down) on algal proliferation over dead corals (Jompa & McCook, 2002; McClanahan et al., 2002; McManus & Polsenberg, 2004), the role of dead coral species' traits in mediating consumer distributions and feeding behavior deserves further study.

Zoanthid "carpet" dynamics remain understudied in coral reefs but are often considered symptomatic of regime shifts in these systems (Cruz et al., 2015, 2016; Yang et al., 2013), although distinct zoanthid-dominated zones (i.e., the "Zoanthus zone") have been observed in coral reefs at least since the 1950s (Goreau, 1959; Karlson, 1980, 1983). Moreover, a recent review of zoanthid phase shifts found that out of 19 locations where zoanthid dominance was reported, only one location in Brazil could be clearly classified as a regime shift (e.g., a persistent state lasting more than 5 years) from coral to *Palythoa* zoanthid cover (Reimer et al., 2021). Zoanthids require similar habitat and nutrient resources as scleractinian corals and can act as competitors that feed on coral larvae (Fabricius & Metzner, 2004) and in some cases overgrow live coral tissue (Cruz et al., 2016; Doucette et al., 2022). However, different zoanthid species may exhibit different degrees of aggressiveness toward neighbors. Although *Palythoa* species have been widely reported to overgrow live corals (Cruz et al., 2016; Ladd et al., 2019), Karlson (1980) found that a *Zoanthus* species in Jamaica was unaggressive and competitively inferior to other corals. Regardless of aggressiveness with other benthic organisms, we recognize that thick zoanthid mats overgrowing the reef substratum represent a monopolization of space that inhibits the growth and colonization of corals and other benthic species through exploitative competition. More work is needed to understand the stability of zoanthids mats and their susceptibility to disturbance and the potential for coral recovery within them.

Zoanthids may have inhibitory effects on coral recovery, but our study demonstrates that high densities of urchins can represent a potent, active destructive force with potential to drive the loss of reef integrity. Urchins can also directly harm or kill coral recruits (O'Leary et al., 2013), and their negative effects may outweigh those driven by zoanthid colonization over dead coral. Although it could be argued that urchin bioerosion could enhance coral resilience by removing dead, brittle corals that act as sinks for settling corals, the reefs in Bocas del Toro are situated upon sand, often without a solid substrate under them. Without the dead skeletons of weedy species such as *Porites*, *Millepora*, and *Agaricia*, there would be an absence of hard substrate for recruitment. Moreover, in separate experiments, we have observed *Porites* coral recruiting into and growing within zoanthid mats (Saldaña, unpublished data), suggesting that these mats are not impenetrable to coral recruitment. Moreover, because branching *Porites* spp. grows from its branching tips, the presence of zoanthids growing on the nonliving colony base below the live tissue may limit the erosion and breakage of these colonies. Because *Zoanthus* can decrease the calcification rates of *Porites* when growing in association (Doucette et al., 2022), the net effects of zoanthids on reef persistence may depend on the intensity of external bioerosion. Other coral competitors, such as some seaweeds, can offer associational refuge to live corals from high consumer pressure (Clements & Hay, 2015), and we suggest that these types of interactions extend to dead corals as we found a benefit from zoanthid overgrowth under high urchin grazing pressure.

Our study demonstrates that death of foundation species can orchestrate species interactions between consumer and basal species that feedback to affect habitat persistence. The death of foundation species can create a context that mediates the cascading effects of species interactions, and organisms typically considered nuisance species may have positive effects on disturbed reefs under high biotic stress. When corals die, associational refuges provided by sessile invertebrates such as zoanthids may provide an underappreciated mechanism of resistance to degradation of the reef framework and thereby extend the window for coral recovery if corals can recruit to zoanthid-covered dead coral. Future work examining coral recruitment dynamics within zoanthid mats, and the temporal/spatial persistence of zoanthids, could further elucidate relationships between zoanthids and coral recovery processes relevant to resilience of reefs facing mortality events.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Saldaña, Lang, & Altieri, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.11583882.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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