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Decreased Diversity and Abundance of Marine Invertebrates at CO₂ 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 $\leq 410 \mu\text{atm}$) and high (mean 971–1484 μatm) levels of seawater $p\text{CO}_2$ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 $p\text{CO}_2$ 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 CO₂ emissions by surface seawater from the Earth's atmosphere. Some shallow-water seeps simulate this process by raising $p\text{CO}_2$ and bicarbonate levels in seawater but lowering seawater carbonate saturation and pH. Studies of the effects of ocean acidification using CO₂ 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 CO₂ 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 CO₂ levels increased.

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Enochs et al. (2015) then showed that as CO₂ 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 CO₂ 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 CO₂ 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 pCO₂ 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 CO₂ 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 CO₂ 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 CO₂ areas. Our focus on invertebrates fills a gap, following-up on similar studies of Shikine Island CO₂ 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 CO₂ 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-

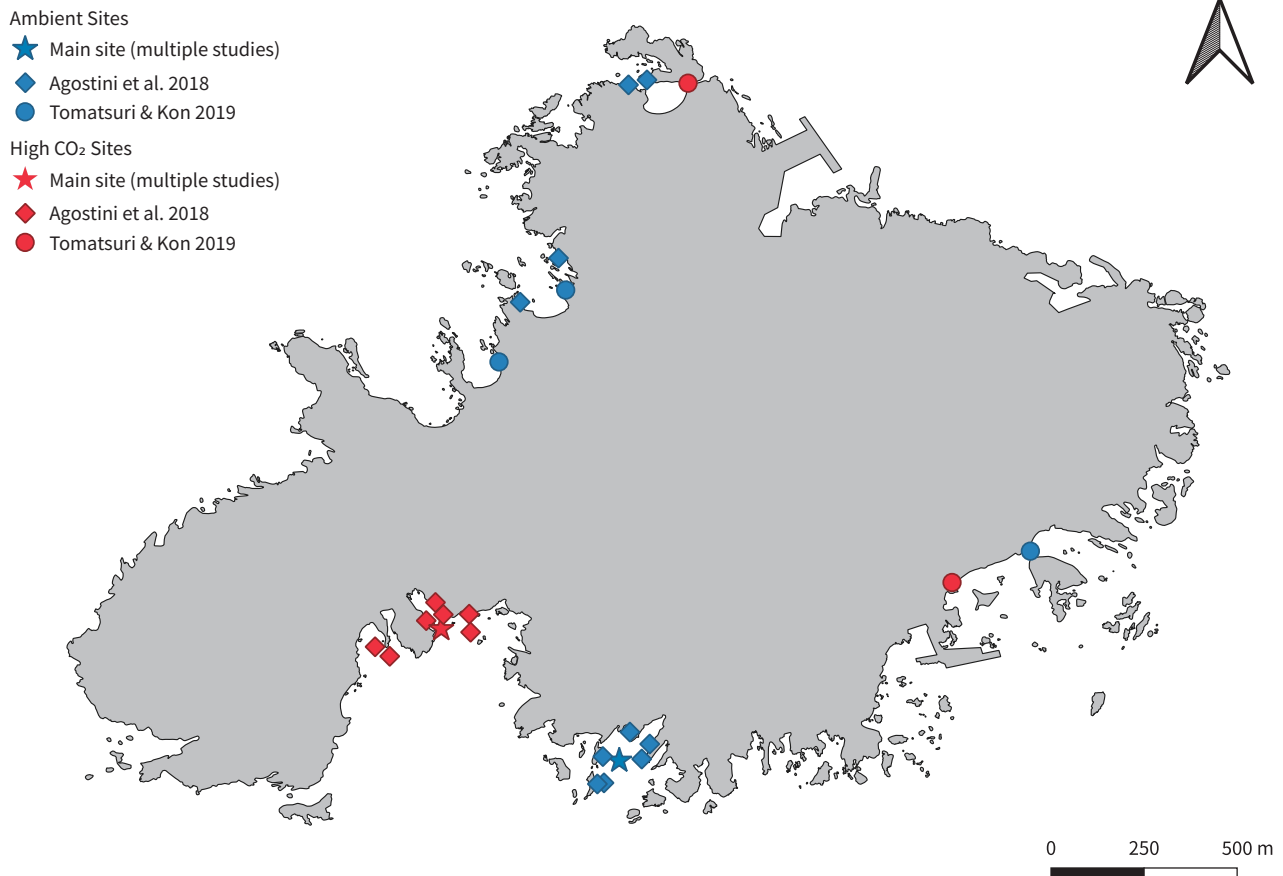


Fig. 1. Shikine island, Japan, showing the main sites used by Agostini et al., 2018, Harvey et al., 2019, and this study (stars) plus other sites that we surveyed less frequently (diamonds and circles). Blue symbols show sites with ambient low levels of pCO₂ in seawater, red symbols show sites with high levels of pCO₂ 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 $p\text{CO}_2$ was $\leq 410 \mu\text{atm}$ ('ambient' sites) and closer to the seeps where $p\text{CO}_2$ in seawater was high ('high CO₂' sites).

Intertidal sites

Agostini et al. (2018) measured the percent cover of encrusting fauna in $25 \times 25 \text{ cm}$ quadrats and counted other sessile macroinvertebrates in $50 \times 50 \text{ cm}$ 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 CO₂ sites. Tomatsuri and Kon (2019) surveyed the diversity and abundance of hermit crabs and live molluscs at three ambient sites and two high CO₂ sites using ten $50 \times 50 \text{ cm}$ 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 $50 \times 50 \text{ cm}$ digital photoquadrats ($n = 8\text{--}11$) at four ambient sites and three high-CO₂ 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 $p\text{CO}_2$ $410 \pm \text{SD } 73 \mu\text{atm}$ characterised by seaweeds and the other with $971 \pm \text{SD } 258 \mu\text{atm}$ and characterised by a diatom mat. Fauna were collected using a SCUBA diver operated airlift to dislodge and lift samples into a $400 \mu\text{m}$ 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 CO₂ zone and one in an ambient CO₂ 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 CO₂ 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 ($< 410 \mu\text{atm } p\text{CO}_2$) and high CO₂ 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 CO₂. Mean (\pm SD) pH_T, temperature, salinity, and total alkalinity (TA) are measured values. Seawater $p\text{CO}_2$, dissolved inorganic carbon and the saturation states for calcite (Ω_{calcite}) and aragonite ($\Omega_{\text{aragonite}}$) are mean values (\pm SD) calculated using the carbonate chemistry system analysis program CO₂SYS.

| Station | | pH | Temp (°C) | Salinity (psu) | TA ($\mu\text{mol kg}^{-1}$) | $p\text{CO}_2$ (μatm) | DIC ($\mu\text{mol kg}^{-1}$) | Ω_{cal} | Ω_{arag} | 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 $p\text{CO}_2$. 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 $p\text{CO}_2$ sites than the ambient sites (Agostini et al., 2018).

Table 2 lists the intertidal benthic macroinvertebrates

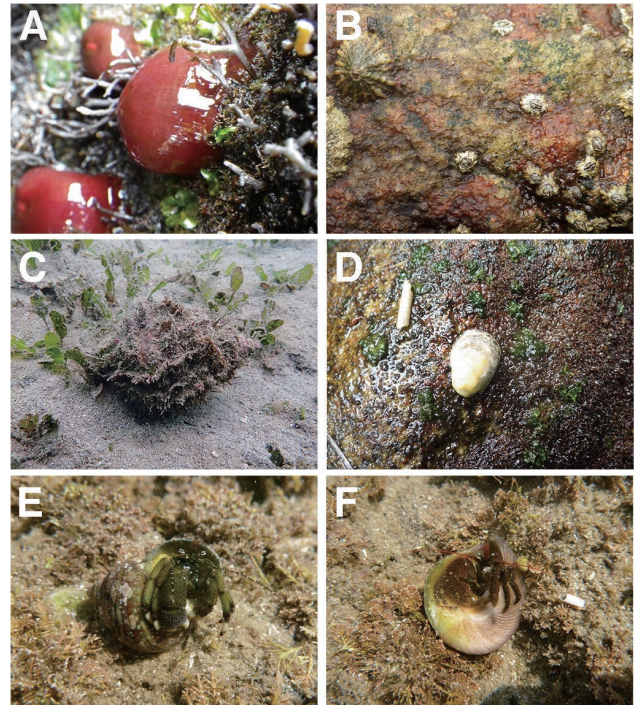


Fig. 2. Benthic invertebrates found at intertidal sites with high seawater $p\text{CO}_2$ (mean 970–1484 μatm) on Shikine Island, Japan. **(A)** Cnidaria *Actinia equina*, **(B)** Crustacea *Chthamalus challengerii* and Mollusca *Siphonaria japonica*, **(C)** Mollusca *Monoplex parthenopeus*, **(D)** 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 $p\text{CO}_2$ 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 | $\leq 402 \mu\text{atm}$ | 1052–1233 μatm | Lifestyle | Feeding | Ref. |
|------------------------------|----------------|--------------------------------|--------------------------|---------------------------|-----------|---------|---------|
| Porifera | Demospongiae | <i>Halichondria okadai</i> | • | • | sessile | SF | 1 |
| Cnidaria | Anthozoa | <i>Actinia equina</i> | | • | sessile | C | 1 |
| | | Sphenopidae sp. | | • | sessile | SF | 1 |
| | | <i>Tubastraea coccinea</i> | • | | sessile | SF | 1 |
| Mollusca | Polyplacophora | <i>Acanthochitona achates</i> | • | • | vagile | G | 1 |
| | | <i>Acanthopleura japonica</i> | • | • | vagile | G | 1 |
| | | Acanthoplurinae gen sp. | 0.5 ± 2.0 | | vagile | G | 3, u.d. |
| | | <i>Onithochiton hirasei</i> | • | | vagile | G | 1 |
| | Gastropoda | <i>Cellana grata</i> | • | • | vagile | G | 1 |
| | | <i>Cellana nigrolineata</i> | 0.3 ± 1.0 | | vagile | G | 3, u.d. |
| | | <i>Cellana rota</i> | 0.3 ± 1.0 | | vagile | G | 3, u.d. |
| | | <i>Cellana toreuma</i> | • | • | vagile | G | 1 |
| | | <i>Cellana toreuma</i> | 0.3 ± 2.0 | | vagile | G | 3, u.d. |
| | | <i>Diloma suavis</i> | | • | vagile | G | 1 |
| | | <i>Drupa ricinus hadari</i> | • | | vagile | C | 1 |
| | | <i>Drupella margariticola</i> | 1.3 ± 2.7 | | vagile | C | 3, u.d. |
| | | <i>Echinolittorina radiata</i> | 8.3 ± 20.4 | | vagile | G | 3, u.d. |
| | | <i>Ergalatax contractus</i> | • | | vagile | S | 1 |
| <i>Japeuthria ferrea</i> | 0.3 ± 3.2 | | vagile | S | 3, u.d. | | |
| <i>Latirus nagasakiensis</i> | • | | vagile | S | 1 | | |
| <i>Lottia kogamogai</i> | • | | vagile | G | 1 | | |

Table 2. Continued.

| Phylum | Class | Species | ≤402 μatm | 1052–1233 μatm | Lifestyle | Feeding | Ref. |
|--|--------------|-----------------------------------|-------------|----------------|-----------------------|---------|---------|
| | | <i>Mancinella echinata</i> | | • | vagile | C | 1 |
| | | <i>Mitrella burchardi</i> | | • | vagile | S | 1 |
| | | <i>Morula granulata</i> | • | | vagile | C | 1 |
| | | <i>Morula iostoma</i> | • | | vagile | C | 1 |
| | | <i>Morula musiva</i> | | • | vagile | C | 1 |
| | | <i>Morula uva</i> | • | | vagile | C | 1 |
| | | Muricidae sp 1. | • | | vagile | C | 1 |
| | | <i>Monoplex parthenopeus</i> | | • | vagile | C | 1 |
| | | Neritidae spp. | 11.0 ± 7.8 | 2.5 ± 7.4 | vagile | G | 3, u.d. |
| | | <i>Nipponacmea</i> sp. | 0.3 ± 1.0 | | vagile | G | 3, u.d. |
| | | Patellidae gen sp. | 0.3 ± 2.0 | | vagile | G | 3, u.d. |
| | | <i>Patelloida saccharina</i> | • | • | vagile | G | 1 |
| | | <i>Patelloida saccharina lanx</i> | • | • | vagile | G | 1 |
| | | <i>Patelloida saccharina lanx</i> | 0.8 ± 2.3 | 0.4 ± 1.2 | vagile | G | 3, u.d. |
| | | <i>Proterato callosa</i> | | • | vagile | G | 1 |
| | | <i>Purpura panama</i> | • | • | vagile | C | 1 |
| | | <i>Reishia bronni</i> | | • | vagile | C | 1 |
| | | <i>Reishia clavigera</i> | • | • | vagile | C | 1 |
| | | <i>Reishia clavigera</i> | 6.0 ± 5.3 | | vagile | C | 3, u.d. |
| | | <i>Reishia luteostoma</i> | | • | vagile | C | 1 |
| | | <i>Sabia conica</i> | | • | vagile | D | 1 |
| | | <i>Scutellastra flexuosa</i> | | • | vagile | G | 1 |
| | | <i>Siphonaria japonica</i> | • | • | vagile | G | 1 |
| | | <i>Siphonaria japonica</i> | 29.1 ± 35.6 | 3.4 ± 4.3 | vagile | G | 3, u.d. |
| | | <i>Siphonaria signa</i> | | • | vagile | G | 1 |
| | | <i>Siphonaria sirius</i> | • | • | vagile | G | 1 |
| | | <i>Siphonaria sirius</i> | 0.4 ± 2.9 | | vagile | G | 3, u.d. |
| | | <i>Strigatella scutula</i> | • | | vagile | C | 1 |
| | | <i>Tenguella granulata</i> | 1.1 ± 2.7 | 0.8 ± 1.8 | vagile | C | 3, u.d. |
| | | <i>Tenguella musiva</i> | 2.7 ± 5.4 | 0.1 ± 1.2 | vagile | C | 3, u.d. |
| | | <i>Trochus rota</i> | • | | vagile | G | 1 |
| | | <i>Turbo stenogyrus</i> | • | | vagile | G | 1 |
| | | <i>Tylothais virgata</i> | • | | vagile | C | 1 |
| | Bivalvia | <i>Hormomya mutabilis</i> | | • | sessile | SF | 1 |
| | | <i>Mytilisepta virgata</i> | 6.4 ± 10.7 | 0.8 ± 1.8 | sessile | SF | 3, u.d. |
| | | <i>Saccostrea kegaki</i> | | • | sessile | SF | 1 |
| | | <i>Saccostrea kegaki</i> | 5.0 ± 6.2 | | sessile | SF | 3, u.d. |
| | | <i>Saccostrea morda</i> | • | | sessile | SF | 1 |
| | | <i>Septifer bilocularis</i> | 1.2 ± 3.7 | • | sessile | SF | 3, u.d. |
| Annelida | Polychaeta | Serpulidae sp 1. | • | • | sessile | SF | 1 |
| | | <i>Spirobranchus</i> sp. | • | | sessile | SF | u.d. |
| | | Spirorbinae sp. | • | • | sessile | SF | 1 |
| Arthropoda | Maxillopoda | <i>Capitulum mitella</i> | • | • | sessile | SF | 1 |
| | | <i>Chthamalus challengerii</i> | • | • | sessile | SF | 1 |
| | | <i>Megabalanus rosa</i> | • | • | sessile | SF | 1 |
| | | <i>Megabalanus volcano</i> | • | | sessile | SF | 1 |
| | | <i>Tetraclita japonica</i> | • | • | sessile | SF | 1 |
| | Malacostraca | <i>Clibanarius virescens</i> | 39.9 ± 43.4 | 3.4 ± 6.0 | vagile | O | 3, u.d. |
| | | <i>Pagurus filholi</i> | 45.2 ± 44.3 | 43.8 ± 35.7 | vagile | O | 3, u.d. |
| | | <i>Pagurus maculosus</i> | | 1.4 ± 4.6 | vagile | O | 3, u.d. |
| | | <i>Pagurus nigrivittatus</i> | 18.7 ± 36.6 | | vagile | O | 3, u.d. |
| | | <i>Pagurus</i> sp. | 0.5 ± 3.0 | | vagile | O | 3, u.d. |
| Total number of taxa per CO ₂ level | | | 57 | 40 | 30% reduction in taxa | | |

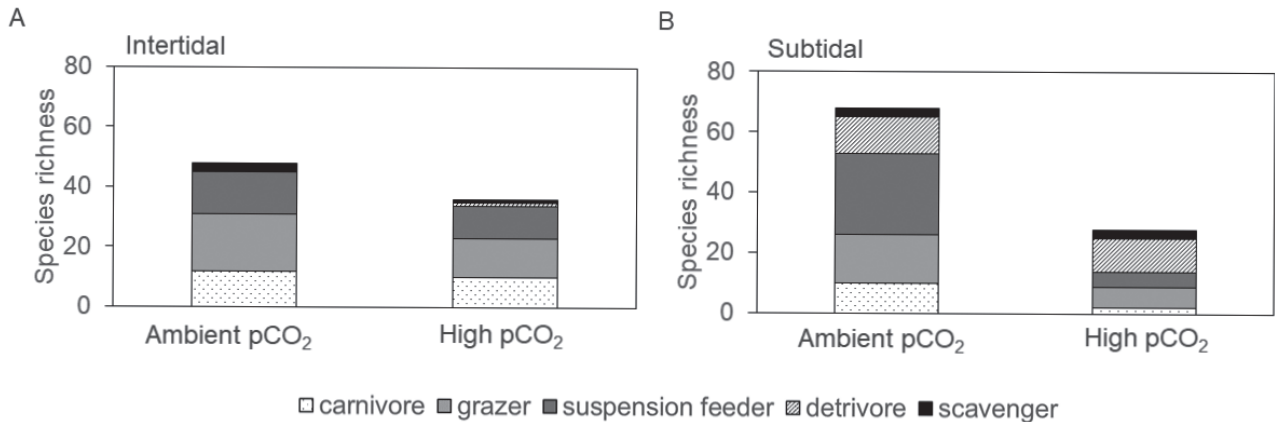


Fig. 3. Macroinvertebrate species richness, divided into feeding guilds, on (A) intertidal and (B) subtidal bedrock at sites with ambient levels of seawater $p\text{CO}_2$ and sites with high levels of $p\text{CO}_2$ around Shikine Island, Japan.

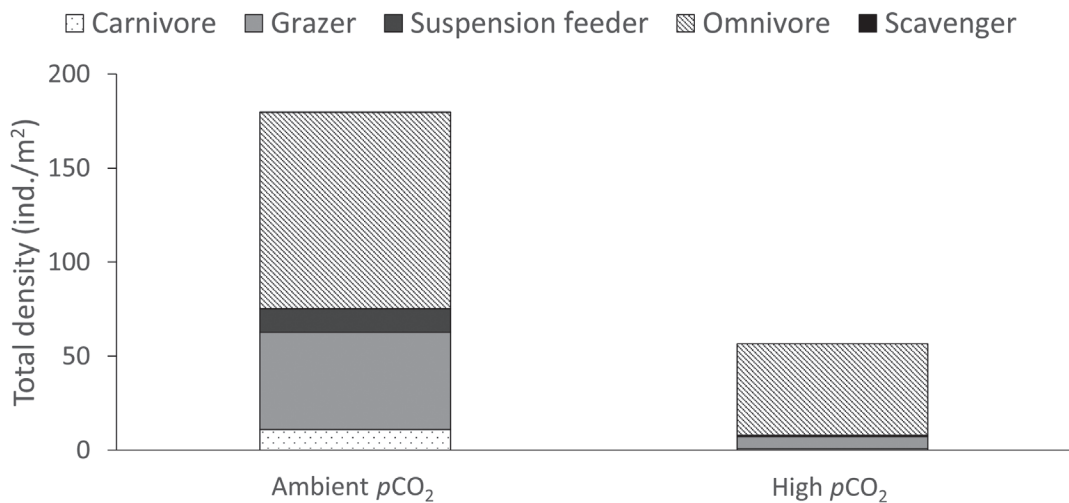


Fig. 4. Abundance of molluscs and hermit crabs (pooled data divided into feeding types) at intertidal rocky shore sites with ambient levels of seawater $p\text{CO}_2$ and sites with high levels of $p\text{CO}_2$ around Shikine Island, Japan.

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 challengerii*, 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-

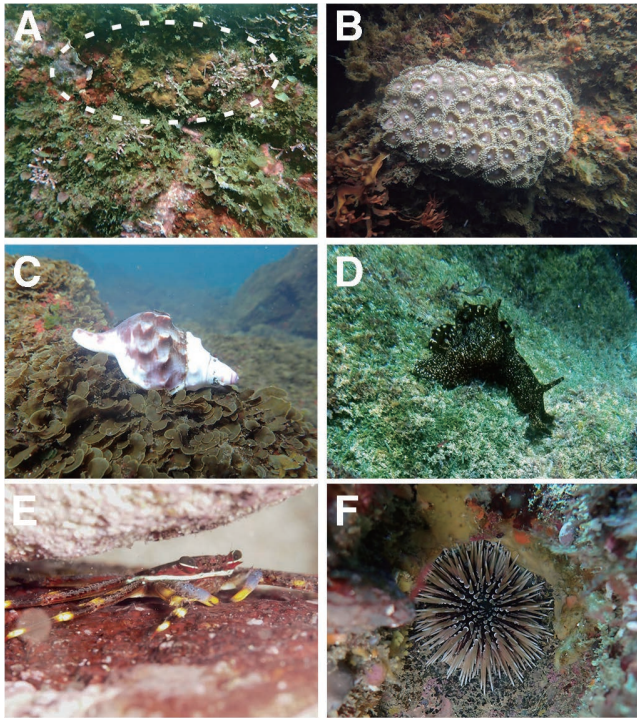


Fig. 5. Benthic invertebrates found at shallow sublittoral rocky sites (< 10 m CD) with high seawater pCO₂ (mean 970–1484 μatm) on Shikine island, Japan. **(A)** Porifera *Aulospongos villosus*, **(B)** Cnidaria *Zoanthus* sp., **(C)** Mollusca *Charonia lampas*, **(D)** Mollusca *Aplysia* sp., **(E)** Crustacea *Percnon planissimum*, and **(F)** Echinodermata *Echinometra* sp.

ian corals and an increase in benthic diatom mats and turf algae at high CO₂. Table 3 lists the benthic invertebrates recorded in ambient and high CO₂ conditions, assigned to lifestyle and feeding groups (using the same reference sources as for Table 1) with quantitative density data converted to numbers per m².

There was a 60% decrease in macrofaunal biodiversity from ambient to high CO₂ 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 CO₂. Scleractinian corals were common in ambient conditions (~11% cover) but comprised < 1% cover at high CO₂ sites. Small gastropods were abundant in ambient conditions but not at high CO₂ 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 CO₂ 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 CO₂ (Fig. 6). Tanaiids, which are less calcified, became the most abundant taxon, comprising on average ~50% of individuals in the elevated pCO₂ 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 pCO₂ 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 | <i>Asteropus simplex</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Aulospongos villosus</i> | | • | sessile | epifauna | SF | new | | |
| | | <i>Axinyssa aculeata</i> | | • | sessile | epifauna | SF | new | | |
| | | <i>Clathria (Thalysias) fasciculata</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Craniella serica</i> | • | | sessile | epifauna | SF | new | | |
| | | Desmospongiae sp. | • | | sessile | epifauna | SF | 1 | | |
| | | <i>Halichondria</i> sp. | • | | sessile | epifauna | SF | new | | |
| | | <i>Hymeniacion halichondroides</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Neofibularia</i> sp. | • | | sessile | epifauna | SF | new | | |
| | | <i>Penares incrustans</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Petrosia ushitsuensis</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Phorbos tanitai</i> | | • | sessile | epifauna | SF | new | | |
| | | <i>Poecillastra tenuilaminaris</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Pseudosuberites perforatus</i> | | • | sessile | epifauna | SF | new | | |
| | | <i>Spheciospongia panis</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Stelletta purpurea</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Strongylacion kaneohae</i> | • | | sessile | epifauna | SF | new | | |
| | | <i>Topsentia kushimotoensis</i> | • | | sessile | epifauna | SF | new | | |
| | | Cnidaria | Anthozoa | <i>Acropora solitaryensis</i> | • | | sessile | epifauna | SF | 1 |
| | | | | <i>Alveopora japonica</i> | • | | sessile | epifauna | SF | 1 |
| <i>Cyphastrea</i> sp. | • | | | | sessile | epifauna | SF | 1 | | |
| <i>Dendronephthya</i> sp. | • | | | | sessile | epifauna | SF | 1 | | |
| <i>Diplastrea speciosa</i> | • | | | | sessile | epifauna | SF | 1 | | |
| <i>Entacmaea quadricolor</i> | • | | | | sessile | epifauna | C | 1 | | |
| <i>Goniastrea complex</i> sp 1. | • | | | | sessile | epifauna | SF | 1 | | |

Table 3. Continued.

| Phylum | Class | Species | ≤410 µatm | 971–1484 µatm | Lifestyle | Habitat | Feeding | Ref. | | |
|--|----------------|--------------------------------------|------------------|----------------------------|-----------------------|-------------|----------|----------|----|-----|
| Mollusca | Gastropoda | <i>Hydnophora exesa</i> | ● | | sessile | epifauna | SF | 1 | | |
| | | <i>Montipora turgescens</i> | ● | | sessile | epifauna | SF | 1 | | |
| | | <i>Paragoniastrea australiensis</i> | ● | | sessile | epifauna | SF | 1 | | |
| | | Phymanthidae sp. | ● | | sessile | epifauna | C | 1 | | |
| | | <i>Porites heronensis</i> | ● | | sessile | epifauna | SF | 1 | | |
| | | <i>Zoanthus</i> sp. | | ● | sessile | epifauna | SF | 1 | | |
| | | <i>Aplysia</i> sp. | | ● | vagile | epifauna | G | 1 | | |
| | | <i>Charonia lampas</i> | ● | ● | 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 | | |
| | | <i>Dolabella auricularia</i> | ● | | 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 | | |
| | | <i>Omphalius pfeifferi pfeifferi</i> | ● | | 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 | | |
| | | Sipuncula | Bivalvia | Lucinidae sp. | 2.6 ± 1.3 | | vagile | infauna | SF | 2 |
| | | | 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 | | |
| Arthropoda | Maxillopoda | Serpulidae sp 2. | ● | | sessile | epifauna | SF | 1 | | |
| | | Syllidae sp. | | 2.6 ± 1.3 | vagile | epifauna | C | 2 | | |
| | | Balanomorpha sp. | ● | | sessile | epifauna | SF | 1 | | |
| | | Malacostraca | Cypridinidae sp. | | 30.6 ± 13.7 | vagile | infauna | S | 2 | |
| | | | Anthuridae sp. | 1.3 ± 1.1 | 5.1 ± 3.2 | vagile | epifauna | D | 2 | |
| | | <i>Archaeomysis</i> sp. | 1.3 ± 1.1 | | vagile | epifauna | O | 2 | | |
| | | Brachyura sp. | ● | | vagile | epifauna | – | 1 | | |
| | | Cancriidae 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 | | |
| | | <i>Monocorophium</i> sp. | | 6.4 ± 3.4 | vagile | infauna | D | 2 | | |
| | | Palapedia sp. | 12.8 ± 7.5 | | vagile | epifauna | O | 2 | | |
| | | <i>Percnon planissimum</i> | ● | ● | vagile | epifauna | G | new | | |
| | | Tanaidae sp. | 210.5 ± 62.7 | 809.9 ± 124.9 | vagile | epifauna | D | 2 | | |
| | | <i>Urothoe</i> 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 | <i>Leiaster leachi</i> | ● | | vagile | epifauna | C | new |
| | | | Holothuroidea | <i>Holothuria pervicax</i> | ● | | vagile | epifauna | D | 1 |
| | | | Ophiuroidea | Ophiura sp. | 24.2 ± 11.7 | 91.8 ± 34.0 | vagile | epifauna | D | 2 |
| | | | Echinoidea | <i>Diadema setosum</i> | ● | ● | vagile | epifauna | G | new |
| | | | | <i>Echinometra</i> sp. | ● | ● | vagile | epifauna | G | new |
| | Echinoidea sp. | 3.8 ± 2.2 | | vagile | epifauna | G | 2 | | | |
| Total number of taxa per CO ₂ level | | | 73 | 29 | 60% reduction in taxa | | | | | |

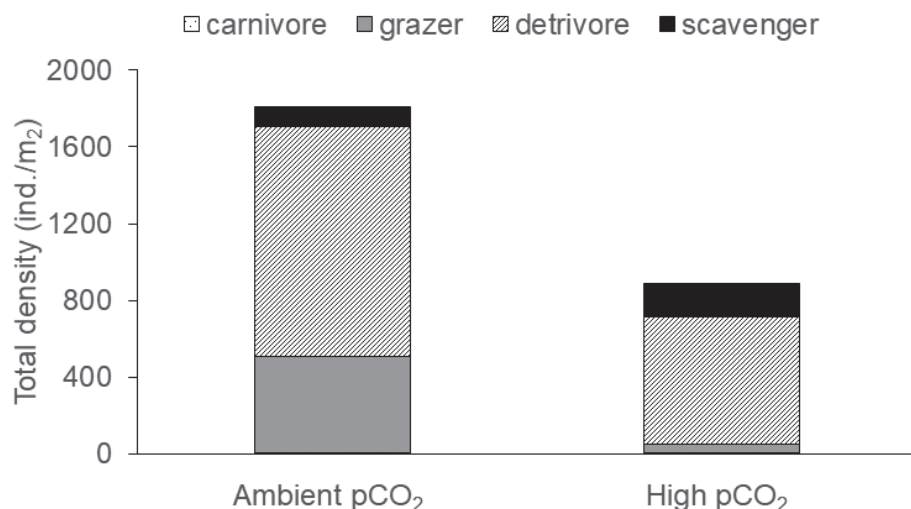


Fig. 6. Abundance of macro-invertebrates in shallow sublittoral (< 10 m CD) air-lift samples (pooled data divided into feeding types) from rocky shore sites with ambient levels of seawater pCO₂ and sites with high levels of pCO₂ around Shikine Island, Japan.

DISCUSSION

The studies synthesised here focused on investigating the biological effects of ocean acidification and so avoided areas that had extremely high levels of CO₂ 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 CO₂ 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 CO₂ 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 (*Mytilus septa 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 CO₂. 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 CO₂ (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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 pCO₂ levels in seawater. The high typhoon resilience of marine communities growing at ambient pCO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ sites (Kroeker et al., 2011). Generalists and small-bodied animals dominate at several Mediterranean CO₂ seep sites, resulting in food web simplification (Vizzini et al., 2017). Similarly, in Papua New Guinea, reductions in invertebrate diversity were observed with increasing CO₂ (Fabricius et al., 2011). A 3-fold decrease in zooplankton biomass was noted in high CO₂ areas near Papua New Guinea seeps compared to ambient nearby sites (Smith et al., 2016). The low biodiversity observed at high CO₂ 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 CO₂. Teixido 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 CO₂ 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 CO₂ compared with 14 in ambient conditions, one anthozoan species at high CO₂ compared with 12 in ambient conditions, and five mollusc species at high CO₂ compared with 19 in ambient conditions. All feeding types were still represented at high CO₂ 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 pCO₂ 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 CO₂ 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 CO₂, 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 CO₂. Our observations suggest that cuts in CO₂ 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.

REFERENCES

- Agostini S, Wada S, Kon K, Omori A, Kohtsuka H, Fujimura H, et al. (2015) Geochemistry of two shallow CO₂ seeps in Shikine Island (Japan) and their potential for ocean acidification research. *Reg Stud Mar* 2: 45–53
- Agostini S, Harvey BP, Wada S, Kon K, Milazzo M, Inaba I, et al. (2018) Ocean acidification drives community shifts towards simplified non-calcified habitats in a subtropical-temperate transition zone. *Sci Rep* 8: 11354
- Agostini S, Harvey BP, Milazzo M, Wada S, Kon K, Floc'h N, et al. (2021) Simplification, not 'tropicalization', of temperate marine ecosystems under ocean warming and acidification. *Glob Chang Biol* 27: 4771–4784
- Aiuppa A, Hall-Spencer JM, Milazzo M, Turco G, Caliro S, Napoli RD (2021) Volcanic CO₂ seep geochemistry and use in understanding ocean acidification. *Biogeochemistry* 152: 92–115
- Allen R, Foggo A, Fabricius K, Balistreri A, Hall-Spencer JM (2017) Tropical CO₂ seeps reveal the impact of ocean acidification on coral reef invertebrate recruitment. *Mar Pollut Bull* 124: 607–613
- Blain CO, Kulins S, Radford CA, Sewell MA, Shears NT (2021) Heterogeneity around CO₂ vents obscures the effects of ocean acidification on shallow reef communities. *ICES J Mar Sci* doi.org/10.1093/icesjms/fsab184
- Cattano C, Agostini S, Harvey BP, Wada S, Quattrocchi F, Turco G, et al. (2020) Changes in fish communities due to benthic habitat shifts under ocean acidification conditions. *Sci Total Environ* 75: 138501
- Cigliano M, Gambi MC, Rodolfo-Metalpa R, Patti FP, Hall-Spencer JM (2010) Effects of ocean acidification on invertebrate settlement at volcanic CO₂ vents. *Mar Biol* 157: 2489–2502
- Enochs IC, Manzello DP, Donham EM, Kolodziej G, Okano R, Johnston L, et al. (2015) Shift from coral to macroalgae dominance on a volcanically acidified reef. *Nat Clim Chang* 5: 1083–1088
- Fabricius KE, Langdon C, Uthicke S, Humphrey C, Noonan S, De'ath G, et al. (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nat Clim Chang* 1: 165–169
- Fabricius KE, De'ath G, Noonan S, Uthicke S (2014) Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proc Royal Soc B*

- 281: 20132479
- Foo SA, Byrne M, Ricevuto E, Gambi MC (2018) The carbon dioxide vents of Ischia, Italy, a natural system to assess impacts of ocean acidification on marine ecosystems: an overview of research and comparisons with other vent systems. *Oceanogr Mar Biol* 56: 237–310
- Garilli V, Rodolfo-Metalpa R, Scuderi D, Brusca L, Parrinello D, Rastrick SPS, et al. (2015) Physiological advantages of dwarfing in surviving extinctions in high-CO₂ oceans. *Nat Clim Chang* 5: 678–682
- Golbuu Y, Gouezo M, Kurihara H, Rehm L, Wolanski E (2016) Long-term isolation and local adaptation in Palau's Nikko Bay help corals thrive in acidic waters. *Coral Reefs* 35: 909–918
- Hall-Spencer JM, Harvey BP (2019) Ocean acidification impacts on coastal ecosystem services due to habitat degradation. *Emerging Top Life Sci* 3: 197–206
- Hall-Spencer JM, Rodolfo-Metalpa R, Martin S, Ransome E, Fine M, Turner SM, et al. (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454: 96–99
- Harvey BP, Agostini S, Wada S, Inaba K, Hall-Spencer JM (2018) Dissolution: the Achilles' Heel of the Triton shell in an acidifying ocean. *Front Mar Sci* 5: 371
- Harvey BP, Agostini S, Kon K, Wada S, Hall-Spencer JM (2019) Diatoms dominate and alter marine food-webs when CO₂ rises. *Diversity* 11: 242
- Harvey BP, Allen R, Agostini S, Hoffmann LJ, Kon K, Summerfield TC, et al. (2021a) Feedback mechanisms stabilise degraded turf algal systems at a CO₂ seep site. *Commun Biol* 4: 219
- Harvey BP, Kon K, Agostini S, Wada S, Hall-Spencer JM (2021b) Ocean acidification locks algal communities in a species-poor early successional stage. *Glob Change Biol* 27: 2174–2187
- Hayashi I (2006) Introduction to useful aquatic invertebrates. Kouseisha Kouseikaku, Tokyo (in Japanese)
- Hooper J (2000) Sponguide: Guide to Sponge Collection and Identification. Queensland Museum, Queensland
- Hooper J, van Soest R (2002) *Systema Porifera: A Guide to the Classification of Sponges*. Springer, Boston
- Hu MY-A, Hagen W, Jeng M-S, Saborowski R (2012) Metabolic energy demand and food utilization of the hydrothermal vent crab *Xenograpsus testudinalis* (Crustacea: Brachyura). *Aquat Biol* 15: 11–25
- Imahara Y (2011) A colour guide to rocky shores of Japan. Tombow Shuppan, Osaka (in Japanese)
- Inaba K, Hall-Spencer JM (2020) Japanese Marine Life, A Practical Training Guide in Marine Biology. Springer Nature, Singapore
- Inoue S, Kayanne H, Yamamoto S, Kurihara H (2013) Spatial community shift from hard to soft corals in acidified water. *Nat Clim Chang* 3: 683–687
- Kroeker KJ, Micheli F, Gambi MC, Martz TR (2011) Divergent ecosystem responses within a benthic marine community to ocean acidification. *Proc Natl Acad Sci USA* 108: 14515–14520
- Kurihara H, Watanabe A, Tsugi A, Mimura I, Hongo C, Kawai T, et al. (2021) Potential local adaptation of corals at acidified and warmed Nikko Bay, Palau. *Sci Rep* 11: 11192
- Lemasson AJ, Fletcher S, Hall-Spencer J, Knights AM (2017) Linking the biological impacts of ocean acidification on oysters to changes in ecosystem services: A review. *J Exp Mar Biol Ecol* 492: 49–62
- Melwani AR, Kim SL (2008) Benthic infaunal distributions in shallow hydrothermal vent sediments. *Acta Oecol* 33: 162–175
- Miura T, Tsukahara J, Hashimoto J (1997) *Lamellibranchia satsuma*, a new species of vestimentiferan worm (Annelida: Pogonophora) from a shallow hydrothermal vent in Kagoshima Bay, Japan. *Proc Biol Soc Wash* 110: 447–456
- Miyake H, Oda A, Wada S, Kodaka T, Kurosawa S (2019) First record of a shallow hydrothermal vent crab, *Xenograpsus testudinalis*, from Shikine-jima Island in the Izu archipelago. *Biogeography* 21: 31–36
- Nishimura S (1992) Guide to Seashore Animals of Japan with Colour Pictures and Keys. Hoikusha, Osaka (in Japanese)
- Okutani T (2017) *Main Molluscs in Japan*. 2nd ed, Tokai University Press, Japan (in Japanese)
- Pitchler T, Biscéré T, Kinch J, Zampighi M, Houlbrèque F, Rodolfo-Metalpa R (2019) Suitability of the shallow water hydrothermal system at Ambitle Island (Papua New Guinea) to study the effect of high pCO₂ on coral reefs. *Mar Pollut Bull* 138: 148–158
- Rützler K (1978) Sponges in coral reefs. In "Coral Reefs: Research Methods: Monographs on Oceanographic Methodology 5" Ed by DR Stoddart, RE Johannes, UNESCO, Paris, pp 299–313
- Suggett DJ, Hall-Spencer JM, Rodolfo-Metalpa R, Boatman TG, Payton R, Pettay DT, et al. (2012) Sea anemones may thrive in a high CO₂ world. *Glob Chang Biol* 18: 3015–3025
- Sunday JM, Fabricius KE, Kroeker KJ, Anderson KM, Brown NE, Barry JP, et al. (2017) Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. *Nat Clim Chang* 7: 81–85
- Tarasov VG (2006) Effects of shallow-water hydrothermal venting on biological communities of coastal marine ecosystems of the western Pacific. *Adv Mar Biol* 50: 267–421
- Teixidó N, Gambi MC, Parravacini V, Kroeker K, Micheli F, Ballesteros E (2018) Functional biodiversity loss along natural CO₂ gradients. *Nat Commun* 9: 5149
- Tomatsuri M, Kon K (2019) Impacts of ocean acidification on hermit crab communities through contrasting responses of *Pagurus filholi* (de Man, 1887) and *Clibanarius virescens* (Krauss, 1843). *Aquat Ecol* 53: 569–580
- Vizzini S, Martinez-Crego B, Andolina C, Massa-Gallucci A, Connell SD, Gambi MC (2017) Ocean acidification as a driver of community simplification via the collapse of higher-order and rise of lower-order consumers. *Sci Rep* 7: 4018
- Wada S, Agostini S, Harvey BP, Omori Y, Hall-Spencer JM (2021) Ocean acidification increases phyto-benthic carbon fixation and export in a warm-temperate system. *Estuar Coast Shelf Sci* 250: 107113
- Zhirmunsky AV, Tarasov VG (1990) Unusual marine ecosystem in the flooded crater of Ushishir volcano. *Mar Ecol Prog Ser* 65: 95–102

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