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Ocean acidification increases the impact of typhoons on algal communities

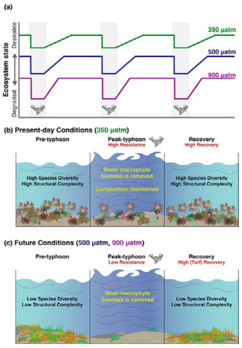
Callum J. Hudson [a,b,1], Sylvain Agostini [c], Shigeki Wada [c], Jason M. Hall-Spencer [a,c], Sean D. Connell [d], Ben P. Harvey [c,*,1]

[a] *Marine Biology and Ecology Research Centre, University of Plymouth, Plymouth PL4 8AA, UK*
[b] *Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna-son, Okinawa 904-0495, Japan*
[c] *Shimoda Marine Research Center, University of Tsukuba, 5-10-1 Shimoda, Shizuoka 415-0025, Japan*
[d] *Southern Seas Ecology Laboratories, School of Biological Sciences, The University of Adelaide, Adelaide, 5005, SA, Australia*

HIGHLIGHTS

- Algal community dynamics studied with three-year monthly surveys at a CO_2 seep
- Acidification consistently altered community composition across all seasons
- Structurally complex communities shifted to degraded 'turf' state with rising pCO_2
- Acidification-driven community changes were maintained by typhoon disturbance
- Turf-dominated communities displayed low resistance to typhoons

GRAPHICAL ABSTRACT



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ABSTRACT

Long-term environmental change, sudden pulses of extreme perturbation, or a combination of both can trigger regime shifts by changing the processes and feedbacks which determine community assembly, structure, and function, altering the state of ecosystems. Our understanding of the mechanisms that stabilise against regime shifts or lock communities into altered states is limited, yet also critical to anticipating future states, preventing regime shifts, and reversing unwanted state change. Ocean acidification contributes to the restructuring and simplification of algal systems, however the mechanisms through which this occurs and whether additional drivers are involved requires further study. Using monthly surveys over three years at a shallow-water volcanic seep we examined how the composition of algal communities change seasonally and following periods of significant physical disturbance by typhoons at three levels of ocean acidification (equivalent to means of contemporary ~350 and future ~500 and 900 µatm pCO_2). Sites exposed to acidification were increasingly monopolised by structurally simple, fast-growing turf algae, and were clearly different to structurally complex macrophyte-dominated reference sites. The distinct contemporary and acidified community states were stabilised and maintained at their respective sites by different mechanisms following seasonal typhoon disturbance. Macroalgal-dominated sites were resistant to typhoon damage. In contrast, significant losses of algal biomass represented a near total ecosystem reset by typhoons for the turf-dominated communities at the elevated pCO_2 sites (i.e. negligible resistance). A combination of disturbance and subsequent turf recovery maintained the same simplified state between years (elevated CO_2 levels promote turf growth following algal removal, inhibiting macroalgal recruitment). Thus, ocean acidification may promote shifts in algal systems towards degraded ecosystem states, and short-term disturbances which reset successional trajectories may 'lock-in' these alternative states of low structural and functional diversity.

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* Corresponding author.
E-mail address: ben.harvey@shimoda.tsukuba.ac.jp (B.P. Harvey).
[1] Equal contribution: Callum J. Hudson and Ben P. Harvey contributed equally to this work.

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1. Introduction

Long-term exposure to gradual environmental change, short periods of significant perturbation, or a combination of both, can alter the structure and functioning of biological communities (Halpern et al., 2008; Petraitis et al., 2009). Ecosystems that are 'stable' against disturbance display 'resistance' (withstanding change in the face of disturbance) and/or 'recovery' (returning to the pre-disturbance state after perturbation), maintaining the same composition, functioning, and internal regulating feedbacks (Meredith et al., 2018). When systems fail to resist or recover following disturbance, regime-shifts may occur (Duarte et al., 2009), tipping ecosystems into new, reconfigured states comprised of different sets of species and controlled by different processes (Rocha et al., 2015; Wernberg et al., 2016). Regime shifts are concerning as they can lead to the dominance of fast-growing, early successional species assemblages, leading to large losses of ecological and economic resources, such as habitat provision, and biodiversity (Hastings and Wysham, 2010). Many drivers of state change have been identified (for review, see deYoung et al., 2008), however our understanding of the mechanisms that stabilise different ecosystems against regime shifts or lock communities into altered states is limited, yet critical to anticipating future states and meeting the challenge of reversing unwanted state change.

Changes in the intensity and duration of disturbances have further implications for their potential to transition communities to a new state and maintain regime shifts, especially when multiple stressors interact and operate together (Folke et al., 2004). Both 'press' (long-term sustained perturbation such as ocean acidification), and 'pulse' (short but intense periods of perturbation such as storm damage) disturbances can push ecosystems beyond tipping points, causing regime shifts (e.g. Hughes, 1994; Möllmann et al., 2009; Harvey et al., 2021a) with consequences for alternate states that are both difficult to predict and prevent. Regime shifts are likely if 'press' and 'pulse' disturbances overlap, and if the frequency, intensity, or duration of disturbances increase (Posey et al., 1996; Peterson, 1996; Wang et al., 2016).

Community stability varies as environmental conditions and ecosystem states change, determined by positive (self-reinforcing) feedback loops arising from species interactions and physiological traits that can either resist disturbance or promote recovery after perturbation (Folke et al., 2004; Connell and Ghedini, 2015; Nimmo et al., 2015). Ocean acidification, a global 'press' disturbance shifting carbonate chemistry conditions as increased atmospheric CO_2 is drawn down by the ocean, is projected to simplify coastal ecosystems due to losses in habitat, structural complexity, and biodiversity (Kroeker et al., 2011; Vizzini et al., 2017; Agostini et al., 2018). This ecosystem reorganization arises due to the unequal impact that ocean acidification has on marine organisms (Connell et al., 2018), acting as both a resource for some primary producers (Koch et al., 2013; Cornwall et al., 2017), and a physiological stressor for other organisms, such as marine calcifiers (Harvey et al., 2018; Agostini et al., 2021b). By promoting the loss of certain functional groups and restructuring community composition, ocean acidification might reduce the ability of marine communities to withstand disturbances and remain unchanged, reducing their stability (Folke et al., 2004).

To capture the complexity of natural systems and investigate the long-term consequences of ocean acidification at the community-level, an increasing number of studies have used marine CO_2 seeps as natural analogues of future conditions (Hall-Spencer et al., 2008; Milazzo et al., 2014; Agostini et al., 2018; Connell et al., 2018; Foo et al., 2018). Some coastal volcanoes cause CO_2 to bubble through the seabed, creating localised gradients of acidification. These offer insights into the long-term consequences of ocean acidification on ecosystems by studying communities that are naturally assembled, complex, and shaped by species interactions (Hall-Spencer and Harvey, 2019). Studies at CO_2 seeps show that ocean acidification increases the probability of regime shifts in many coastal ecosystems with the large-scale loss of complex habitat-forming species (e.g. kelp forests, corals) and more homogenous algal dominance (Enochs et al., 2015; Connell et al., 2018; Harvey et al., 2021a). The degradation of community stability is often associated with shifts to lower baselines of diversity and complexity (Allison, 2004; Hughes and Stachowicz, 2004). Simplified communities may also be more susceptible to additional perturbation, including short-term 'pulse' disturbance events such as storms. As such, acidification-driven changes in species interactions, composition, and community dynamics, by indirectly altering responses to additional stressors, may promote and entrench regime-shifts, maintaining conditions which enable alternative, opportunistic assemblages to dominate.

Typhoons are tropical cyclones with sustained winds that exceed 33 m s^{-1} (Japan Meteorological Agency, 2021). These powerful low-pressure weather systems can be both disruptive and dangerous to marine organisms and human populations (Zhan et al., 2012). Prevalent throughout the Northern and Western Pacific, typhoons typically form in the tropics before tracking poleward (Zhan et al., 2012; Hsu et al., 2013). Typhoons are highly seasonal, peaking in frequency during late summer to early autumn, and contribute to annual variation within marine communities (which for algal assemblages remains understudied). Typhoons represent a major physical 'pulse' disturbance for coastal ecosystems, generating large waves that can severely damage structurally important habitats such as coral reefs (Done, 1992; Harmelin-Vivien, 1994), mangroves (Diele et al., 2013), seagrasses (Wilson et al., 2020), and macroalgae (Vroom et al., 2005; Hall-Spencer and Harvey, 2019; Cattano et al., 2020). Typhoons also alter the community structure and functioning of species living in association with these habitats (Gardner et al., 2005; Teixidó et al., 2013), such as fish (Cattano et al., 2020), invertebrates (Harmelin-Vivien, 1994; Diele et al., 2013), and seaweeds (Pocklington et al., 2018; Wernberg et al., 2020). The amount of damage caused is determined by the frequency and magnitude of typhoons (Lee et al., 2012; Hsu et al., 2013) and the stability of the marine community against physical disturbance. Rising sea surface temperatures in the western North Pacific over the past 30 years have meant that the average latitude at which typhoons reach their peak intensity has increased (Kossin et al., 2016). The impacts of strong typhoons on temperate coastal communities have and will continue to become increasingly common, exacerbated by climate heating (Webster et al., 2005; Mann and Emanuel, 2006; Lee et al., 2012; Murakami et al., 2012; Zhan et al., 2012).

Prior to this study we observed that algal community coverage and composition varied seasonally and was greatly affected following typhoon disturbance, however this response appeared to differ between the ambient and elevated pCO_2 areas of our study site (Fig. 1). In this study, we test this observation and investigate algal communities along a natural pCO_2 gradient in Japan to assess how their composition varies with increasing pCO_2. We also investigate the seasonality of algal communities to understand patterns of compositional change and how this is altered by ocean acidification. We then examine how ocean acidification-driven changes in community structure mediates their stability (resistance and recovery) against seasonal 'pulses' of typhoon disturbance. By conducting the study over three years, we were able to test the responses (resistance and recovery) of algal communities to several typhoon seasons. This temporal replication provides new insights into the future impact of typhoons on acidified oceans.

2. Materials and methods

2.1. Study site and environmental context

Algal community assessments were carried out in three locations along a pCO_2 gradient around Shikine Island, Japan (34°19′9″ N, 139° 12′18″ E) from September 2016 to December 2019. These three locations were 1) a reference area outside the influence of the CO_2 seep, 2) a 'near-future' elevated pCO_2 area, and 3) an 'end-of-the-century' elevated pCO_2 area (hereafter referred to as '350 μatm', '500 μatm' and '900 μatm', respectively). The acidified sites offer potential for space-for-time analyses, serving as analogues for future conditions under projections of changing ocean pH (RCP 8.5 scenario, IPCC, 2013). The Shikine Island seep site has been surveyed since 2014, and its carbonate chemistry and biology

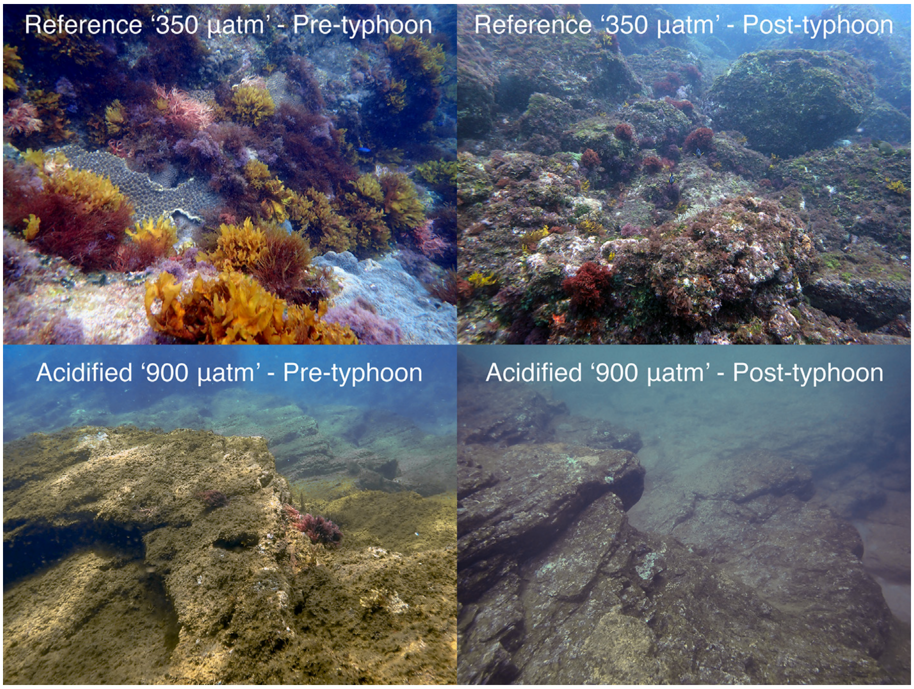

Fig. 1. Examples of seascapes found at Reference '350 µatm' and acidified '900 µatm' pCO_2 locations before typhoon disturbance (pre-typhoon) and after (post-typhoon).

are well characterised (Agostini et al., 2015, 2018, 2021a; Harvey et al., 2018, 2019, 2021a, 2021b; Witkowski et al., 2019; Kerfahi et al., 2020; Cattano et al., 2020). Located at 34° north, Shikine Island is within the temperate-subtropical biogeographic boundary zone (see Fig. S1). Here, the coastal communities on rocky reef habitats are dominated by large stands of macroalgae (Harvey et al., 2021b). The pCO_2 conditions are temporally stable over the long-term, whilst still following natural diurnal and seasonal variation, and are not confounded by differences in temperature, salinity, dissolved oxygen, total alkalinity, nutrients or depth relative to reference sites (Agostini et al., 2015, 2018; Harvey et al., 2019, 2021b; Agostini et al., 2021a). The '350 µatm' location had a mean pH_T of 8.137 ± 0.056 (SD), the '500 µatm' location area had a mean pH_T of 7.983 ± 0.119 (SD), and the '900 µatm' location had a mean pH_T of 7.781 ± 0.105 (SD). The mean carbonate chemistry of each location is presented in Table 1. A full description of the locations is provided in the supplementary material (Fig. S1). Shikine Island is exposed to frequent and significant disturbance from tropical cyclones (including typhoons), which peak in frequency during the late summer and early autumn (August–September) (Yumoto and Matsuura, 2001). For specific information regarding typhoon characteristics and dates during the study period, see Table S1.

2.2. Experimental design and analysis

2.2.1. Data collection

To determine how ocean acidification influences the composition and structure of algal communities over time, eight permanent quadrats (50 × 50 cm) were marked using anchor bolts (8.5 mm width, 70 mm length) at each of the three locations ('350 µatm', '500 µatm' and '900 µatm'). Quadrats within these locations were deployed haphazardly over a ca. 400 m^2 area with at least 3 m between them, fixed to upward-facing substrata. As algae were the focus of this study, random stratified sampling was used to prevent the inclusion of coral within quadrats. Individual quadrats at each location were photographed (Tough TG-5, Olympus, Japan) monthly (with four exceptions when poor conditions prevented access) a total of 36 times over a period of three years (September 2016–December 2019) for community assessment.

2.2.2. Community analysis

Following methods used by Harvey et al. (2021b), algal community composition was assessed using the ImageJ Fiji processing package. An 8 × 8 grid of points (n = 64) was superimposed onto each of the photoquadrats, before the abundance of the algal functional group under

Table 1

Summary of the carbonate chemistry for the 350 µatm and 900 µatm locations. The pH_T (350 µatm, n = 1964; 500 µatm, n = 1760; 900 µatm, n = 10,818), salinity (350 µatm, n = 1964; 500 µatm, n = 1760; 900 µatm, n = 10,818), and total alkalinity (A_T; 350 µatm, n = 56; 500 µatm, n = 10; 900 µatm, n = 47) are measured values. All other values were calculated using the carbonate chemistry system analysis program CO2SYS: Seawater pCO_2, dissolved inorganic carbon (DIC), bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), carbon dioxide (CO_2), saturation states for calcite (Ωcalcite), and aragonite (Ωaragonite). Values are presented as mean, with standard deviation below. NOTE: Carbonate chemistry data are sourced from Agostini et al. (2018), Harvey et al. (2019), and Harvey et al. (2021b).

Location	pH_T	Salinity (psu)	A_T (µmol kg^{-1})	pCO_2 (µatm)	DIC (µmol kg^{-1})	HCO_3^- (µmol kg^{-1})	CO_3^{2-} (µmol kg^{-1})	Ωcalcite	Ωaragonite
'350 µatm'	8.137	34.504	2264.29	316.057	1962.694	1740.629	211.979	5.087	3.301
	0.056	0.427	15.34	47.466	34.376	55.084	22.221	0.534	0.348
'500 µatm'	7.990	34.17	2264.35	471.30	2031.16	1852.31	163.71	3.94	2.56
	0.086	0.44	16.62	117.01	40.16	60.59	24.88	0.59	0.39
'900 µatm'	7.788	34.351	2268.33	841.148	2125.785	1984.889	115.150	2.771	1.805
	0.106	0.484	19.45	291.762	39.381	52.510	21.308	0.512	0.336

each point was identified and recorded. Functional groups were assigned following descriptions provided by Steneck and Dethier (1994), sorting algal groups based on their morphology, thallus size and complexity: filamentous algae, foliose algae, corticated foliose algae, corticated macrophytes, turf algae, microalgae, leathery macrophytes, articulated calcareous algae, and crustose coralline algae (CCA). For a list of the dominant species and associated functional groups at each location, refer to the supplementary material (Table S2). The complexity of the algal community within each quadrat was also determined following Steneck and Dethier (1994), whereby ranks (0–5) assigned to the biogenic habitat complexity provided by each functional group were combined with their relative abundance within each of the communities that they occurred. The total structural complexity was calculated using the following ranking categories: other = 0 (i.e. macroinvertebrates), bare rock = 0, microalgae = 1, turf = 1, filamentous algae = 2, foliose algae = 3, CCA = 3, corticated foliose algae = 3.5, articulated calcareous algae = 4, corticated macrophytes = 4, and leathery macrophytes = 5. To calculate overall community complexity, the complexity value associated with the group represented under each superimposed point were summed (for example, for a community consisting entirely of filamentous algae: $64 \times 2 = 128$). Complexity values were then standardised between 0 and 1 (dividing total quadrat score by the maximum potential score of 320).

2.2.3. Algal community stability

Changes in community percentage cover and complexity were assessed between different stages of the typhoon season hereby referred to as 'Before', 'After', and 'Recovery' respectively. For all $p\text{CO}_2$ levels, communities possessed their highest level of algal coverage and structural complexity during the 'Before' period (April–June) prior to the peak typhoon season, facilitated by summer growth and low-levels of disturbance. The 'After' period (October–December) refers to the months following the peak typhoon season when typhoons had reduced communities to low levels of algal cover and structural complexity. A 'Recovery' period (January–March) coincided with the start of the spring algal bloom, during which the algae began to grow following disturbance.

2.3. Statistical analysis

Statistical analyses were conducted using R (version 4.04; R Development Core Team, 2022), with the 'vegan' (Oksanen et al., 2019) and 'lme4' (Bates et al., 2015) packages. The 'ggplot2' (Wickham, 2016) and 'ggpubr' (Kassambara, 2019) packages were used for figure production. For each of the analyses performed, the package and specific function used in R are listed below as 'package::function'.

Differences in community composition (based on the relative percentage cover of different functional groups) between locations (three levels: ('350 μatm', '500 μatm' and '900 μatm')) were visualised using principal component analysis (PCA; ggord::biplot). The significance of these differences were then determined using one-way and post-hoc pairwise permutational analysis of variance (PERMANOVA) comparisons based on Bray–Curtis dissimilarity (vegan::vegdist and vegan::adonis). Multivariate homogeneity of groups dispersions was also tested (vegan::betadisper), and did not significantly differ.

To test for differences in the responses of both the percentage cover and structural complexity of algal communities exposed to different levels of typhoon disturbance and $p\text{CO}_2$, general linear mixed effect models (GLMM) were made, with 'Timing' (three levels: 'Before', 'After', and 'Recovery') and 'Location' (three levels: ('350 μatm', '500 μatm' and '900 μatm')) as fixed factors, and 'Quadrat', 'Month', and 'Year' as nested random effects (lme4::lmer and emmeans::pairwise). The typhoon period itself was excluded from these analyses as changes in community composition is confounded by the exact timing, strength, and number of storms in relation to sampling, reducing the accuracy of interannual comparisons. The same models were also used to test how differences in algal functional group abundance at different times (relative to the peak typhoon season) explained these patterns of community percentage cover and complexity change. By assessing how communities respond following typhoon disturbance, we could assess whether mechanisms of resistance (low immediate impact of disturbance), resilience (rapid return to pre-disturbance states), or both were controlling community dynamics.

3. Results

3.1. Community differences between $p\text{CO}_2$ conditions and seasons

For all three locations ('350 μatm', '500 μatm' and '900 μatm'), the percentage cover and community composition of the algal communities showed clear patterns within and between years (Fig. 2). High algal coverage was observed during the 'pre-typhoon' spring and summer months (around April to June), whereas the occurrence of bare rock increased in the autumn to winter months (around September to December) following the typhoon season when physical disturbance was greatest (Fig. 2).

Overall community composition was clearly separated by 'Location', associated with changes in $p\text{CO}_2$ (PERMANOVA: Location, $F_{2,\ 858} = 63.61$, $p < 0.001$; Fig. 3; Table 2). Community composition at the 350 μatm location showed clear and consistent differences to both the 500 μatm and 900 μatm locations (Fig. 3; Table S3 PERMANOVA *post-hoc*: all $p < 0.01$). Communities in the 350 μatm location had higher structural complexity, with greater coverage of corticated macrophytes, foliose algae, and crustose coralline algae, compared to the turf and bare rock dominated acidified sites (Fig. 2). Communities with each $p\text{CO}_2$ conditions varied and responded similarly between seasons, however differences were consistently maintained between $p\text{CO}_2$ conditions (Fig. 2). At the 350 μatm location, the spring and summer months had extensive growth of species such as *Asparagopsis taxiformis* and *Gelidium elegans* (Fig. 2; Table S2). Although typhoons removed significant algal biomass (Fig. 1) macroalgal persistence through the typhoon season, emerging as 'new growth' in winter, formed the basis of the summer community composition, maintaining a more consistent structure between seasons (Fig. 2; Table S2).

At both the 500 μatm and 900 μatm locations, community composition was more variable between seasons (Figs. 4 (g–i) and S2). The highly productive spring and summer months saw the rapid growth of thick turf algal mats, compared to a mix of corticated foliose alga (*Zonaria* sp.) and bare rock present during the autumn and winter months due to the impacts of typhoon disturbance – i.e. the physical removal of turf (Figs. 1 and S2). Despite significant differences between the 500 μatm and 900 μatm locations (Table S3), their community composition had a higher degree of overlap due to the similarities in their functional groups (structurally simpler turf algae and corticated foliose algae). For nine of the 12 months, the composition of communities at the 500 μatm and 900 μatm locations did not significantly differ, suggesting that they respond to environmental change in similar ways (Fig. 3 PERMANOVA results).

3.2. Effects of ocean acidification on community stability

Algal communities under different $p\text{CO}_2$ conditions responded to typhoon disturbance differently (Figs. 1 and 2). The percentage cover (%) of algal communities was significantly impacted by 'Timing', but not $p\text{CO}_2$ condition ('Location'), with a significant interactive effect demonstrating changes in the response of the community over time (Type III ANOVA: Timing*Location, $X^2 = 46.58$, $p \leq 0.001$; Table 3 and Fig. 4a–c). Algal percentage cover (% ± SD) 'Before' (93.48 ± 8.21, 90.33 ± 8.58, and 91.27 ± 9.85) and 'After' (72.75 ± 16.50, 52.93 ± 19.45, and 49.15 ± 19.39) typhoons differed significantly at each location ('350 μatm', '500 μatm' and '900 μatm') (Fig. 4a–c). The algal coverage of 'Before' and 'Recovery' (89.92 ± 12.41, 82.01 ± 13.76, and 78.00 ± 18.81) communities (growing in the months following typhoons) also significantly differed for acidified communities, but not under reference $p\text{CO}_2$ conditions (Table S4). The coverage of reference communities remained more stable over time due to resistance to physical disturbance and algal recovery. Although typhoons had a lasting effect on the coverage of acidified communities, these faced far more significant reductions in algal coverage due to

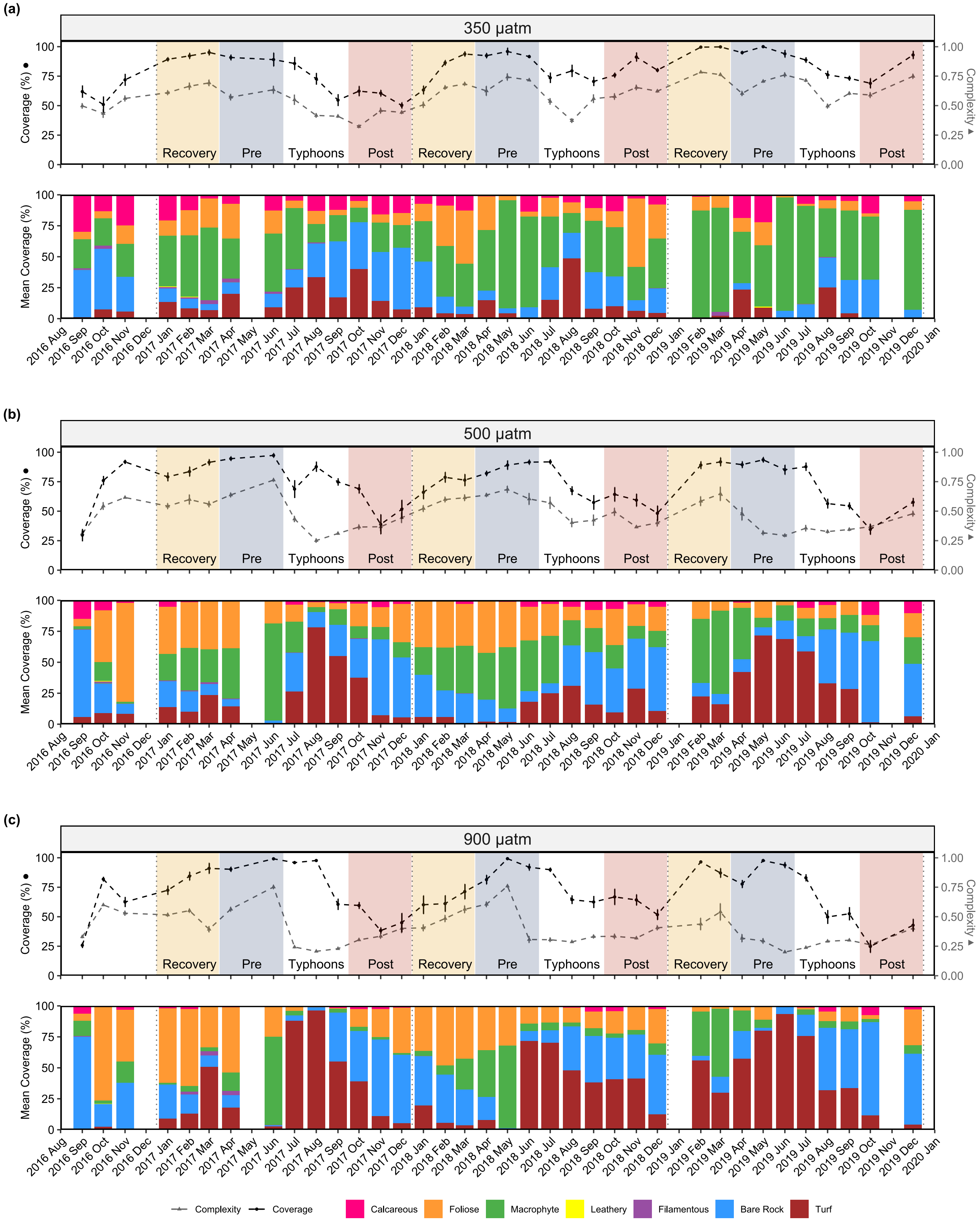

Fig. 2. Average percentage cover (Black); complexity (Grey); and mean coverage (by functional group) of algal communities across each sampling month over a three-year sampling period at (a) 350 µatm CO_2; (b) 500 µatm CO_2; and (c) 900 µatm CO_2. Pre-typhoon periods ("Pre"; April to June; blue), post-typhoon periods ("Post"; October to December; red), and recovery periods ("Recovery"; January to March; yellow) are indicated on the figure. Typhoon periods (July to September) are marked as "Typhoons". Dotted vertical lines denote the start of each new year (2017–2020).

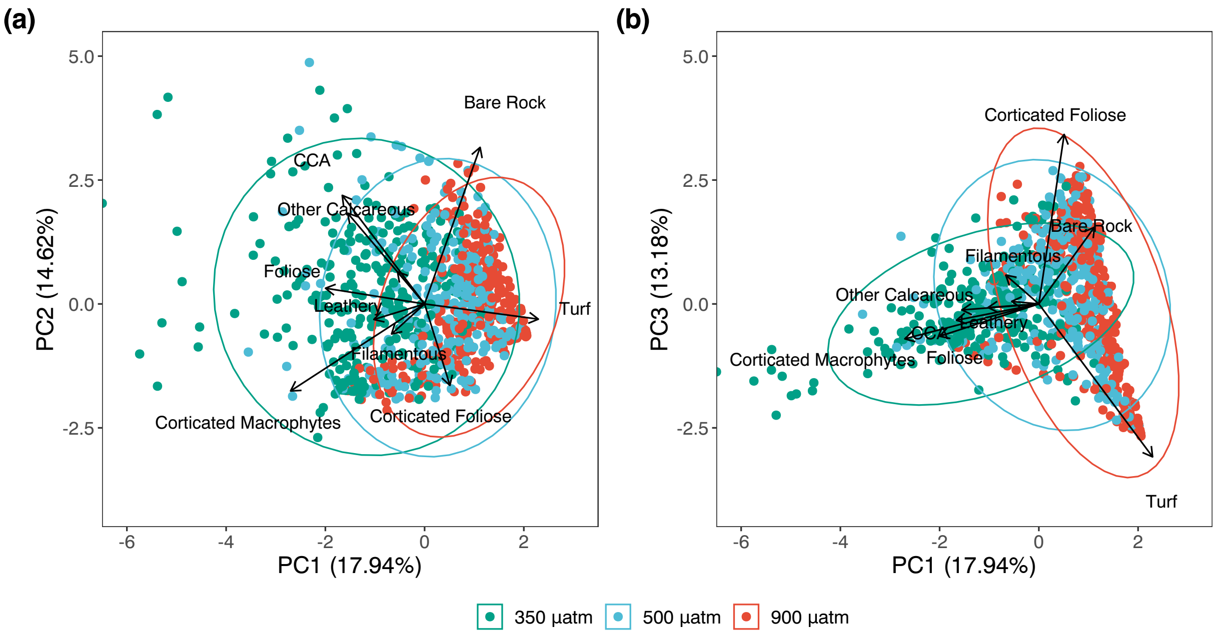

Fig. 3. Community composition of algal functional groups between the three locations, 350 µatm CO_2 (Green), 500 µatm CO_2 (Blue) and 900 µatm CO_2 (Red), as assessed by principal component analysis for (a) PC1 vs. PC2 and (b) PC1 vs. PC3. See Fig. S2 for comparisons of the locations at each month.

typhoon disturbance yet still rapidly recovered, returning to near pre-disturbance conditions (Fig. 4a–c; Table S4).

The structural complexity of algal communities was also significantly impacted by both 'Timing' (ANOVA: $X^2 = 33.30, p \leq 0.001$) and 'Location' (ANOVA: $X^2 = 77.88, p \leq 0.001$; Table 3 and Fig. 4d–f). Structural complexity was significantly reduced in the 'After' communities when compared to the 'Before' and 'Recovery' communities either side of the peak typhoon season (Fig. 4d–f). The structural complexity of these communities did not significantly differ, indicating a return to pre-disturbance levels within the 6 months following the typhoon season. Unlike percentage cover, which started at similar levels for each of the communities prior to disturbance, the mean structural complexity (±SD) of the algal communities in the pre-typhoon season ('Before') was significantly higher for the Reference pCO_2 communities ('350 µatm' = 0.670 ± 0.095; '500 µatm' = 0.552 ± 0.182; '900 µatm' = 0.471 ± 0.215; PERMANOVA *post-hoc*: all $p < 0.001$). Despite displaying similar losses in structural complexity 'After' typhoon disturbance (0.552 ± 0.139, 0.411 ± 0.093, and 0.345 ± 0.076) and a subsequent 'Recovery' of complexity to pre-disturbance levels at each location (0.670 ± 0.097, 0.584 ± 0.101, and 0.487 ± 0.119), the communities exposed to increased pCO_2 remained less complex than the communities found at the reference location (Fig. 4d–f; Table 3, Fig. 5; PERMANOVA *post-hoc*: all $p < 0.001$). As they began at low levels of structural complexity, the increased pCO_2 communities had less structure to lose following disturbance, and lower baselines to recover to.

Acidification-driven changes in community composition, and differences in the response of individual algal functional groups to typhoon disturbance explained changes in community percentage cover and structural complexity (Fig. 4g–i; Figs. S3, S4). Typhoons had a large impact on algal community composition, which differed significantly between all timing pairs, apart from the 'Before' and 'Recovery' communities at '350 µatm' (Fig. 4; Fig. S4 PERMANOVA results). Calcareous and filamentous algae did not significantly change in abundance between pCO_2 conditions or timings (remaining at low frequency), whereas fleshy macrophytes had reduced abundance following disturbance at every location. Bare rock and turf algae increased in abundance following typhoon disturbance and had a stronger association with typhoon seasonality, underpinning the main differences between the 'After' communities and those of the 'Before' and 'Recovery' timings for each location (Fig. S4).

Table 2
PERMANOVA summary for the effects of pCO_2 ('350 µatm' vs. '500 µatm' vs. '900 µatm') on algal community composition. For *p*-values, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Term	*df*	Sum Sq.	Mean Sq.	*F*	*p*
pCO_2	2	21.96	10.98	63.13	0.001***
Residuals	858	148.1	0.173		
Total	860	170.0			

4. Discussion

Whilst other environmental factors also influence community assembly, composition, and dynamics, global research at CO_2 seeps has consistently demonstrated clear ecosystem shifts towards simplified communities at sites with elevated pCO_2 levels (Johnson et al., 2012; Enochs et al., 2015; Sunday et al., 2017; Connell et al., 2018; Foo et al., 2018; Cattano et al., 2020; Harvey et al., 2021a, 2021b; Agostini et al., 2021a). These acidified communities not only have reduced ecological and structural complexity (Figs. 1, 4), but also lower biodiversity, raising concerns about the loss of ecosystem services (Hall-Spencer and Harvey, 2019). Most studies investigating the ecological effects of ocean acidification have not taken seasonality into account, leaving community dynamics between seasons largely unknown (but see Godbold and Solan, 2013, Baggini et al., 2014, Cattano et al., 2020, Harvey et al., 2021b). Here, we found that algal community structure consistently differed between locations with different pCO_2 levels (Fig. 3; Fig. S2), and this persisted across seasons despite profound physical disturbance from typhoons, a seasonal environmental stress which maintained the differences. Increased levels of pCO_2 caused consistent reductions in macrophyte cover (Fig. 2), leaving communities dominated by turf algae, characterised by low functional diversity and structural complexity (Harvey et al., 2021a, 2021b; Agostini et al., 2021a). Conversely, reference communities had greater algal diversity, with more extensive cover of macrophytes and calcareous algae.

Community differences between elevated pCO_2 and reference locations were seen year-round, however they became more pronounced during

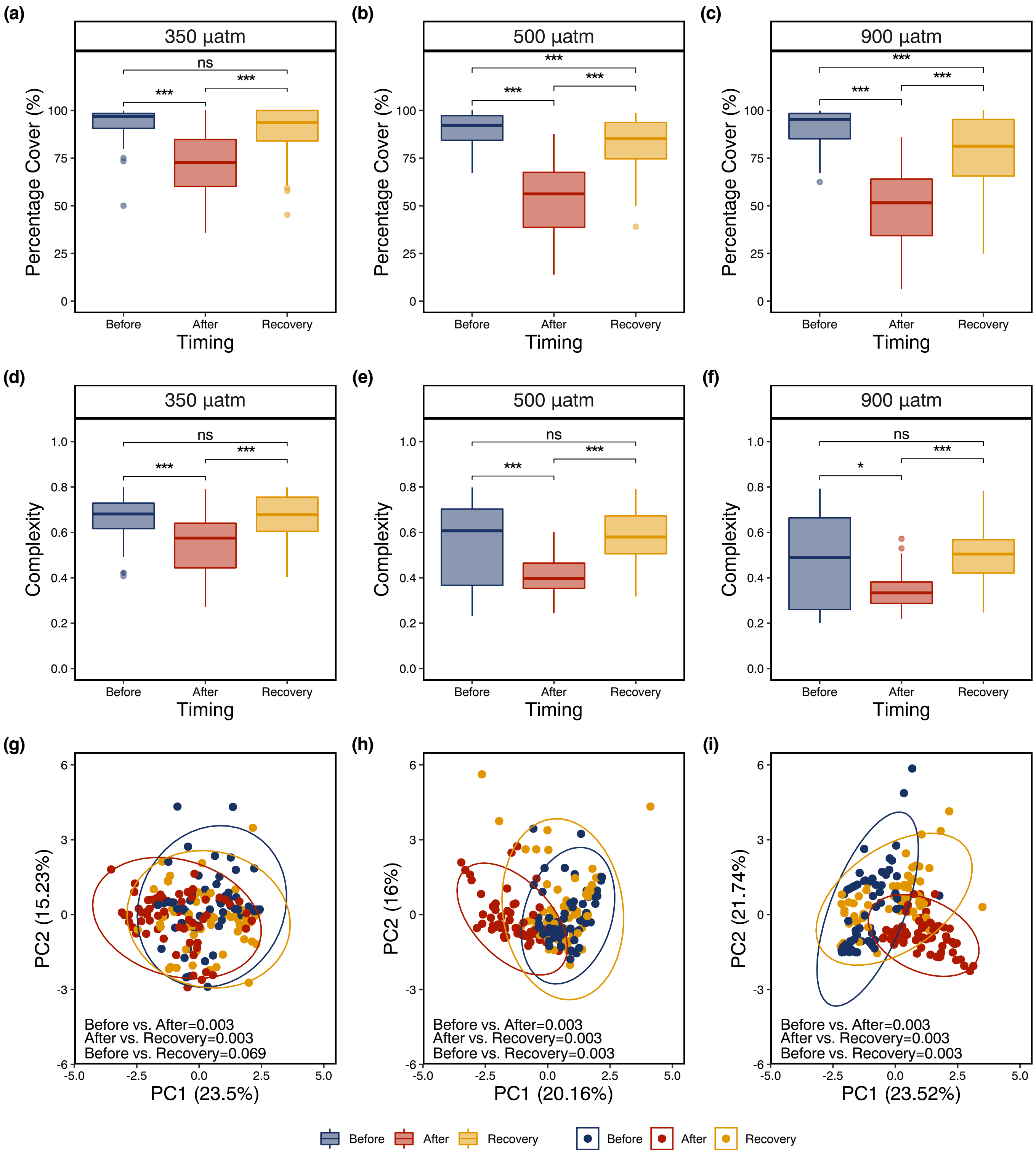

Fig. 4. Percentage cover (a–c), complexity (d–f) and composition (g–i) of communities 'Before' (Blue) and 'After' the typhoon season peak (Red), and the subsequent 'Recovery' period (Orange). The 350 μatm location is shown on the left (a, d, g), the 500 μatm location in the center (b, e, h), and the 900 μatm location on the right (c, f, i). NOTES: Pairwise comparisons within Panels a–f are carried out by Type III ANOVA following GLMM (ns, $p > 0.05$; *$p < 0.05$; **$p < 0.01$;***$p < 0.001$) with the individuals points in a-f indicating outliers. Pairwise PERMANOVA analysis between Timing ('Before', 'After' and 'Recovery') are shown in g–i. To see the Panels a-f separated by year, see Fig. S3, and for more detailed statistics, see Tables S4 and S5.

(1) the spring algal bloom, and (2) the autumn peak typhoon season, associated with large environmental change. During spring, algal biomass peaked, and the elevated and high $p\mathrm{CO}_2$ communities became dominated by thick mats of turf algae (Harvey et al., 2019; Fig. 2). Reference communities did not become turf-dominated, but instead burgeoned with canopy-forming species (e.g. *Asparagopsis taxiformis*, *Gelidium elegans*, *Sarcodia ceylanica*). The lack of turf is likely due to several factors, including the year-round persistence of macrophytes (lack of empty space), removal

Table 3

GLMM Type III Wald chi-square Analysis of Deviance summary for the effect of timing ('Before' vs. 'After' vs. 'Recovery') and pCO_2 condition ('350 µatm' vs. '500 µatm' vs. '900 µatm') on algal community (a) percentage cover (%) and (b) complexity. For p-values, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Term	X^2	df	p
a) Cover (%)			
Intercept	1875	1	<0.001***
Timing	73.43	2	<0.001***
pCO_2	1.208	2	0.547
Timing × pCO_2	46.58	4	<0.001***
b) Complexity			
Intercept	1539	1	<0.001***
Timing	33.30	2	<0.001***
pCO_2	77.88	2	<0.001***
Timing × pCO_2	3.193	4	0.5261

by physical abrasion from fleshy macroalgal thalli (Cheroske et al., 2000), greater top-down control by grazers (Cattano et al., 2020), and a lack of CO_2 enrichment to boost their competitive ability. Autumn typhoons removed the turf algal mats, exposing bare rock; a profound reset of the ecosystem state (Figs. 1 and 2). Typhoon disturbance caused less change in the composition, coverage, and structural complexity of communities at reference pCO_2 levels (Figs. 4 and 5). Algal persistence as low biomass 'new growth' through the winter following typhoon disturbance meant that reference community structure was more stable between seasons and did not differ between the winter (after typhoon disturbance) and the following spring. Our method of calculating structural complexity was limited in that only the functional group and not the size or biomass of the algae was considered. For example, whilst both winter and summer communities were dominated by macrophytes under ambient conditions (receiving similar scores for structural complexity), they differed markedly; summer communities had high biomass and 3-D structure, whereas winter communities had high coverage of the same functional groups, but lower biomass providing less habitat and structure.

Short periods of intense physical disturbance interacted with the effects of long-term acidification exposure on community composition to alter their dynamics. Acidified assemblages were less resistant (reduction of algal coverage and structural complexity) to disturbance from typhoons with more pronounced losses at higher pCO_2 levels (Figs. 2, 4, and 5). Community composition and associated life-histories, traits, and physiological susceptibilities underpinned these differences in community resistance. Complex macroalgal habitats can buffer the influence of climate change (Krause-Jensen et al., 2018), such as mitigating storm surge intensity due to their capacity to attenuate water flow (Rosman et al., 2007) resisting change until disturbances of a greater magnitude are experienced (Schowalter, 2006; Levin and Möllmann, 2015). The weaker attachment strength and low complexity of the algal groups associated with acidified conditions, such as turfs (Peterson, 1996; Harvey et al., 2021a), leaves acidified communities more susceptible to removal by physical disturbance (Wada et al., 2021), representing low levels of resistance (Figs. 4 and 5).

Differences were also observed in the recovery of algal communities following disturbance due to acidification-driven shifts in succession trajectories. Despite experiencing a greater initial impact, assemblages found under elevated pCO_2 rapidly recovered to levels of algal coverage near to those seen pre-disturbance. Enrichment of CO_2 promotes the fast and opportunistic growth of turf algae, leading to rapid turf expansion during the springtime community succession which follows the ecosystem reset of acidified sites by the typhoon season (Connell et al., 2018; Ferreira et al., 2021). Previous studies have shown that turf removal can promote the recovery of macroalgal canopies (Gorman and Connell, 2009), however here turf-dominance was consistently regained at the acidified sites. Due to the proximity of our sites when considered relative to the average radius of typhoons (roughly 3–6 latitude degrees), our study lacked 'disturbance-free' treatments. Despite this, previous studies suggest that even in the absence of disturbance, due to turf-mediated reinforcing feedback loops (sediment trapping, alteration of substrate chemistry, physicochemical environment change, and recruitment inhibition), the development of macroalgal assemblages will not eventually replace established turf communities under acidified conditions (Harvey et al., 2021a). As the acidified communities were less complex than those at reference locations before typhoon disturbance, their recovery only had a low baseline to reach (Fig. 4). This simplified community represents an alternate stable state maintained by a combination of boosted turf growth, the turf-mediated inhibition of slower-growing, structurally complex macrophytes (Ghedini and Connell, 2017a), and regular resetting of succession by physical disturbance under elevated pCO_2 conditions (Gorman and Connell, 2009; Harvey et al., 2021a).

Similar to patterns seen in systems enriched with nutrients (Worm et al., 1999; Gorman et al., 2009), shifts in dominance towards fast-growing *r*-selected species have been widely documented under acidified conditions (Connell and Russell, 2010; Harvey et al., 2019, 2021a; Agostini et al., 2021a), whereby opportunistic species rapidly monopolize primary space, replacing algal canopies (Airoldi, 2003; Gorman and Connell, 2009). Under reference conditions grazing (top-down control) and competition (bottom-up effects) rapidly exclude turf algae, preventing such a regime shift (Kéfi et al., 2016). Concern is growing that rising pCO_2 will remove the feedbacks that stop turfs from monopolising space, and additional coincidental biotic and abiotic change may further reinforce the competitive advantages turf gain over slower growing, typically dominant groups (such as macroalgae; Hughes, 1994, Connell and Russell, 2010, Ghedini and Connell, 2017a), making state transitions within algal systems more likely (Ghedini et al., 2015; Harvey et al., 2021a).

The strength and likelihood of typhoons in temperate latitudes is being enhanced by global warming (Webster et al., 2005; Mann and Emanuel, 2006; Lee et al., 2012; Murakami et al., 2012; Zhan et al., 2012; Wang et al., 2022). The competitive edge of turf algae over macroalgal canopy formers are limited to their early life-history stages (O'Brien and Scheibling, 2018) and is therefore weak under stable conditions. Reductions in recovery time between typhoons and extension of the typhoon season alters the competitive balance of algal communities however, particularly those exposed to other stressors such as ocean acidification (Kroeker et al., 2013; Pessarrodona et al., 2021). Although communities with extensive foundation species coverage display resistance to turf-system regime shifts (Falkenberg et al., 2012), if sufficiently high-levels of disturbance were to remove slower-growing macroalgal canopies, their recovery and recruitment could be inhibited in favour of *r*-selected turf algae (O'Brien and Scheibling, 2018; Harvey et al., 2021b). Facilitated by rapid recruitment and fast rates of growth, turf algae might monopolize the space created by stronger typhoons, during the shortened periods occurring between disturbance events, and following the end of the typhoon season, helping to further drive regime shifts from macroalgal to turf-dominated communities (Pessarrodona et al., 2021).

Natural analogues provide many benefits for advancing our knowledge on the responses of shallow water marine communities following exposure to ocean acidification conditions, but they are not perfect analogues. Carbonate chemistry at some CO_2 seeps can be highly variable close to the venting areas, requiring care to be taken in the selection of study sites. The two elevated pCO_2 study sites used in this study are >300 m and 400 m away from the main vent, thereby making mean carbonate conditions temporally stable (see Harvey et al., 2021b), although intermittently of higher amplitude. The depth and remoteness of CO_2 seep sites also makes them logistically demanding (Rastrick et al., 2018), which can place constraints on the replicability of sites and treatments. Ideally, multiple sites are used for the same treatments, however, the unique nature of our site (which allows investigations into both ocean acidification and storm disturbances) prevented this. Given these constraints, we ensured that our approach was as robust as possible by spreading our quadrats over a wide region (~ 400 m^2 within each site) to lessen the dependence between quadrats and ensure that we covered the full variability of benthic cover within each site. Moreover, we temporally replicated our study over three years to strengthen the inference, observing consistent patterns over the full period.

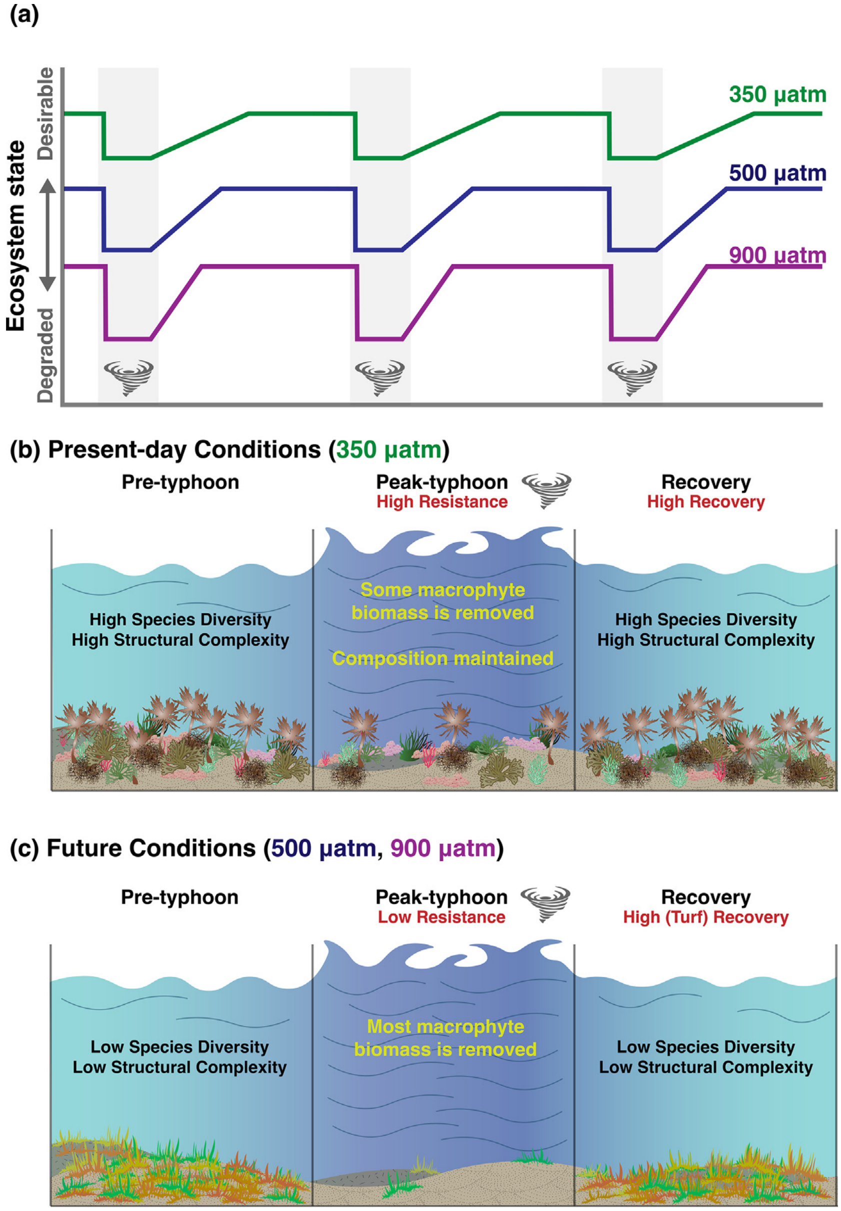

Fig. 5. Schematic summary of the differences in community stability between Present-day (350 µatm = Green) and future (500 µatm = Blue, 900 µatm = Purple) CO_2 conditions in response to physical disturbance from typhoons. The ecosystem state of present-day communities is higher than those under future pCO_2 conditions due to persistent press disturbance from ocean acidification (leading to community compositional changes, lower functional diversity, and structural complexity). Through time, ecosystem state fluctuates with seasonal and environmental change (temperature, nutrients, disturbance), with larger fluctuations for acidified communities. Periods of intense 'pulse' disturbance from seasonal factors such as typhoons have significant effects on ecosystem state. Differences in the functional traits and life-history strategies of the species forming present-day (macroalgal-dominated) and future (turf-dominated) communities lead to reductions in ecosystem stability. Macroalgal assemblages are resistant to disturbance from typhoons, maintaining a more consistent composition between seasons and recovering to pre-disturbance baselines following physical disturbance. Turf-dominated communities display low resistance to typhoons, which almost entirely removes the algal community, reducing the benthos to bare substrate. Turf resilience, promoted by boosted primary production and growth under elevated pCO_2 conditions, meant that the empty space created was later recolonised by turf algae. In the absence of physical disturbance feedback mechanisms maintain turf-dominance and inhibit macroalgal recruitment (see Harvey et al., 2021a, 2021b). Regular disturbance stabilised this pattern, locking the community into an early successional stage.

Despite these caveats, the use of CO_2 seeps is still invaluable for providing insights into the future impacts of ocean acidification on organisms, communities, and ecosystems (Rastrick et al., 2018).

Our findings reveal that the globally observed tendency for complex ecosystem states to be replaced by simple ecosystem states due to human impacts is likely to become entrenched by ocean acidification. Algal communities differed in their composition with increasing pCO_2 and this was maintained across the year, with the largest changes coinciding with associated environmental change (spring algal blooms and stormy typhoon seasons). Between years, the same ecosystem states were maintained within each respective pCO_2 condition. Acidification-driven changes in algal community structure (with different life-histories and traits altering the mechanism of response to disturbance by typhoons) have significant implications for the structure and stability of future temperate rocky reef systems (Fig. 5). Over three annual cycles of near total ecosystem reset by typhoons following extensive algal removal (i.e. negligible resistance), communities in acidified conditions rapidly returned to the same state (i.e. high recovery). This comprised of dominance by highly productive, opportunistic algal turfs which provide little structural complexity but cover the substrate and inhibit macroalgal recruitment. Whilst the persistence of macroalgal-dominated communities relies on both initial resistance to and subsequent recovery from typhoons, the combination of ocean acidification and typhoons increases the probability of ecosystem shifts to simpler states dominated by fast-growing 'weedy' species with low resistance but fast recovery that 'locks-in' the new ecosystem state (Harvey et al., 2021a). The anticipated increase in typhoon intensity, frequency, and duration would further reinforce this low complexity state, reducing the time for algal recovery and keeping the community in an early successional stage. Crucially, shifts that reduce marine ecosystem complexity can also reduce ecosystem productivity and associated species diversity. Future work should examine how reductions of community stability against disturbance might change ecosystem function following perturbation.

CRediT authorship contribution statement

Callum J. Hudson: Investigation, Writing – original draft, Formal analysis, Writing – review & editing, Visualization. **Sylvain Agostini:** Investigation, Writing – review & editing. **Shigeki Wada:** Investigation, Writing – review & editing. **Jason M. Hall-Spencer:** Investigation, Writing – review & editing, Supervision, Funding acquisition. **Sean D. Connell:** Writing – review & editing. **Ben P. Harvey:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Data availability

Raw data and the R code used for Figure Production and Analysis is supplied in the Appendix.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.161269.

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