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Decreased Diversity and Abundance of Marine Invertebrates at CO_2 Seeps in Warm-temperate Japan

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Japan has many coastal carbon dioxide seeps as it is one of the most volcanically active parts of the world. These shallow seeps do not have the spectacular aggregations of specialist fauna seen in deep-sea vent systems but they do have gradients in seawater carbonate chemistry that are useful as natural analogues of the effects of ocean acidification on marine biodiversity, ecosystem function and fisheries. Here, we compare macroinvertebrate diversity and abundance on rocky habitats at ambient (mean ≤ 410 µatm) and high (mean 971–1484 µatm) levels of seawater pCO_2 in the warm-temperate region of Japan, avoiding areas with toxic sulphur or warm-water conditions. We show that although 70% of intertidal taxa and 40% of shallow subtidal taxa were able to tolerate the high CO_2 conditions, there was a marked reduction in the abundance of corals, bivalves and gastropods in acidified conditions. A narrower range of filter feeders, grazers, detritivores, scavengers and carnivores were present at high CO_2 resulting in a simplified coastal system that was unable to retain the high standing stocks of marine carbon biomass found in ambient conditions. It is clear that cuts in CO_2 emissions would reduce the risks of climate change and ocean acidification impacts on marine biodiversity, shellfish production and biomass in the rocky coastal shores of this region.

Key words: climate change, corals, hydrothermal vents, marine biodiversity, ocean acidification

INTRODUCTION

Since their discovery in 1977, the diversity and abundance of marine invertebrates around deep-sea (> 200 m) hydrothermal vents has received much more scientific attention than their shallow-water counterparts. Deep-sea vents have obligate animal communities that are reliant upon chemosynthetic processes whereas shallow-water seeps have an abundance of photoautotrophs and few obligate fauna (Tarasov, 2006). Marine CO_2 seeps occur where plate tectonics create volcanoes; Japan has many as it sits on the 'Ring of Fire' that extends around the landward rim of the Pacific from New Zealand to Chile.

One of the best studied shallow CO_2 seeps in the NW Pacific ocean basin is on Yankicha Island (47°31′N, 152°26′E), part of the Kuril archipelago north of Hokkaido. Here, high biomass communities of anemones, holothurians and sea urchins (up to several kg m^{-2}) benefit from elevated chemosynthetic and photosynthetic primary production in an enclosed coastal lagoon (Zhirmunsky and Tarasov, 1990). Guishan Island, off Taiwan (24°50′N, 121°57′E), is another well-studied shallow NW Pacific CO_2 seep, but it is so strongly sulphurous that zooplankton are killed when they are brought into the seep area by currents (Hu et al., 2012). Thus, the marine zoology of hydrothermal systems is highly site-specific.

Research into shallow-water seeps increased once it was realised that these systems can have gradients in seawater pCO_2 that provide natural analogues for the future effects of ocean acidification (Hall-Spencer et al., 2008). Ocean acidification is happening due to the uptake of human CO_2 emissions by surface seawater from the Earth's atmosphere. Some shallow-water seeps simulate this process by raising pCO_2 and bicarbonate levels in seawater but lowering seawater carbonate saturation and pH. Studies of the effects of ocean acidification using CO_2 seeps require persistent gradients in seawater carbonate chemistry without toxic levels of metals and sulphur that would otherwise confound the experiments and observations (Pichler et al., 2019; Aiuppa et al., 2021; Blain et al., 2021).

In the NW Pacific, research using CO_2 seeps to study ocean acidification began at Iwotorishima Island (27°52′N, 128°14′E) in tropical Japan (Inoue et al., 2013). That study showed that soft corals replaced hard corals and the diversity of benthic invertebrates fell as CO_2 levels increased.

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Enochs et al. (2015) then showed that as CO_2 levels increased at a tropical seep site off Maug Island (47°31′N, 152°49′E) the diversity and abundance of calcified algae and scleractinians decreased, being replaced by fleshy macroalgae. This natural analogue approach has been applied to other acidified reef systems, such as at a lagoon in Nikko Bay, Palau (7°20′N, 134°29′E) where the phenotypic plasticity and adaptive potential of tropical corals can be assessed because genetic flow from outside the lagoon is restricted (Golbuu et al., 2016; Kurihara et al., 2021). Studies of genetic adaptation to ocean acidification and warming are difficult at most CO_2 seeps because these sites are easily colonised by larvae that drift in from outside the acidified area (Allen et al., 2016).

Agostini et al. (2015) began studies of warm-temperate CO_2 seeps at a temperate/tropical biogeographic boundary, paving the way for investigations into range shifts and the balance between temperate kelp forest and tropical coral communities. They selected Shikine Island (34°19′N, 139°12′E), 150 km southwest of Tokyo, as this island has areas with increased levels of pCO_2 in the seawater but the same temperature, salinity, dissolved oxygen, total alkalinity, nutrients, wave exposure, current strength, substratum type, and depth as nearby reference sites (Agostini et al., 2018, 2021). Knowledge of the types of organisms that live around Shikine Island CO_2 seeps has been growing steadily over the past 5 years but is scattered in the published literature.

The present paper provides a checklist of benthic macroinvertebrate diversity around warm-temperate CO_2 seeps off Shikine Island. This list reflects the authors' collective zoological knowledge of the area and draws extensively on surveys by Agostini et al. (2018), Harvey et al. (2019) and Tomatsuri and Kon (2019). Here, we assess how the diversity, abundance, and function of macrobenthic fauna change from ambient to high CO_2 areas. Our focus on invertebrates fills a gap, following-up on similar studies of Shikine Island CO_2 gradients that focused on microbial biofilms (Kerfahi et al., 2020), algae (Harvey et al., 2021a, b; Wada et al., 2021), and fish (Cattano et al., 2020).

MATERIALS AND METHODS

Shikine is a volcanic island south-east of the Izu Peninsula in Japan. It has many hydrothermal CO_2 seeps, several of which have been surveyed from the shore or using RV *Tsukuba II* since 2014 (Fig. 1). Agostini et al. (2018), Harvey et al. (2019), and Tomatsuri and Kon (2019) describe the methods used for measuring pH, temperature, salinity and total alkalinity and associated environmental factors at our study sites through in situ measurements and/or dis-

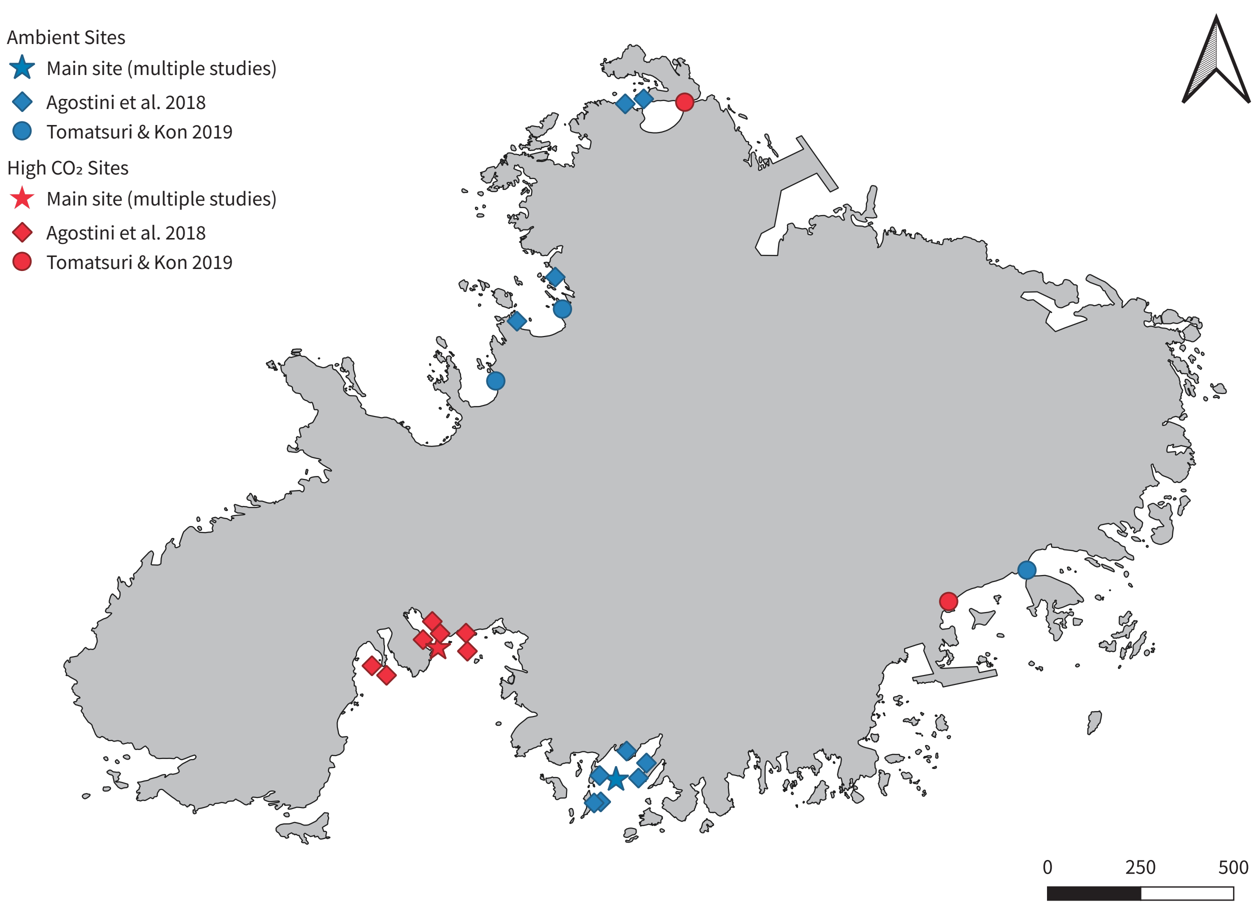

Fig. 1. Shikine island, Japan, showing the main sites used by Agostini et al., 2018, Harvey et al., 2019, and this study (stars) plus other sites that we surveyed less frequently (diamonds and circles). Blue symbols show sites with ambient low levels of pCO_2 in seawater, red symbols show sites with high levels of pCO_2 in seawater. Source: Geospatial Information Authority of Japan (https://www.gsi.go.jp/kankyochiri/gm_japan_e.html).

crete sampling. The diversity and abundance of macroinvertebrates were surveyed outside the influence of the seeps where seawater pCO_2 was ≤ 410 µatm ('ambient' sites) and closer to the seeps where pCO_2 in seawater was high ('high CO_2' sites).

Intertidal sites

Agostini et al. (2018) measured the percent cover of encrusting fauna in 25 × 25 cm quadrats and counted other sessile macroinvertebrates in 50 × 50 cm quadrats by snorkelling, when the tide was in. In both cases, 10–15 replicate quadrats were deployed at least a metre apart on steeply sloping rock faces at nine ambient sites and three high CO_2 sites. Tomatsuri and Kon (2019) surveyed the diversity and abundance of hermit crabs and live molluscs at three ambient sites and two high CO_2 sites using ten 50 × 50 cm quadrats per site when the tide was out. Their previously unpublished live mollusc data are included here. We collated these data and standardised them to numbers m^{-2}.

Subtidal sites

Agostini et al. (2018) assessed rocky reef community structure 3–6 m below Chart Datum by SCUBA diving using haphazardly placed 50 × 50 cm digital photoquadrats (*n* = 8–11) at four ambient sites and three high-CO_2 sites. Photographs were analysed using ImageJ (Developed at the National Institutes of Health and the Laboratory for Optical and Computational Instrumentation (University of Wisconsin), released in 1997) by overlaying 64 points on a grid, and recording the organisms at each point. Harvey et al. (2019) sampled two sites for macroinvertebrates, one with mean pCO_2 410 ± SD 73 µatm characterised by seaweeds and the other with 971 ± SD 258 µatm and characterised by a diatom mat. Fauna were collected using a SCUBA diver operated airlift to dislodge and lift samples into a 400 µm mesh net for later analysis from four 25 cm diameter circular plots at each site. Samples were fixed in 70% ethanol prior to sorting and identification under a dissecting microscope, and abundance counted.

We assessed sponge diversity on 25 September 2019, 29 October 2019 and 16 December 2019. On each of these days two SCUBA dives were carried out on rocky seabed at 3–6 m below Chart Datum along 10 m long, 4 m wide transect lines (*n* = 3), one in a high CO_2 zone and one in an ambient CO_2 zone. To minimize other factors that influence sponge distribution, such as light exposure, depth and inclination of the rock, the two sites selected had similar topographic features. Each sponge found on each transect was photographed before a small sample was removed using a knife and placed in a ziplock bag and later put in 70% ethanol. Spicule analysis followed methods in Rützler (1978); the samples were hand-cut, put in nitric acid, then washed twice with 70% ethanol before mounting on slides using clear nail varnish. Following Hooper (2000), hand-cut sections were prepared to analyse skeleton morphology, where possible comparing ectosome (tangential) and choanosome (transversal) sides, before being fixed on microscope slides as above. Photographs of the sponge spicules and skeletal structure were taken using a microscope-mounted camera and eyepiece graticule for scale. Identification to genus was made using keys in Hooper and Van Soest (2002) and to species using the World Porifera Database (available from www.marinespecies.org/porifera).

The authors collectively spent hundreds of hours at the seeps carrying out tasks such as helping media teams film the research programme (e.g., https://8billionangels.org/). This allowed incidental observations of bacterial mats/sulphurous conditions at the seeps as well as noting which rocky shore organisms can tolerate high CO_2 conditions and which were only seen far from the seeps. Our quantitative data on abundance were standardised to numbers m^{-2} whereas qualitative *ad hoc* observations were recorded as presence/absence.

RESULTS

Differences in seawater carbonate chemistry between ambient (< 410 µatm pCO_2) and high CO_2 conditions at

Table 1. Seawater carbonate chemistry at intertidal and subtidal sites used in three studies off Shikine Island, Japan in ambient conditions and at high CO_2. Mean (± SD) pH_T, temperature, salinity, and total alkalinity (TA) are measured values. Seawater pCO_2, dissolved inorganic carbon and the saturation states for calcite (Ωcalcite) and aragonite (Ωaragonite) are mean values (± SD) calculated using the carbonate chemistry system analysis program CO_2SYS.

Station		pH	Temp (°C)	Salinity (psu)	TA (µmol kg-1)	pCO_2 (µatm)	DIC (µmol kg-1)	Ωcal	Ωarag	Source
Intertidal										
Ambient	mean	8.17	18.5	34.6	2256	402	2033	3.8	2.5	Agostini et al., 2018
	SD	0.03	0.4	0.0	3	33	22	0.3	0.2	
High-CO_2	mean	7.83	17.6	34.8	2262	1052	2173	2.2	1.4	Agostini et al., 2018
	SD	0.06	0.3	0.1	7	344	39	0.4	0.3	
Ambient	mean	8.32	23.5	30.5	2237	186	–	7.2	4.7	Tomatsuri & Kon, 2019
	SD	0.10	6.2	4.0	35	44	–	1.1	0.8	
High-CO_2	mean	7.72	22.8	28.0	2264	1233	–	3.4	2.2	Tomatsuri & Kon, 2019
	SD	0.60	5.5	3.8	136	1506	–	2.6	1.7	
Subtidal										
Ambient	mean	8.21	18.5	34.0	2244	359	1984	4.5	2.9	Agostini et al., 2018
	SD	0.07	0.8	0.1	2	67	36	0.6	0.4	
High-CO_2	mean	7.75	19.9	34.1	2255	1484	2168	2.1	1.4	Agostini et al., 2018
	SD	0.26	0.6	0.2	2	1084	142	1.0	0.7	
Ambient	mean	8.04	23.1	34.1	2282	410	2007	4.8	3.1	Harvey et al., 2019
	SD	0.07	0.6	0.7	7	73	39	0.6	0.4	
High-CO_2	mean	7.72	22.9	34.9	2272	971	2145	2.6	1.7	Harvey et al., 2019
	SD	0.10	0.9	0.2	3	258	33	0.4	0.3	

Shikine Island hydrothermal seeps were reported in detail by Agostini et al. (2018), Harvey et al. (2019) and Tomatsuri and Kon (2019) and are synthesised here in Table 1. In brief, whilst there were no significant differences in salinity or total alkalinity between sites, the mean values of seawater pH fell from ≥ 8.0 in ambient conditions to ≤ 7.8 near the seeps. At ambient sites the mean aragonite saturation of seawater was > 2.5 (with no episodes of aragonite undersaturation) but this fell to means as low as 1.4 in our high CO_2 sites where there were frequent episodes of aragonite undersaturation.

Intertidal observations

In ambient conditions thick biogenic carbonate crusts formed by coralline algae, serpulids, barnacles, oysters and mussels characterised bedrock on the lower shore of Shikine Island. Sponges, polychaetes and sipunculids bored into these biogenic carbonate crusts on the low shore but this species-rich habitat was lost in high CO_2 areas. Figure 2 shows seven examples of macroinvertebrate taxa that were found living on bedrock in the intertidal where the seawater had high levels of pCO_2. The acidified habitats were less complex than in ambient conditions, with a clear reduction in calcareous organisms and an increase in the amount of bare rock and turf algae (see Agostini et al., 2018 for quantitative data on these changes). Of all the intertidal taxa recorded, only the sea anemone *Actinia equina* was more common in the high pCO_2 sites than the ambient sites (Agostini et al., 2018).

Table 2 lists the intertidal benthic macroinvertebrates

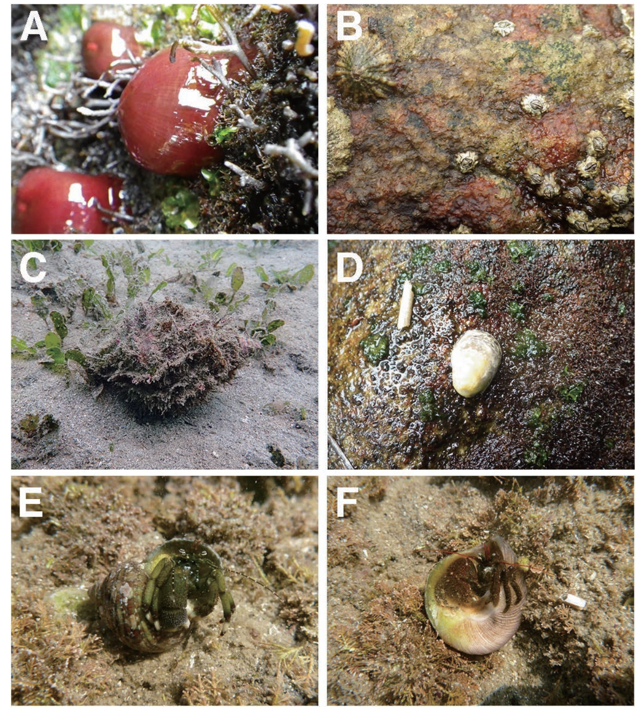

Fig. 2. Benthic invertebrates found at intertidal sites with high seawater pCO_2 (mean 970–1484 μatm) on Shikine Island, Japan. **(A)** Cnidaria *Actinia equina*, **(B)** Crustacea *Chthamalus challengeri* and Mollusca *Siphonaria japonica*, **(C)** Mollusca *Monoplex parthenopeus*, **(D)** Mollusca *Nerita albicilla*, **(E)** Crustacea *Pagurus filholi*, and **(F)** Crustacea *Pagurus maculosus*.

Table 2. Presence (dot) or abundance (number m^{-2}) of intertidal species at ambient and high mean levels of seawater pCO_2 at Shikine island, Japan. 1: Agostini et al., 2018; 2: Harvey et al., 2019; 3: Tomatsuri and Kon, 2019; 4: Harvey et al., 2018; u.d.: unpublished data. Notes indicate sessile vs. vagile along with feeding type (SF = suspension feeders, D = detritivores, G = grazers, C = carnivores and S = scavengers); they were all epifaunal.

Phylum	Class	Species	≤402 μatm	1052–1233 μatm	Lifestyle	Feeding	Ref.
Porifera	Demospongiae	*Halichondria okadai*	•	•	sessile	SF	1
Cnidaria	Anthozoa	*Actinia equina*		•	sessile	C	1
		Sphenopidae sp.		•	sessile	SF	1
		Tubastraea coccinea	•		sessile	SF	1
Mollusca	Polyplacophora	*Acanthochitona achates*	•	•	vagile	G	1
		Acanthopleura japonica	•	•	vagile	G	1
		Acanthoplurinae gen sp.	0.5 ± 2.0		vagile	G	3, u.d.
		Onithochiton hirasei	•		vagile	G	1
	Gastropoda	*Cellana grata*	•	•	vagile	G	1
		Cellana nigrolineata	0.3 ± 1.0		vagile	G	3, u.d.
		Cellana rota	0.3 ± 1.0		vagile	G	3, u.d.
		Cellana toreuma	•	•	vagile	G	1
		Cellana toreuma	0.3 ± 2.0		vagile	G	3, u.d.
		Diloma suavis		•	vagile	G	1
		Drupa ricinus hadari	•		vagile	C	1
		Drupella margariticola	1.3 ± 2.7		vagile	C	3, u.d.
		Echinolittorina radiata	8.3 ± 20.4		vagile	G	3, u.d.
		Ergalatax contractus	•		vagile	S	1
		Japeuthria ferrea	0.3 ± 3.2		vagile	S	3, u.d.
		Latirus nagasakiensis	•		vagile	S	1
		Lottia kogamogai	•		vagile	G	1

Table 2. Continued.

Phylum	Class	Species	≤402 µatm	1052–1233 µatm	Lifestyle	Feeding	Ref.
		Mancinella echinata		●	vagile	C	1
		Mitrella burchardi		●	vagile	S	1
		Morula granulata	●		vagile	C	1
		Morula iostoma	●		vagile	C	1
		Morula musiva		●	vagile	C	1
		Morula uva	●		vagile	C	1
		Muricidae sp 1.	●		vagile	C	1
		Monoplex parthenopeus		●	vagile	C	1
		Neritidae spp.	11.0 ± 7.8	2.5 ± 7.4	vagile	G	3, u.d.
		Nipponacmea sp.	0.3 ± 1.0		vagile	G	3, u.d.
		Patellidae gen sp.	0.3 ± 2.0		vagile	G	3, u.d.
		Patelloida saccharina	●	●	vagile	G	1
		Patelloida saccharina lanx	●	●	vagile	G	1
		Patelloida saccharina lanx	0.8 ± 2.3	0.4 ± 1.2	vagile	G	3, u.d.
		Proterato callosa		●	vagile	G	1
		Purpura panama	●	●	vagile	C	1
		Reishia bronni		●	vagile	C	1
		Reishia clavigera	●	●	vagile	C	1
		Reishia clavigera	6.0 ± 5.3		vagile	C	3, u.d.
		Reishia luteostoma		●	vagile	C	1
		Sabia conica		●	vagile	D	1
		Scutellastra flexuosa		●	vagile	G	1
		Siphonaria japonica	●	●	vagile	G	1
		Siphonaria japonica	29.1 ± 35.6	3.4 ± 4.3	vagile	G	3, u.d.
		Siphonaria signa		●	vagile	G	1
		Siphonaria sirius	●	●	vagile	G	1
		Siphonaria sirius	0.4 ± 2.9		vagile	G	3, u.d.
		Strigatella scutula	●		vagile	C	1
		Tenguella granulata	1.1 ± 2.7	0.8 ± 1.8	vagile	C	3, u.d.
		Tenguella musiva	2.7 ± 5.4	0.1 ± 1.2	vagile	C	3, u.d.
		Trochus rota	●		vagile	G	1
		Turbo stenogyrus	●		vagile	G	1
		Tylothais virgata	●		vagile	C	1
	Bivalvia	*Hormomya mutabilis*		●	sessile	SF	1
		Mytilisepta virgata	6.4 ± 10.7	0.8 ± 1.8	sessile	SF	3, u.d.
		Saccostrea kegaki		●	sessile	SF	1
		Saccostrea kegaki	5.0 ± 6.2		sessile	SF	3, u.d.
		Saccostrea morda	●		sessile	SF	1
		Septifer bilocularis	1.2 ± 3.7	●	sessile	SF	3, u.d.
Annelida	Polychaeta	Serpulidae sp 1.	●	●	sessile	SF	1
		Spirobranchus sp.	●		sessile	SF	u.d.
		Spirorbinae sp.	●	●	sessile	SF	1
Arthropoda	Maxillopoda	*Capitulum mitella*	●	●	sessile	SF	1
		Chthamalus challengeri	●	●	sessile	SF	1
		Megabalanus rosa	●	●	sessile	SF	1
		Megabalanus volcano	●		sessile	SF	1
		Tetraclita japonica	●	●	sessile	SF	1
	Malacostraca	*Clibanarius virescens*	39.9 ± 43.4	3.4 ± 6.0	vagile	O	3, u.d.
		Pagurus filholi	45.2 ± 44.3	43.8 ± 35.7	vagile	O	3, u.d.
		Pagurus maculosus		1.4 ± 4.6	vagile	O	3, u.d.
		Pagurus nigrivittatus	18.7 ± 36.6		vagile	O	3, u.d.
		Pagurus sp.	0.5 ± 3.0		vagile	O	3, u.d.
Total number of taxa per CO_2 level			57	40	30% reduction in taxa		

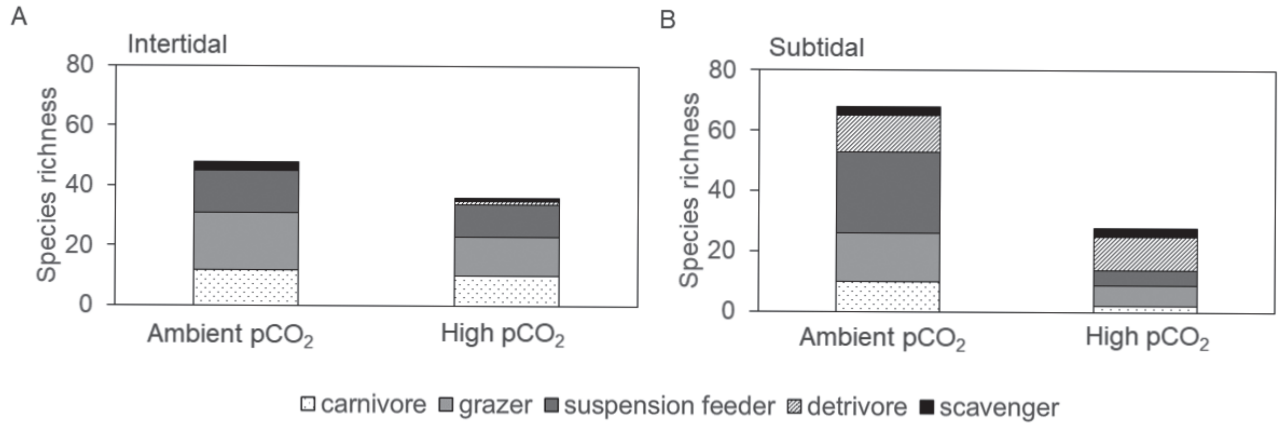

Fig. 3. Macroinvertebrate species richness, divided into feeding guilds, on **(A)** intertidal and **(B)** subtidal bedrock at sites with ambient levels of seawater pCO_2 and sites with high levels of pCO_2 around Shikine Island, Japan.

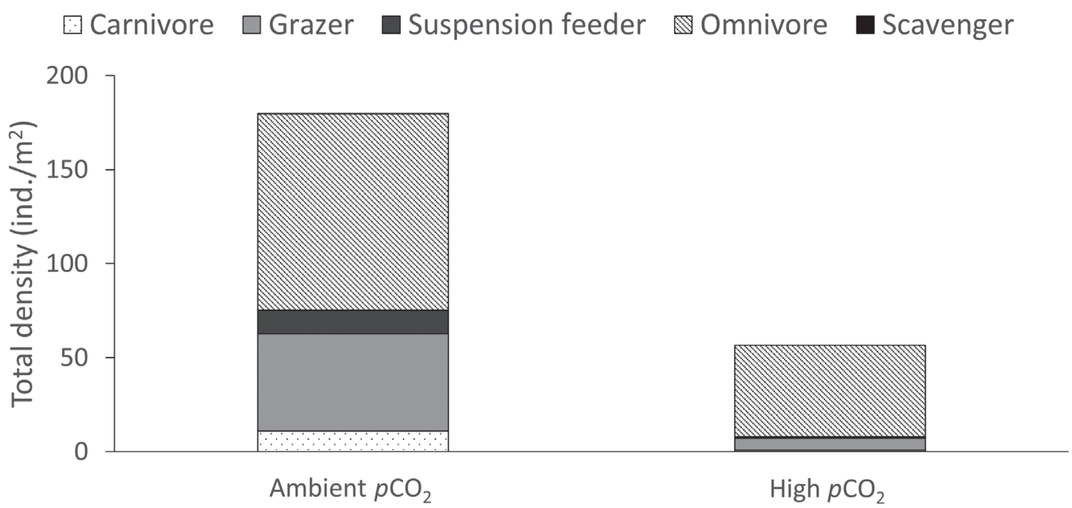

Fig. 4. Abundance of molluscs and hermit crabs (pooled data divided into feeding types) at intertidal rocky shore sites with ambient levels of seawater pCO_2 and sites with high levels of pCO_2 around Shikine Island, Japan.

recorded, arranged by phylum, class, genus and species. The table includes notes on whether these animals have a vagile or sessile lifestyle and on their feeding types. This natural history information was obtained from Nishimura (1992), Hayashi (2006), Imahara (2011) and Okutani (2017). In the high CO_2 areas 30% fewer taxa were recorded than in ambient conditions. This reduction affected both vagile and sessile taxa and reduced the diversity of suspension feeders, grazers, carnivores and scavengers (Fig. 3). The abundance of calcifying fauna (e.g., the barnacle *Chthamalus challengeri*, the limpet *Siphonaria japonica* and the gastropods *Monoplex parthenopeus* and *Nerita albicilla*) decreased in the high CO_2 areas where rock was mainly covered in fleshy algal turf or biofilm.

Sponge percentage cover decreased and the average number of calcifying organisms fell from several hundred individuals per m^2 in ambient conditions to fewer than 40 individuals per m^2 at high CO_2. The abundance of large barnacles (> 1 cm in diameter, including *Capitulum mitella*, *Megabalanus volcano* and *Megabalanus rosa*) fell from over 60 per m^2 in ambient conditions to around 20 individuals per m^2 at high CO_2 before petering out to zero individuals in the highest CO_2 areas (Agostini et al., 2018). Mussels were also reduced in abundance, from around 28 per m^2 in ambient conditions to 8 per m^2 in the high CO_2 areas (Agostini et al., 2018).

There was also a reduction in abundance of intertidal molluscs and hermit crabs from around 175 individuals per m^2 in ambient conditions to around 60 per m^2 at high CO_2 and an associated reduction in the diversity of feeding types (Fig. 4). Hermit crab species richness was lower in acidified areas, although *Pagurus filholi* was abundant in all areas. Hermit crabs in the high CO_2 areas had a lower diversity of carried shells and there were fewer empty gastropod shells available to them in the high CO_2 areas (see Tomatsuri and Kon, 2019 for these datasets).

Subtidal observations

Figure 5 shows six examples of macroinvertebrates found living at high CO_2 sites in shallow subtidal waters off Shikine Island. This figure illustrates the acidified rocky habitats in which the organisms were found, which were less complex than the ambient conditions with a notable reduction in the amount of crustose coralline algae and scleractin-

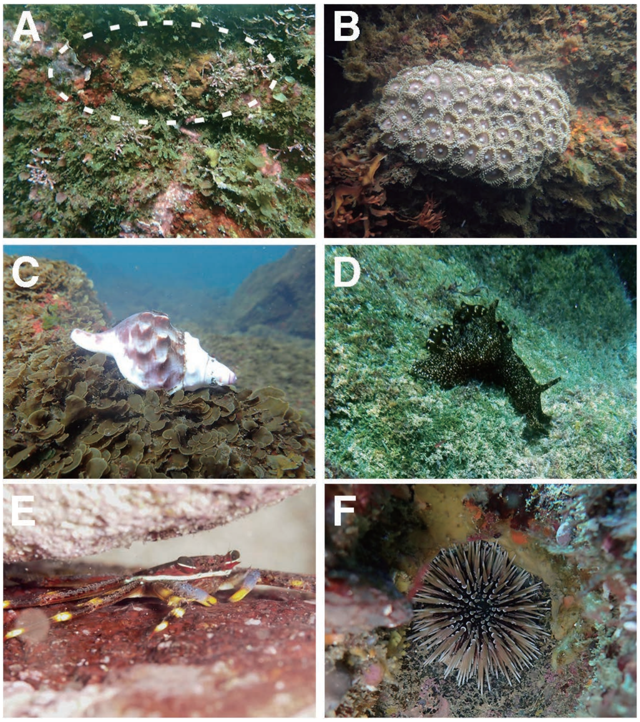

Fig. 5. Benthic invertebrates found at shallow sublittoral rocky sites (< 10 m CD) with high seawater pCO_2 (mean 970–1484 µatm) on Shikine island, Japan. **(A)** Porifera *Aulospongus villosus*, **(B)** Cnidaria *Zoanthus* sp., **(C)** Mollusca *Charonia lampas*, **(D)** Mollusca *Aplysia* sp., **(E)** Crustacea *Percnon planissimum*, and **(F)** Echinodermata *Echinometra* sp.

ian corals and an increase in benthic diatom mats and turf algae at high CO_2. Table 3 lists the benthic invertebrates recorded in ambient and high CO_2 conditions, assigned to lifestyle and feeding groups (using the same reference sources as for Table 1) with quantitative density data converted to numbers per m^2.

There was a 60% decrease in macrofaunal biodiversity from ambient to high CO_2 conditions, although the surviving communities retained examples of suspension feeders, detritivores, grazers, carnivores and scavengers. Many benthic taxa were only found in ambient conditions, including species of sponge, polychaete, mollusc, arthropod and echinoderm (Table 3, Fig. 4). There were significantly reduced abundances of calcifying invertebrate macrofauna at high CO_2. Scleractinian corals were common in ambient conditions (~11% cover) but comprised < 1% cover at high CO_2 sites. Small gastropods were abundant in ambient conditions but not at high CO_2 sites and the shells of large marine snails showed obvious signs of external dissolution by corrosive seawater (e.g., *Charonia lampas*, Fig. 5).

Air-lift samples confirmed lower species richness at high CO_2 sites, and in these samples there was an absence of calcified bivalve molluscs, decapods, mysids and echinoderms. There was about a 50% reduction in the numbers of individuals collected at high CO_2 (Fig. 6). Tanaids, which are less calcified, became the most abundant taxon, comprising on average ~50% of individuals in the elevated pCO_2 conditions but only ~10% in the ambient air-lift samples (Harvey et al., 2019).

Table 3. Presence (dot) or abundance (number m^{-2}) of subtidal species at ambient and high mean levels of seawater pCO_2 at Shikine island, Japan. 1: Agostini et al., 2018; 2: Harvey et al., 2019; 3: Tomatsuri and Kon, 2019; 4: Harvey et al., 2018; new: new data. Notes on sessile vs. vagile and epifauna vs. infauna provided along with feeding type (SF = suspension feeders, D = detritivores, G = grazers, C = carnivores and S = scavengers).

Phylum	Class	Species	≤410 µatm	971–1484 µatm	Lifestyle	Habitat	Feeding	Ref.
Porifera	Demospongiae	*Asteropus simplex*	•		sessile	epifauna	SF	new
		Aulospongus villosus		•	sessile	epifauna	SF	new
		Axinyssa aculeata		•	sessile	epifauna	SF	new
		Clathria (*Thalysias*) *fasciculata*	•		sessile	epifauna	SF	new
		Craniella serica	•		sessile	epifauna	SF	new
		Desmospongiae sp.	•		sessile	epifauna	SF	1
		Halichondria sp.	•		sessile	epifauna	SF	new
		Hymeniacidon halichondroides	•		sessile	epifauna	SF	new
		Neofibularia sp.	•		sessile	epifauna	SF	new
		Penares incrustans	•		sessile	epifauna	SF	new
		Petrosia ushitsuensis	•		sessile	epifauna	SF	new
		Phorbas tanitai		•	sessile	epifauna	SF	new
		Poecillastra tenuilaminaris	•		sessile	epifauna	SF	new
		Pseudosuberites perforatus		•	sessile	epifauna	SF	new
		Spheciospongia panis	•		sessile	epifauna	SF	new
		Stelletta purpurea	•		sessile	epifauna	SF	new
		Strongylacidon kaneohe	•		sessile	epifauna	SF	new
		Topsentia kushimotoensis	•		sessile	epifauna	SF	new
Cnidaria	Anthozoa	*Acropora solitaryensis*	•		sessile	epifauna	SF	1
		Alveopora japonica	•		sessile	epifauna	SF	1
		Cyphastrea sp.	•		sessile	epifauna	SF	1
		Dendronephthya sp.	•		sessile	epifauna	SF	1
		Diplastrea speciosa	•		sessile	epifauna	SF	1
		Entacmaea quadricolor	•		sessile	epifauna	C	1
		Goniastrea complex sp 1.	•		sessile	epifauna	SF	1

Table 3. Continued.

Phylum	Class	Species	≤410 µatm	971–1484 µatm	Lifestyle	Habitat	Feeding	Ref.
		Hydnophora exesa	●		sessile	epifauna	SF	1
		Montipora turgescens	●		sessile	epifauna	SF	1
		Paragoniastrea australiensis	●		sessile	epifauna	SF	1
		Phymanthidae sp.	●		sessile	epifauna	C	1
		Porites heronensis	●		sessile	epifauna	SF	1
		Zoanthus sp.		●	sessile	epifauna	SF	1
Mollusca	Gastropoda	*Aplysia* sp.		●	vagile	epifauna	G	1
		Charonia lampas	●	●	vagile	epifauna	C	4
		Columbellidae sp. 1	3.8 ± 2.2		vagile	epifauna	G	2
		Columbellidae sp. 2	●		vagile	epifauna	S	1
		Columbellidae sp. 3	●		vagile	epifauna	S	1
		Dolabella auricularia	●		vagile	epifauna	G	new
		Haminoeidae sp.		3.8 ± 2.2	vagile	epifauna	G	2
		Mitridae sp. 1	●		vagile	epifauna	C	1
		Mitridae sp. 2	●		vagile	epifauna	C	1
		Mitridae spp.	7.7 ± 5.4		vagile	epifauna	G	2
		Muricidae sp 2.	●		vagile	epifauna	C	1
		Muricidae sp 3.	●		vagile	epifauna	C	1
		Muricidae sp 4.	●		vagile	epifauna	C	1
		Muricidae spp.	2.6 ± 1.3		vagile	epifauna	G	2
		Nassariidae sp.		5.1 ± 3.2	vagile	epifauna	S	2
		Omphalius pfeifferi pfeifferi	●		vagile	epifauna	G	new
		Sorbeoconcha sp. 1	●		vagile	epifauna	–	1
		Sorbeoconcha sp. 2		●	vagile	epifauna	–	1
		Tegulidae sp.	●		vagile	epifauna	G	1
		Trochidae sp1	11.5 ± 5.0		vagile	epifauna	G	2
		Trochidae sp2	6.4 ± 3.4		vagile	epifauna	G	2
		Trochidae spp.	●		vagile	epifauna	G	1
	Bivalvia	Lucinidae sp.	2.6 ± 1.3		vagile	infauna	SF	2
Sipuncula	Sipunculidea	Sipunculidae sp.		3.8 ± 2.2	vagile	infauna	D	2
Annelida	Polychaeta	Lumbrineridae sp.		1.3 ± 1.1	vagile	infauna	D	2
		Phyllodocidae sp.	2.6 ± 1.3		vagile	epifauna	C	2
		Serpulidae sp 2.	●		sessile	epifauna	SF	1
		Syllidae sp.		2.6 ± 1.3	vagile	epifauna	C	2
Arthropoda	Maxillopoda	Balanomorpha sp.	●		sessile	epifauna	SF	1
		Cypridinidae sp.		30.6 ± 13.7	vagile	infauna	S	2
	Malacostraca	Anthuridae sp.	1.3±1.1	5.1±3.2	vagile	epifauna	D	2
		Archaeomysis sp.	1.3±1.1		vagile	epifauna	O	2
		Brachyura sp.	●		vagile	epifauna	–	1
		Cancridae sp.	2.6±1.3		vagile	epifauna	C	2
		Caprellidae sp1	12.8±5.4	34.4±17.2	vagile	epifauna	G	2
		Caprellidae sp2	30.6±10.3	7.7±5.4	vagile	epifauna	G	2
		Caprellidae sp3	435.5±69.7		vagile	epifauna	G	2
		Haustoridae sp.	14.0±7.7	2.6±1.3	vagile	infauna	D	2
		Hyalidae sp.		11.5±5.0	vagile	epifauna	D	2
		Ischyroceridae sp1	248.7±51.3	150.5±48.4	vagile	epifauna	D	2
		Ischyroceridae sp2	162.0±62.1		vagile	epifauna	D	2
		Ischyroceridae sp3	355.9±134.4		vagile	epifauna	D	2
		Ischyroceridae sp4	11.5±5.9		vagile	epifauna	D	2
		Lysianassidae sp.	102.0±34.1	136.5±62.2	vagile	infauna	S	2
		Melitidae sp.	273.0±118.9	327.8±83.2	vagile	epifauna	D	2
		Monocorophium sp.		6.4±3.4	vagile	infauna	D	2
		Palapedia sp.	12.8±7.5		vagile	epifauna	O	2
		Percnon planissimum	●	●	vagile	epifauna	G	new
		Tanaidae sp.	210.5±62.7	809.9±124.9	vagile	epifauna	D	2
		Urothoe sp.	76.5±27.4	63.8±20.6	vagile	infauna	D	2
		Urothoidae sp.	29.3±15.0		vagile	infauna	D	2
Echinodermata	Asteroidea	*Leiaster leachi*	●		vagile	epifauna	C	new
	Holothuroidea	*Holothuria pervicax*	●		vagile	epifauna	D	1
	Ophiuroidea	Ophiura sp.	24.2±11.7	91.8±34.0	vagile	epifauna	D	2
	Echinoidea	*Diadema setosum*	●	●	vagile	epifauna	G	new
		Echinometra sp.	●	●	vagile	epifauna	G	new
		Echinoida sp.	3.8±2.2		vagile	epifauna	G	2
Total number of taxa per CO_2 level			73	29	60% reduction in taxa			

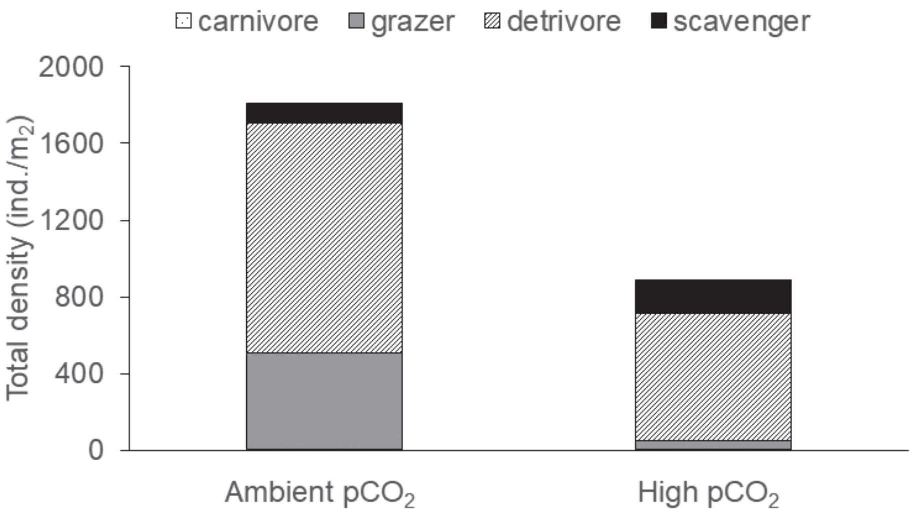

Fig. 6. Abundance of macro-invertebrates in shallow sublittoral (< 10 m CD) air-lift samples (pooled data divided into feeding types) from rocky shore sites with ambient levels of seawater pCO_2 and sites with high levels of pCO_2 around Shikine Island, Japan.

DISCUSSION

The studies synthesised here focused on investigating the biological effects of ocean acidification and so avoided areas that had extremely high levels of CO_2 and were characterised by bacterial mats supporting very low levels of invertebrate diversity, as reported at many shallow-water hydrothermal seeps worldwide (Aiuppa et al., 2021; Blain et al., 2021). At our high CO_2 sites the seawater was not heated or sulphurous and this allowed observations of the long-term effects of ocean acidification.

Intertidal findings

We found that most (70%) of the intertidal warm-temperate epifauna recorded could survive in high CO_2 conditions. This resilience reflects the fact that intertidal organisms have evolved to cope with extreme fluctuations in physicochemical conditions, including hypercapnia (Inaba and Hall-Spencer, 2020). However, there were large reductions in the abundance and size of calcareous organisms in the intertidal. Body size reductions have been noted as a way in which organisms cope with seawater acidification (Harvey et al., 2018). Large oysters (*Saccostrea* spp.), mussels (*Mytilsepta virgata*), limpets (*Siphonaria* spp.) and barnacles (e.g., *Capitulum mitella* and *Megabalanus* spp.) were abundant in ambient conditions but were sparsely distributed and smaller at high CO_2. This caused a loss in habitat complexity and a reduction in filter feeding and grazing functions (Agostini et al., 2018), which amount to a loss in ecosystem services such as shellfish productivity and maintenance of good water quality (Lemasson et al., 2017). The diversity and abundance of shells available to hermit crabs and the abundance of these crabs were all significantly reduced at high CO_2 (Tomatsuri and Kon, 2019). An increased abundance of anemones in acidified conditions ties in with similar observations in the Mediterranean and may relate to a decrease in competition with calcareous animals for living space (Suggett et al., 2012).

Subtidal findings

Most taxa listed in Table 3 are epifauna because we carried out our surveys on bedrock. A wider range of habitats have been studied at CO_2 seeps in Ischia (Italy), including artificial substrata, and for this reason the range of taxa found able to cope with acidified conditions is large (we list 69 resistant taxa compared with around 250 resistant invertebrate species listed by Foo et al., 2018). Deployment of scouring pads has worked well for sampling a diverse range of fauna at CO_2 seeps (Cigliano et al., 2010; Allen et al., 2017) and settlement tiles are a convenient way of collecting bryozoans, serpulids and tunicates (Kroeker et al., 2011; Harvey et al., 2021). Care is needed when interpreting such studies since ocean acidification decreases habitat complexity (Cattano et al., 2020; Sunday et al., 2017) an aspect that can be obscured when using artificial substrata.

Subtidal sponges and scleractinian corals were looked at in detail, reflecting the expertise of Belfiore and Agostini, but for some taxa our list of shallow sublittoral macroinvertebrate fauna will be incomplete. Bringing in experts with taxonomic knowledge of polychaetes, hydroids, bryozoans and ascidians would help fill this knowledge gap. Nevertheless, our faunal inventory provides insights into how ocean acidification can alter marine ecosystems.

The sublittoral invertebrate macrofauna showed a 60% loss of biodiversity at high CO_2 levels, with the loss of scleractinian corals and many other calcified organisms. This exceptionally high susceptibility of shallow sublittoral rocky reef communities to ocean acidification appears to be linked to the high exposure of Shikine Island to wave action. During relatively calm spring and summer months, high CO_2 levels allow turf algae to rapidly grow and dominate rocky habitats near to the seeps. During each autumn typhoon season, very rough seas hit our study sites. Rough seas decimated the rocky reef communities at the acidified sites, removing most of the algal biomass, but the typhoons had much less effect at the sites with ambient pCO_2 levels in seawater. The high typhoon resilience of marine communities growing at ambient pCO_2 levels meant that they could store more carbon biomass and retain a higher diversity than marine communities growing at the acidified sites (Harvey et al., 2019, 2021a, b; Wada et al., 2021).

Research at other CO_2 seeps

Similar patterns to those seen at Shikine Island occur at seeps on tropical coral reefs in the NW Pacific ocean basin, with habitat degradation and loss of biodiversity in acidified areas (Fabricius et al., 2014; Enochs et al., 2015). These systems have proven very useful for showing which organisms can survive high CO_2 conditions and how ecosystem services are affected (Foo et al., 2018; Hall-Spencer and

Harvey, 2019).

Work on the ecosystem effects of ocean acidification began at CO_2 seeps in Ischia, Italy, where shore access is easy and the gas bubbles out of the seafloor at ambient temperature with no influence of toxic metals or sulphur (Foo et al., 2018). The high CO_2 areas have 30% fewer invertebrate taxa and lower animal biomass, although the number of individuals does not differ due to a higher number of small-bodied, tolerant species at the high CO_2 sites (Kroeker et al., 2011). Generalists and small-bodied animals dominate at several Mediterranean CO_2 seep sites, resulting in food web simplification (Vizzini et al., 2017). Similarly, in Papua New Guinea, reductions in invertebrate diversity were observed with increasing CO_2 (Fabricius et al., 2011). A 3-fold decrease in zooplankton biomass was noted in high CO_2 areas near Papua New Guinea seeps compared to ambient nearby sites (Smith et al., 2016). The low biodiversity observed at high CO_2 is linked to the loss of habitat-forming corals (Fabricius et al., 2014; Sunday et al., 2017).

In a similar study to ours, using quadrats to quantify benthic diversity and abundance, Teixido et al. (2018) recorded 24 macroinvertebrate species in ambient conditions near shallow water seeps in Ischia, Italy but only 13 species at high CO_2. Teixdo et al. (2018) explain that ocean acidification caused a loss in functional diversity as, for example, scleractinian corals, molluscs, and sea urchins were present in ambient conditions but absent from their high CO_2 quadrats. We recorded similar major reductions in biodiversity and function in warm-temperate Japan with, for example, only four sponge taxa able to live at high CO_2 compared with 14 in ambient conditions, one anthozoan species at high CO_2 compared with 12 in ambient conditions, and five mollusc species at high CO_2 compared with 19 in ambient conditions. All feeding types were still represented at high CO_2 but a narrower range of filter feeders, grazers, detritivores, scavengers, and carnivores were present, resulting in a simplified coastal system that was unable to retain the high standing stocks of marine carbon biomass found in ambient conditions. Collectively, these results support the hypothesis that as seawater pCO_2 levels increase there is a loss in macroinvertebrate diversity and a proliferation of tolerant species that alter ecosystem function along the warm temperate coast of Japan, to the detriment of shellfish fisheries.

CONCLUSION

Comparisons of intertidal and subtidal rocky reef communities living under ambient and high CO_2 conditions show that ocean acidification is a threat to many marine organisms, driving fundamental shifts in coastal marine ecosystems towards simplified communities with reduced capacity to store carbon. Although intertidal macroinvertebrates retained 70% of their surrounding diversity at high CO_2, they decreased in abundance and so their provision of ecosystem services, such as shellfish production and water filtration, was reduced. The shallow sublittoral communities retained only 40% of their diversity, with a proliferation of small opportunist taxa such as tanaeids at high CO_2. Our observations suggest that cuts in CO_2 emissions will reduce the risks of ocean acidification, helping to ensure that the coastlines of Japan remain highly biodiverse, resilient, and able to provide ecosystem services such as fisheries, good water quality, and carbon storage.

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COMPETING INTERESTS

The authors have no relevant financial interests that may influence the interpretation of our results.

AUTHOR CONTRIBUTIONS

SA initiated studies at the Shikine island. GB collected the sponge data. JMH-S prepared the first draft, and all authors interpreted the data and co-wrote the manuscript.

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