

Prior predation alters community resistance to an extreme climate disturbance

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Abstract. Short-term physical disturbances occur amid a backdrop of longer-term biotic interactions, including predation, which shape communities. Effects of consumer interactions typically begin in early stages of assembly and continue throughout post-disturbance recovery. Despite decades of predation and disturbance research, few studies examine how consumer interactions during these different time periods may affect community responses to disturbance. Here we use replicate communities of tropical, sessile invertebrates to ask whether fish predation during initial assembly (before) and recovery (after) influences community resistance to a hurricane-level low-salinity event. Results revealed that pre-event predation determined whether communities shifted in biomass and community structure following disturbance. Communities that assembled without predators responded to the low-salinity event strongly, with large shifts in community composition and a mean loss of 54% of pre-disturbance biomass after a one-month recovery period. In contrast, those that experienced predation during initial assembly were strikingly resistant to disturbance, which had no effect on species composition or biomass. Results were driven by predator removal of a dominant competitor, which gave rise to more disturbance-resistant communities. These findings highlight the potential for past trophic interactions to shape community stability in the face of physical disturbances predicted to escalate with global change.

Key words: benthic communities; biotic resistance; climate change; extreme events; hurricanes; predation; resilience; resistance; stability; temporal ecology; time dependence.

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INTRODUCTION

As a future of more severe and frequent extreme weather events ratchets up disturbance regimes for ecosystems worldwide, ecologists increasingly look to untangle the factors that shape ecological stability (Easterling et al. 2000, Jentsch et al. 2007, and e.g., Lloret et al. 2012, Hoover et al. 2014, Isbell et al. 2015). At the same time, many systems have experienced shifts—often declines—in consumer populations, with cascading effects on community composition and diversity (Estes et al. 2011, Ripple et al. 2015). The concurrence of these

global changes underscores the potential for alterations in predation and herbivory regimes to affect community stability in the face of escalating physical disturbances, although this question has rarely been explored directly.

Previous research examining interactive effects of predation and disturbance does, however, suggest mechanisms by which predation could alter community responses to physical disturbance. For example, the relative importance of disturbance and predation along gradients of environmental stress is well explored. We can therefore consider these questions in a temporally dynamic

Menge–Sutherland framework (Menge and Sutherland 1987) where background conditions of low stress (during which predation is predicted to be of prime importance) may affect how communities respond to acute periods of extreme environmental stress (predicted to override the relative importance of other interactions). Numerous studies have also investigated consumer effects on the magnitude or intensity of disturbances such as fire (Bowman et al. 2011), and ways that concurrent predation and disturbance treatments influence diversity, composition, or biomass (e.g., in grassland experiments: Belsky 1992, Royo et al. 2010, and mesocosms: Kneitel and Chase 2004). This latter work in particular demonstrates that consumers can modify key community traits that may mediate the capacity to resist or recover from physical perturbations. For example, predation can enhance species diversity (Olf and Ritchie 1998, Hillebrand et al. 2007). Where it does so prior to a disturbance, diversity may in turn increase community stability, as it does in at least some systems (Tilman 1999, Ives and Carpenter 2007). Similarly, predation could also influence other community-level traits, such as species composition and biomass (Freestone et al. 2013), which in turn may affect stability. Direct experimentation in systems where predator communities are still robust can provide insight into ecological conditions under which these pathways may operate.

Importantly, predation tends to occur over fundamentally different timescales than those of physical disturbance events. Consequently, predation may influence stability in ways that depend on the time period considered. Consumer effects are typically long term, often beginning during early community assembly and persisting indefinitely, including after acute physical disturbances. Predation may or may not continue during an actual disturbance event—as consumers may move or suspend feeding temporarily (e.g., during large storms, hypoxic events, fires)—but generally resumes afterward. Predator effects on disturbance response could therefore occur prior to an event, via the aforementioned mechanisms, as predation influences the structure of communities experiencing disturbance. Consumer effects on stability may also occur post-disturbance by altering community processes if, for example, disturbance-driven declines in prey populations lead

to greater per-capita predation rates on survivors (Sinclair et al. 1998). Enhanced post-event predation on weak or damaged individuals could also exacerbate disturbance impacts, or reduce them if cleared space facilitates re-colonization (Turner et al. 1998). Such possibilities emphasize the likely time dependence of predator effects on stability, and the need therefore to examine these temporal dynamics explicitly.

Here we use replicate communities of sessile marine invertebrates in the tropical eastern Pacific as a model prey system. We ask how predation during initial, pre-disturbance assembly and post-event recovery affects the extent to which prey communities resist change following a simulated hurricane-level low-salinity disturbance. Predation can strongly influence community structure in such systems (Lubchenco et al. 1984, Freestone et al. 2011, 2013), and these interactions may be shifting as marine predator populations continue to be depleted. At the same time, massive rainfall events driven by storms generate low-salinity pulses that are also capable of altering benthic assemblages (Przeslawski et al. 2008), and the frequency of very severe storms is predicted to increase with climate change (Knutson et al. 2010). We quantified resistance to this type of low-salinity event as a lack of change, on a per-community basis, between pre-disturbance and post-recovery values of biomass, species richness, and community composition, measured as relative cover per species in each community. We use “assembly” to describe initial community development, understanding that assembly processes can continue indefinitely. For simplicity, we use the term “resistance” here, understanding it may include some aspect of resilience, since separation of these stability metrics depends to some extent on temporal perspective (Grimm and Wissel 1997), and various processes can complicate the distinction (e.g., lagged mortality, disturbance-enhanced reproduction). Our findings provide experimental evidence that past predation, by shaping community structure during assembly, can substantively enhance community resistance to change following an extreme physical disturbance.

METHODS

We used a three-phase experiment to untangle effects of predation at different time periods on the

resistance of sessile invertebrate communities to change following a low-salinity disturbance event. We conducted field experiments on Flamenco Island in the Gulf of Panama (8°54'43.3" N, 79°31'18.3" W), and laboratory work on adjacent Naos Island at the Smithsonian Tropical Research Institute (STRI) Naos Marine Laboratory (NML) from November 2015 to March 2016. Sessile invertebrate communities like those examined here occupy rock surfaces around these and other rocky islands in the Gulf, as well as structures like pilings, docks, and concrete rubble along shorelines. These communities are rich in species, including numerous non-indigenous ones (NIS). Predatory fishes (especially triggerfish, puffers, and wrasses) drive the majority of predation on these species in subtidal habitats (Lubchenco et al. 1984). The Gulf of Panama largely prevents hurricanes from striking the Pacific coast directly, but Caribbean storms often generate enormous rainfall across the narrow isthmus. We calibrated low-salinity treatments to mimic those accompanying the most severe storms in the last forty years (details below). After a three-month field phase (Phase 1) in which communities developed under two predator treatments (with and without; N = 32 per treatment), we exposed 16 communities from each assembly treatment to a low-salinity disturbance and the other 16 to seawater control conditions in the laboratory (Phase 2; N = 16 per treatment) and then returned them to the field for a one-month recovery period (Phase 3) in which half of the communities from each prior treatment combination were re-caged and half were exposed to predation (randomly assigned), yielding eight final treatments with eight replicates each (diagrammed in Appendix S1: Fig. S3).

Phase 1: Predation during initial community assembly

We deployed 64 polyvinyl chloride (PVC) settlement panels (14 × 14 cm) face down at 1 m depths (± 0.1 m) on individual weighted lines suspended from floating docks at Flamenco Marina on 30 November 2015. We randomly chose half of these to remain fully open to predators, and these were spatially interspersed at deployment with the remainder, which we enclosed in 8 cm tall cages made of heavy-duty plastic mesh designed to eliminate predation by organisms larger than the 0.635-cm mesh gaps (adult fishes and most macro-invertebrates such as crabs). We

deployed panels for three months to enable an adult community to assemble (at one month, 95–100% of space was occupied). Every two weeks, we manually cleaned cages to prevent fouling and exposed other panels to air briefly to ensure similar levels of maintenance-related stress.

Following this initial assembly period, and prior to imposing salinity treatments, we non-destructively assessed species richness, wet biomass, and cover per species for sessile marine invertebrates on each panel community. We first transported the panels in seawater to NML in batches of 8–10 panels per day for 7 days (17–23 February 2016) to avoid impacts associated with communities sitting in the laboratory awaiting analysis. We took high-resolution digital photographs of each panel community and measured its wet mass to 0.1 g with a digital scale (Scout Pro-2001, Ohaus, Parsippany, New Jersey, USA). We assessed species richness under a dissecting microscope, identifying each organism to the lowest possible taxonomic level, typically species. When that was not possible, we used morphological traits to assign a morpho-species classification, following the approach of other researchers (Freestone et al. 2011). To avoid observer bias, the same individual visually estimated cover of primary and secondary substrate occupying taxa, and canopy-forming species, using calibration templates and cross-verification with imaging software (ImageJ; <https://imagej.nih.gov>). To assess possible cage artifacts, we deployed cage control panels (partially caged, but open to predators) with additional un-caged panels for the 3-month assembly period (N = 5 per treatment, randomly spaced).

Predator identification

We used a separate predator-exposure experiment at the same field location to identify diurnal predators that may have been interacting with the invertebrate communities during our experimental period. We exposed five panel communities assembled without predators (3-month assembly in cages) to predation for 3 days (15–17 March 2016), using GoPro cameras set either to video or 1-s time-lapse photography to record predator visits between 07:00 hours (at the onset of sufficient light) and dusk (~17:00 hours) daily. Video began immediately with initial exposure. We then identified predators (in all cases, fish) from these high-resolution images.

Phases 2 and 3: Hurricane-level salinity treatments and predation during recovery

We imposed the low-salinity treatment at a salinity level parameterized by examining historical low-salinity events associated with major storms. Severe tropical storms typically occur in this area between June and December. We began our experiments toward the end of this season, in late November, to avoid storm-driven variability in salinity that could confound community responses to experimental treatment conditions, while maintaining rough proximity to relevant seasonality. We monitored ambient salinity at the treatment depth every two weeks with a hand-held digital probe (YSI Pro 2030, YSI Incorporated, Yellow Springs, Ohio, USA; mean = 31.2 ppt, standard deviation [SD] = 1.3). Salinity varies seasonally in this region, with wet-season (typically May to early January) lows rarely <25 ppt (Appendix S1: Figs. S1, S2). We focused on mimicking both the magnitude and duration of a particularly extreme low-salinity event at a disturbance level. To do so, we used a treatment level of 20 ppt, reflecting that reached by the two most severe low-salinity events recorded in Panama Bay since 1968, the latter of which was associated with Hurricane Irene in 2011 (Appendix S1: Figs. S1, S2). Our time series indicated that salinity tended to decrease rapidly with such storms and stay at low levels for roughly 24–72 h. We therefore imposed our low-salinity treatment for 48 h at 20 ppt with 6-h ramp-down and ramp-up periods.

After collecting community data from panels following the initial assembly period, we randomly selected half the communities assembled in each predation treatment (N = 16 per treatment) for exposure to low-salinity water. For both control treatments, we placed each panel community in a 15-L container containing 12 L constantly aerated seawater at the designated salinity, surrounded by running seawater at ambient bay temperature (23.0°–25.1°C) in shaded outdoor seawater tables. We measured salinity, temperature, and dissolved oxygen every hour during the 6-h ramp-down and ramp-up periods with a digital probe (YSI Pro 2030). For the low-salinity treatment, we reduced salinity hourly over the course of six hours to the final treatment level (20 ± 0.2 ppt) by adding ~1.5 L of de-chlorinated freshwater per hour (exact quantity adjusted for initial salinity). For ambient-salinity controls, we added

1.5 L of seawater (31.4–32.3 ppt). We changed water twice daily during the experiment and fed communities after each water change with 1 mL Kent Marine MicroVert concentrated invertebrate food per container.

We then returned each panel to the field on its original weighted line for a one-month recovery period (Phase 3) to allow fitness effects including mortality, which may not occur immediately, to accrue. Following Phase 3, we brought batches of panels to NML in the same sequence as Phase 2, and measured biomass, species richness, and cover as previously described.

Recruitment patterns

Interpretation of post-disturbance patterns in community responses could be complicated by temporal variation in the abundance of juveniles joining communities. We monitored this recruitment at 14-day (±1 day) intervals throughout the duration of the experiment, deploying three bare PVC panels every two weeks inside each predation treatment (un-caged, cage control, and fully caged) for a total of nine panels per two weeks. We counted individual recruits identified to the lowest taxonomic level possible on each panel under a dissecting microscope.

Our ability to confidently identify individuals to taxonomic levels lower than phylum varied with each individual, based on its developmental stage and taxon (some taxa display distinguishing morphological traits before others). For example, we could readily identify most tunicates to genus or species after days to weeks of development, but many individuals had settled too near the end of the 14-day recruitment window for us to identify beyond phylum (e.g., immediately post-metamorphosis). We therefore pooled abundance data into higher taxonomic groupings in which we were confident to examine trends over time and to test for cage effects.

Data analysis

We first asked how predation during assembly affected community structure in ways that might influence subsequent responses to disturbance. We compared species richness and biomass after initial assembly (before disturbance), between communities open to predators and those where predators were excluded (N = 32 per treatment) with *t* tests. We compared community

composition by considering the relative cover of each species for primary substrate holders, and also the total, pooled cover of all taxa present (including secondary substrate and canopy cover). We analyzed compositional differences by treatment with PERMANOVA in PRIMER (v.6; Anderson 2001), using a Bray-Curtis matrix of per-species cover (999 permutations).

Next, we examined how predation influenced the extent to which communities changed following disturbance by comparing shifts in species richness, biomass, and composition among the final eight treatments, relative to pre-disturbance values. Since each final treatment had a unique temporal trajectory of experimental conditions, we treated each of these eight treatments as unique for these analyses (rather than nested or crossed) and compared differences among them to interpret results. We analyzed the univariate responses (changes in richness and biomass) with ANOVA and examined treatment effects by comparing specific treatment pairs with post hoc tests (Tukey honestly significant difference procedure [HSD]). We examined the relative strength of changes in community composition across treatments by constructing a distance matrix in which cells represented the Euclidian distance between final cover (as a proportion of the panel) of each species present and the pre-disturbance cover of that species in that panel community. We did this for primary cover species only and for the total, pooled cover of all species present. We analyzed each matrix with PERMANOVA in PRIMER (v.6), using 999 permutations ($P = 0.001$ is the lowest possible value), and conducted post hoc SIMPER analyses to examine species that contributed most to differences in the extent of compositional changes. For interpretation relative to our main question, we emphasize comparisons among communities exposed to low salinity, and we used the aforementioned analyses to explicitly ask whether predation before or after the event had greater influence on changes in species richness, biomass, and per-species cover following disturbance.

For recruitment analyses, we examined whether cage treatment or two-week time period affected the abundance of recruits by taxon with generalized linear models (Poisson GLM) in R (base R, log link function). Because of the nature of these questions, we incorporated both factors in the models as fixed effects (time period here is binned and we

wanted to understand which periods differed from others). We used a quasi-GLM to correct the standard errors after encountering overdispersion and applied an analysis of deviance approach (drop1 function in R, “ F ” test). We report deviance-based statistics. We plotted response, Pearson, scaled Pearson, and deviance residuals to validate models and found no patterns that would suggest violation of model assumptions. We also analyzed potential cage artifacts by comparing species richness and biomass in panels assembled in cage controls (partial cages) relative to open panels with t tests. We examined differences in species composition between open and partially caged panels with PERMANOVA of Jaccard matrix of species present on the panels.

RESULTS

Predation during initial community assembly

After three months, all experimental panels were covered in diverse invertebrate communities (species pool = 50 taxa), but those assembled in the presence vs. absence of predators were consistently different in composition (Fig. 1; total cover: pseudo- $F = 184.8$; $df = 1, 62$; $P[\text{perm}] = 0.001$; primary cover taxa: pseudo- $F = 29.2$; $df = 1, 62$; $P[\text{perm}] = 0.001$). Panel communities from caged treatments were typically dominated by the large-bodied solitary tunicate, *Ascidia sydneiensis* (Fig. 1;

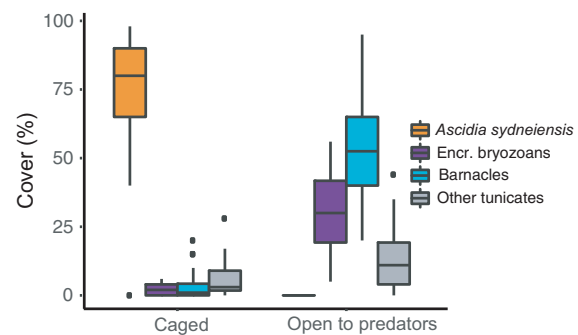


Fig. 1. Box plot of compositional differences in dominant primary substrate taxa between invertebrate communities assembled inside (left) and outside (right) predator-exclusion cages. Except for the solitary tunicate *Ascidia sydneiensis*, which comprised substantial cover on its own, we pooled species for depiction into the following groups: encrusting (“Encr.”) bryozoans, barnacles, and other tunicates (see Appendix S2: Table S1 for a list of these species).

Appendix S1: Fig. S4), and had roughly three times greater biomass than those exposed to predators during assembly (caged mean = 347.6 ± 119.2 g SD; uncaged mean = 104.1 ± 29.7 g SD; $t = 11.2$, $df = 34$, $P < 0.0001$). In contrast, *A. sydnei* was absent from all 32 panels open to predators during assembly. These were instead comprised mostly of barnacles, encrusting bryozoans, and colonial tunicates (Fig. 1; Appendix S1: Fig. S4; full list in Appendix S2: Table S1). Other taxa present at lower frequencies in both treatments included a broad assortment of polychaete worms, anemones, bivalves, sponges, hydroids, one alga, and one tube-forming (vermetid) gastropod. We found no effect of predation treatment on species richness (means: 15.4 species/panel on caged and 14.5 on uncaged panels; $t = 1.4$, $df = 58$, $P = 0.17$). Communities therefore differed between treatments in biomass and species composition, but not richness, prior to receiving disturbance in the next experimental phase.

Predation effects on disturbance resistance

Comparisons among the final eight treatments enabled us to examine how, and whether, predation during assembly or recovery affected communities' resistance to change following the low-salinity disturbance. We found significant differences in compositional changes following disturbance among predation treatments for both primary substrate holders (Fig. 2; pseudo- $F = 14.03$; $df = 7, 25$; $P[\text{perm}] = 0.001$; Appendix S2: Table S3) and full communities (pseudo- $F = 8.70$; $df = 7, 25$; $P[\text{perm}] = 0.001$; Appendix S2: Table S3). Large shifts in biomass and species composition occurred after the low-salinity disturbance for communities assembled in predator-exclusion cages, including a complete loss of the formerly dominant *A. sydnei*, and growth of distinctly different communities comprised mostly of encrusting bryozoans, colonial tunicates, and barnacles (Fig. 2). After a month of recovery, disturbed panels assembled without predation had lost a mean 42–66% of their pre-disturbance biomass, depending on final predation treatment (Fig. 2). In contrast, all communities exposed to predators during assembly gained biomass relative to pre-disturbance measures, resulting in significant biomass differences among treatments ($F = 55.57$; $df = 5, 42$; $P < 0.0001$) and suggesting normal growth processes were largely

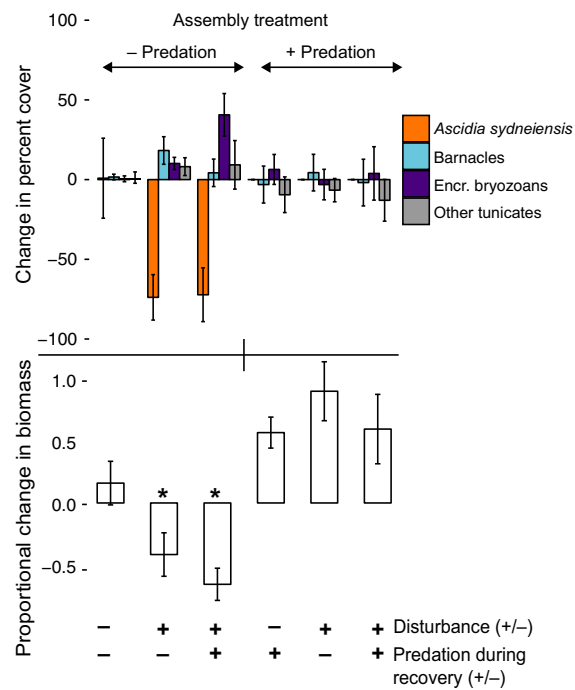


Fig. 2. Shifts in cover of dominant taxa (upper panel) and per-community biomass (lower panel) after low-salinity disturbance (except for controls) and a one-month recovery period with or without predation, relative to pre-disturbance values. We pooled encrusting ("Encr.") bryozoan, barnacle, and tunicate species other than *Ascidia sydnei* into these broader groups for depiction (full list in Appendix S2: Table S1). Asterisks denote biomass changes significantly different from others (Tukey honestly significant difference procedure, $P < 0.05$). We depict proportional shifts in biomass since initial predation conditions drove large differences in biomass prior to disturbance. The magnitude of biomass shifts ranged from mean increase of 95 g to a mean loss of 250 g depending on treatment. For simplicity, two of four control groups are shown (but see Appendix S2: Fig. S3).

uninterrupted. We depict these shifts as proportional changes in Fig. 2, since pre-disturbance biomass in communities assembled without predators was roughly triple that in those assembled with predators. Changes in biomass per community ranged from a mean increase of 95 g (SD = 23.8 g) in communities assembled with predators, exposed to low salinity, and recovered without predation, to a mean loss of 250 g (SD = 163.0 g) for communities assembled without predation,

exposed to low salinity, and recovered in the presence of predators. Surprisingly, we detected no shifts in species composition relative to pre-disturbance assemblages in communities assembled in the presence of predators (Fig. 2; Appendix S2: Tables S3, S4). Retrieval batches did not affect results (Appendix S2: Tables S3, S4).

Following disturbance, predation during the recovery period only influenced composition for communities assembled without fish predation (Fig. 2, upper panel; see also Appendix S2: Tables S3, S4). Although pre-event predation strongly affected biomass responses to disturbance, predation during recovery did not (Fig. 2, lower panel; Tukey HSD for initially open panels: $P = 0.30$, and initially caged ones: $P = 0.61$). For communities assembled in cages, fish access during recovery modified the relative cover of species in the emergent assemblage (Fig. 2). Post-disturbance predation did not affect species composition for communities open to predators during assembly (primary cover: $t = 0.96$, $P[\text{perm}] = 0.48$; total cover: $t = 0.93$, $P[\text{perm}] = 0.64$). Final predation treatments alone also had no effect on species richness ($F = 0.39$; $df = 7, 56$; $P = 0.90$). Predation during recovery therefore had less overall impact on disturbance responses than predation during assembly.

In SIMPER analyses, differences in how community structure changed with disturbance among treatments were dominated primarily by the following taxa, to an extent that depended on the treatment comparison in question: the solitary tunicate *A. sydnei* (decreases of 72.3–73.9% cover per panel for initially caged panels, contributing >50% of the differences between treatments in which it had been present prior to disturbance), the encrusting bryozoan *Schizoporella pungens* (increase of 5.9–23.3% cover per panel, contributing up to 10% of treatment differences), and the colonial tunicate *Sympyga brakenhielmi* (up to 1.3% cover increases, contributing up to 13% of treatment differences). These summaries include communities in both post-disturbance predation treatments for initially caged panels (those initially open to predators had no significant changes in per-species cover after disturbance).

Although *A. sydnei* drove a substantial portion of treatment effects, differences remained significant when we removed *A. sydnei* from analyses (primary cover: $F = 4.08$; $df = 7, 56$;

$P[\text{perm}] = 0.001$). We note that this analysis does not remove the ecological effect of *A. sydnei*, since other species' responses may have been linked to the loss of this competitor.

Control treatments not receiving low-salinity disturbance did not change in composition (Fig. 2), richness, or biomass except (predictably) in the single treatment in which predators were given access to previously caged, undisturbed panels (Appendix S2). We emphasize two of these four control treatments in our figures for simplicity (but see Appendix S2: Fig. S3).

Recruitment patterns, cage artifacts, and predator identification

All taxa recruited at some level of abundance both before and after the disturbance treatments, but recruitment varied by two-week sampling period (Appendix S2: Fig. S1). We found no significant effect of cage treatment on the number of tunicates recruiting ($F_2 = 1.1$, $P = 0.34$; Fig. S2), but significant differences by 2-week time period ($F_7 = 7.3$, $P < 0.0001$; Fig. S1). The abundance of tunicate recruits was lower overall during the post-disturbance recovery period, although tunicate recruits were still present on all recruitment panels (7–52 individuals per panel). Lower recruitment post-disturbance may have influenced overall tunicate cover following disturbance, although non-*Ascidia* tunicates were abundant in mature communities even after disturbance (Appendix S2: Fig. S3). We found solitary tunicates, including *A. sydnei*, on 40% of recruitment panels collected during the post-disturbance recovery period. Although these were too small for conclusive taxonomic identification, many of these appeared to be *A. sydnei*, which is not similar even at this stage to other tunicates known to be present in the region. Recruitment of encrusting bryozoans was also low during this post-disturbance period, despite their high proportional representation in final community structure assessments (Fig. S3). Like tunicates, results of recruitment analyses showed no effect of cage treatment but significant differences by time period for encrusting bryozoans (cage: $F_2 = 0.80$, $P = 0.46$; time period: $F_7 = 20.0$, $P < 0.0001$), for barnacles (cage: $F_2 = 0.64$, $P = 0.53$; time period: $F_7 = 4.22$, $P < 0.0001$), and also for less-dominant taxa like sabellid worms (cage: $F_2 = 0.72$, $P = 0.49$; time period: $F_7 = 6.49$,

$P < 0.0001$). The consistent lack of cage treatment effects suggests that predation on older individuals, rather than predation on new recruits or cage artifacts, was the likeliest driver of the community structure patterns we found.

We found no difference in adult communities (developed for three months) between cage control (partial cage) treatments and un-caged treatments in terms of biomass ($t = 0.077$, $df = 7$, $P = 0.94$), species richness ($t = 1.37$, $df = 6$, $P = 0.21$), or composition (pseudo- $F = 0.99$; $df = 1, 7$; $P[\text{perm}] = 0.44$), suggesting that effects of caging apart from excluding predators were minimal.

Cameras trained on the five adult communities exposed to predators for the first time revealed removal of large amounts of invertebrate biomass, including up to an estimated 60% of one panel's cover of *A. sydneiensis*, within the first 8 h of exposure by puffer fishes, notably the white-spotted puffer *Arothron hispidus* and the balloonfish *Diodon holocanthus*.

DISCUSSION

Our results demonstrate how past predation, by shaping community structure, can dramatically influence community stability in the face of acute disturbance. Shifts in marine invertebrate communities would generally be expected following an extreme low-salinity event of the kind we imposed here, the level of which has only occurred twice in the record over roughly fifty years. Theory developed in the context of mostly ongoing, or pressed, stress conditions predicts that such extreme levels of an environmental stressor should overwhelm the importance of species interactions (Menge and Sutherland 1987). However, we found that prior predation during low-stress periods strongly shaped community resistance to acute (pulse) stress conditions. Indeed, predation during assembly essentially eliminated community-level impacts of the disturbance. In contrast, predation after the event only affected disturbance response if there was no predation beforehand, and did so by modifying species composition without affecting biomass (Fig. 2). Early predation had no effect on species richness, but instead increased disturbance resistance by altering community composition via removal of a high-biomass, non-indigenous species (*Ascidia sydneiensis*) that was intolerant of

low-salinity conditions. By keeping this species from dominating communities, predation during assembly enabled development of more disturbance-resistant assemblages.

By considering ecological characteristics underlying these findings, we can envision how legacy effects of consumers may affect stability in a broad suite of systems via various pathways (Fig. 3). These include pathways mediated by species diversity, or by composition and biomass. Findings here emphasize one of these scenarios, in which a competitively dominant species is vulnerable to both consumers and disturbance, while more consumer-resistant taxa are also more robust to physical perturbation. Both criteria may be met in systems with “weedy” species (Parker and Hay 2005, Ortega et al. 2012), including those with palatable dominant or invasive species that have little resistance to extreme climate conditions such as drought, severe freezes or heat waves, storms, or salinity extremes. These dynamics are unlikely to apply in systems where dominant native or NIS are less susceptible than other community members to predation. However, where consumer control of NIS is strong, they may remain undetected (such as may have occurred with *A. sydneiensis* here, had we not used anti-predation cages). This possibility sets up the potential for rapid, unforeseen shifts in disturbance responses to occur where consumer declines release biotic control of potential invaders.

At the same time, other physical and ecological factors could modify or override the types of responses that we found here. Milder events like seasonal shifts in physical conditions may control weedy species vulnerable to physical stress. In our model system, for example, a very wet season could reduce cover of *A. sydneiensis* and reduce the strength of the predation–stability relationship. The strength of that relationship may also depend on the timing of events relative to species’ phenology. Other species interactions, which we did not explicitly test for, may also affect the outcomes of disturbance. These include competition and facilitation, which we allowed to progress without manipulation in these experiments. Alternative communities with different species composition may also respond differently of course, including algae-dominated communities that may be susceptible not only to salinity minima, but also to longer-term consequences of

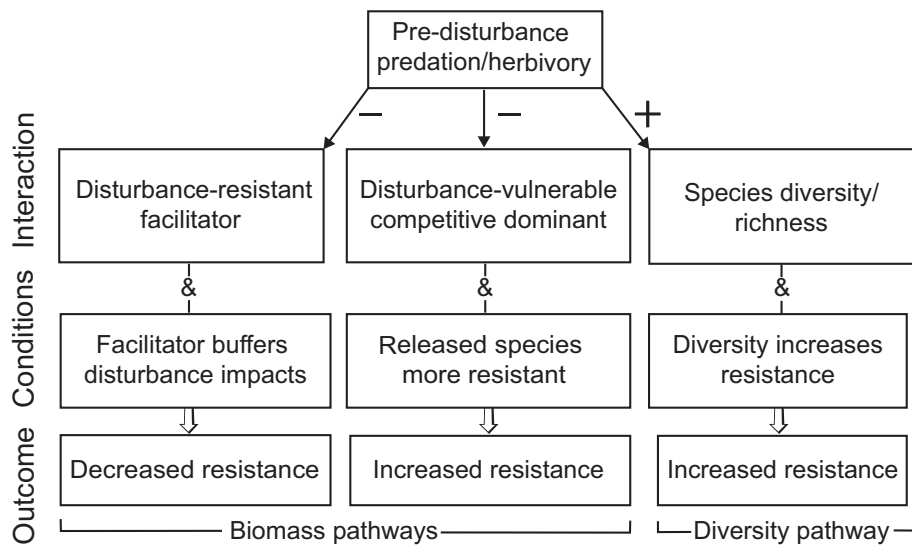


Fig. 3. Key pathways by which predation during assembly could shape community responses to acute physical disturbances. From the top down, symbols accompanying initial arrows denote negative (–) or positive (+) effects of predation on the species or community traits at the “Interaction” level. The “Conditions” level depicts conditions required for the responses described in the lowermost “Outcomes” level. The two left pathways operate by removing biomass of taxa playing key roles as facilitators or dominant competitors. The right pathway shows how predator effects on species diversity could mediate community stability.

severe storms like changes in nutrient concentrations and turbidity.

Alternative routes by which predation prior to disturbance could affect stability include diversity-mediated pathways and systems in which consumers limit foundation species that buffer others from environmental stress (Fig. 3). In the latter situation, prior predation or herbivory could erode community-level resistance by decreasing the abundance of protective habitat present when a disturbance strikes. Certainly, we know consumers can degrade biogenic habitats, some of which buffer environmental stresses. For example, ungulate grazing can shift grassland community composition to less fire-resistant species (Radloff et al. 2014). Similarly, crown-of-thorns starfish damage fringing coral reef structure that, when intact, may buffer other taxa from hurricane-driven mechanical damage (Wilson et al. 2006). In each of these scenarios, consumer effects on community resistance to physical disturbance could occur well before an event itself, as findings here emphasize.

Such historical or “ghost” interactions may be important considerations when attempting to predict current responses to escalating physical

disturbance regimes under global change, especially in the many systems that have already lost large populations of consumers (Estes et al. 2011, Ripple et al. 2015). Although the tropical invertebrate communities we studied here assemble relatively quickly, predator influences may have occurred in the more distant past in other systems, and could influence disturbance resistance even if their populations have been reduced or removed altogether. Our results provide experimental evidence of one of the multiple pathways whereby ecological impacts of escalating physical disturbances could be exacerbated by current or past declines in consumers. More optimistically, findings here imply that in at least some systems, strategies to maintain food webs could also enhance resilience to increased physical disturbances associated with climate change.

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DATA AVAILABILITY

Data are available at <https://figshare.com/s/b37c8a832766b722fd2d>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1986/full>