








Simplification, not “tropicalization”, of temperate marine ecosystems under ocean warming and acidification

Sylvain Agostini¹  | Ben P. Harvey¹  | Marco Milazzo^{2,3}  | Shigeki Wada¹  |
Koetsu Kon¹  | Nicolas Floc'h⁴ | Kosei Komatsu⁵  | Mayumi Kuroyama⁵  |
Jason M. Hall-Spencer^{1,6} 

¹Shimoda Marine Research Center,
University of Tsukuba, Shimoda, Shizuoka,
Japan

²Dipartimento di Scienze della Terra e del
Mare, University of Palermo, Palermo,
Italy

³Consorzio Nazionale Interuniversitario
per le Scienze del Mare (CoNISMa, Rome,
Italy

⁴Ecole Européenne Supérieure d'Art de
Bretagne, Rennes, France

⁵Atmosphere and Ocean Research Institute,
University of Tokyo, Kashiwa, Japan

⁶Marine Biology and Ecology Research
Centre, University of Plymouth, Plymouth,
UK

Correspondence

Jason M. Hall-Spencer and Sylvain
Agostini, Shimoda Marine Research
Center, University of Tsukuba, 5-10-1
Shimoda, Shizuoka 415-0025, Japan.
Emails: jhall-spencer@plymouth.ac.uk
(J.M.H.-S.); agostini.sylvain@shimoda.
tsukuba.ac.jp (S.A.)

Funding information

Travel costs were funded by the Daiwa
Foundation (Grant Number: 10777/11517)
for J.M.H.-S., and by a Japan Society for
the Promotion of Science Short Term
Invitation Fellowship (Grant Number:
S16073) for M.M. This project was
supported by JSPS KAKENHI Grant in Aid
(Grant No: 17K17621). We acknowledge
funding support from the Ministry of
Environment, Government of Japan
(Suishinhi: 4RF-1701) and this publication
contributes towards the International
Education and Research Laboratory
Program, University of Tsukuba.

Abstract

Ocean warming is altering the biogeographical distribution of marine organisms. In the tropics, rising sea surface temperatures are restructuring coral reef communities with sensitive species being lost. At the biogeographical divide between temperate and tropical communities, warming is causing macroalgal forest loss and the spread of tropical corals, fishes and other species, termed “tropicalization”. A lack of field research into the combined effects of warming and ocean acidification means there is a gap in our ability to understand and plan for changes in coastal ecosystems. Here, we focus on the tropicalization trajectory of temperate marine ecosystems becoming coral-dominated systems. We conducted field surveys and in situ transplants at natural analogues for present and future conditions under (i) ocean warming and (ii) both ocean warming and acidification at a transition zone between kelp and coral-dominated ecosystems. We show that increased herbivory by warm-water fishes exacerbates kelp forest loss and that ocean acidification negates any benefits of warming for range extending tropical corals growth and physiology at temperate latitudes. Our data show that, as the combined effects of ocean acidification and warming ratchet up, marine coastal ecosystems lose kelp forests but do not gain scleractinian corals. Ocean acidification plus warming leads to overall habitat loss and a shift to simple turf-dominated ecosystems, rather than the complex coral-dominated tropicalized systems often seen with warming alone. Simplification of marine habitats by increased CO₂ levels cascades through the ecosystem and could have severe consequences for the provision of goods and services.

KEYWORDS

biogeography, climate change, kelp forests, natural analogues, range shift, scleractinian corals, warm-temperate

Agostini and Harvey contributed equally to this study.

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1 | INTRODUCTION

Rising anthropogenic carbon dioxide levels are fundamentally altering the physicochemical and biological properties of the ocean, driving changes in marine biogeography (i.e., what lives where; Tittensor et al., 2010). Major biogeographical shifts are already underway due to global warming, with the redistribution of species moving at different rates (Pecl et al., 2017). Considerable changes have been noted in areas with rapid increases in seawater temperature along the paths of strong poleward currents, resulting in novel marine communities (Kumagai et al., 2018; Pinsky et al., 2013). Similarly, ocean acidification can also alter the structure and function of biological communities (Gattuso et al., 2015) but there remains very limited knowledge about how these changes will alter the biogeography of marine organisms (but see Coni et al., 2021), as most ocean acidification research has been focused on isolated elements of ecosystems (Dupont & Pörtner, 2013). The response of marine ecosystems to the combined effects of future ocean warming and acidification remains highly uncertain, due to a lack of empirical observations.

Japan spans more than 2000 km from north to south, with kelp forests in the north and coral reefs in the south. The southern limit of Japanese kelp forests is located where seawater temperatures do not exceed 25–28°C in August and 15–18°C in February (Komazawa et al., 2015). Kelp forests are being lost globally at their low-latitude boundaries due to marine heatwaves and the gradual warming of surface seawater temperatures (Merzouk & Johnson, 2011). In Japan, this widespread loss of kelp is known as “Isoyake” which means “burnt seashore” in Japanese (Fujita, 2010; Vergés et al., 2014). In the far south of Japan, islands such as Okinawa have extensive shallow-water coral reefs with highly biodiverse coral communities containing more than 400 scleractinian species (Nishihira & Veron, 1995). The poleward limit for the formation of tropical coral reefs is around where winter seawater temperatures fall below 18°C (Kleypas et al., 1999). Although a few warm-water hermatypic coral species can extend their northern limit to where temperature minima reach 10°C, these species do not form reefs under these conditions (Veron & Minchin, 1992). Since the 1990s, global warming has threatened coral reefs by causing mass bleaching events that are now increasing in frequency. Japan is no exception: in 2016–2017, a marine heatwave caused a mass bleaching event that killed 50% of the scleractinian corals in this country's largest coral reef located within the Iriomote-Ishigaki National Park, Okinawa (Nakamura, 2017).

Poleward shifts of several tropical coral species are underway in Japan (Yamano et al., 2011) as well as in other parts of the world (Baird et al., 2012; Soares et al., 2016) and this could continue further (Guinotte et al., 2003; Takao et al., 2015; Yara et al., 2016) where land masses or counter-currents do not limit these shifts. Biogeographical shifts in Japanese coral distribution are driven by regional warming and enhanced by larval spread via the Kuroshio (warm water) current (Kang et al., 2020; Kumagai et al., 2018). Some people hope that higher latitudes will offer a refuge for tropical scleractinian corals (Beger et al., 2014; Nakabayashi et al., 2019),

although this requires suitable conservation strategies to be enacted (Makino et al., 2014; Veron, 1992). Taken together, the expansion of corals at their leading (poleward) edge and the retraction of kelp on their trailing (equatorward) edge are changing marine ecosystems at the boundary between subtropical and temperate biogeographical zones.

As warm-water species increasingly colonize temperate reefs and replace cold-water species, temperate reefs start to become “tropicalized”. Three tropicalization trajectories are thought to be possible, with the main habitat-forming species becoming either coral, tropical seaweed or turf algae (Vergés et al., 2019). The higher structural complexity and biodiversity associated with a coral-dominated tropicalized reef are likely to support greater ecosystem goods and services compared to seaweed- or turf-dominated reefs. However, it remains uncertain which tropicalization trajectory will be followed and how these novel tropicalized systems will compare to existing temperate reefs.

Most research on tropicalization has solely focused on the effects of rising seawater temperature but does not consider the other major effect of rising atmospheric CO₂ levels on marine ecosystems: ocean acidification. The ecosystem effects of future acidification against a background of warming remain poorly understood, as very few studies have combined these stressors (Alessi et al., 2019; Coni et al., 2021; Rodolfo-Metalpa et al., 2011). We know that acidification of seawater by CO₂ increases the amount of dissolved inorganic carbon and that this may boost the growth of kelp forests (Falkenberg et al., 2013). We also know that this acidification lowers carbonate saturation state which can adversely affect a wide range of calcified marine organisms, including corals (Albright et al., 2016; Doney et al., 2020). This lowering of the aragonite saturation state could slow down the poleward range expansion of scleractinian corals, acting in the opposite direction to warming (van Hooidonk et al., 2014; Yara et al., 2012). While ocean warming is clearly affecting the distribution of marine organisms, the effects of ocean acidification are not as readily visible, despite the fact that it is known to already be affecting organisms and ecosystems from the tropics (Albright et al., 2016; Smith et al., 2020) to the poles (Moy et al., 2009). Differences in the time scales at which ocean warming and acidification affect marine ecosystems add to the uncertainties regarding the future distribution of marine organisms.

The effects of ocean acidification and warming involve changes in the physical, chemical and biological environment that are difficult to reproduce in laboratory conditions. For this reason, natural analogues of futuristic conditions are increasingly being used to assess the likely effects of rising atmospheric CO₂ emissions on marine ecosystems. Carbon dioxide seeps (Agostini et al., 2018; Enochs et al., 2015; Fabricius et al., 2011; Hall-Spencer et al., 2008; Inoue et al., 2013), upwelling zones (Feely et al., 2008) and enclosed bays (Barkley et al., 2015; Camp et al., 2017) can be used to study the ecosystem effects of ocean acidification. However, this approach seldom assesses the combined effects of ocean warming and acidification (Alessi et al., 2019; Coni et al., 2021; Milazzo et al., 2014; Rodolfo-Metalpa et al., 2011). On the other hand, latitudinal

gradients can be used to study the effects of warming on marine ecosystems (Smale & Moore, 2017; Veron & Minchin, 1992) but they do not assess the effects of ocean acidification. Here, we used three locations (Figure 1) at a similar latitude. The first with present-day conditions that is representative of a temperate ecosystem with abundant kelp forests (Biodiversity Center of Japan, 2019; Serisawa, Akino, et al., 2002; Wada et al., 2007), the second as an analogue of future conditions under warming whereby the ecosystem has recently shifted from a temperate-type ecosystem to a more tropicalized one with various corals cohabiting with macroalgae (Agostini et al., 2018; Biodiversity Center of Japan, 2008; Nakabayashi et al., 2019), and the third with ocean warming plus ocean acidification which has a simplified, homogeneous ecosystem dominated by turf algae that lacks habitat complexity and supports less biodiversity (Agostini et al., 2018; Cattano et al., 2020; Harvey et al., 2019, 2021). These last two locations, remote from the "Present" location, provide space for time analogues for an ocean warming alone scenario and an ocean acidification and warming combined scenario. This allows us to assess the likely effects of rising atmospheric CO₂ levels at the leading edge of hermatypic corals and the trailing edge of kelp forests. Our chosen locations took advantage of the influence of the warm Kuroshio current, which causes different coastal temperature regimes over short distances (Murazaki et al., 2015), and a CO₂ seep off Shikine Island, Japan (Agostini et al., 2018). We conducted field surveys to characterize the existing coral and kelp communities at these three locations and we carried out transplantation experiments of kelp (to assess herbivory) and of two hermatypic corals (to study their growth, photosystem efficiency and metabolic rates) at these natural analogues for future conditions. One of the coral species, *Acropora solitaryensis*, represents a fast-growing, branching species that possesses complex morphology but is vulnerable to OA (Agostini et al., 2021) and has shown a rapid poleward expansion

over the last few decades (Yamano et al., 2011). The other species, *Porites heronensis*, is a slow-growing, encrusting species that provide relatively low complexity, although it is resistant to OA (Agostini et al., 2021). We expected that increased temperature would favour the growth and metabolism of corals but that this gain would be negated by combined ocean warming and acidification for the most vulnerable species. We also expected kelp to suffer under warming conditions and that any potential benefit of ocean acidification, as an increased source of carbon for growth, would be overwhelmed by an increase in fish herbivory due to warming.

2 | MATERIALS AND METHODS

2.1 | Study locations and sites

We carried out our observations and experiments at three locations on rocky reefs at 3–10 m depth. One location is representative of temperate marine ecosystems (hereafter referred to as "Present") and situated off the Izu Peninsula (34°39'58.4"N 138°56'33.2"E) close to the Shimoda Marine Research Center, University of Tsukuba (Japan). The other two locations are warmer than the "Present" location and are situated off the shore of Shikine Island, Japan, 50 km from the "Present" location. One is an analogue of ocean warming (hereafter: "OW"; 34°19'01.7"N 139°12'35.9"E) and a second is additionally acidified by a natural carbon dioxide seep, making it an analogue of ocean acidification and warming (hereafter: "OAW"; 34°19'15.0"N 139°12'18.2"E). Surveys to characterize the biological communities were conducted at three separate sites within each location. Due to logistical constraints, transplantation experiments were only conducted at one of the three sites within each location. As these sites showed no discernible differences in their environmental conditions

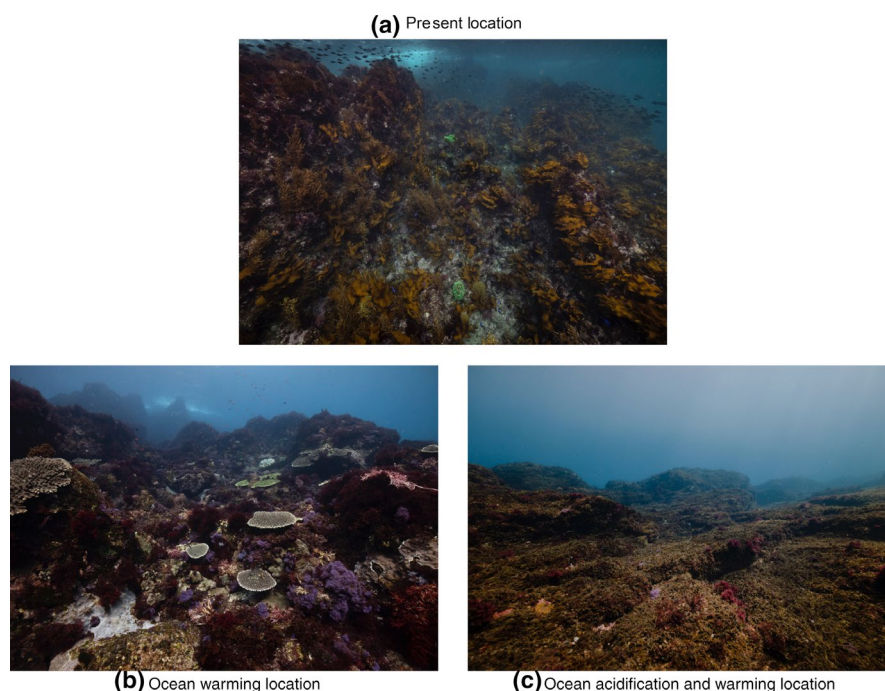


FIGURE 1 Seascapes at the three study locations representative of present-day temperate ecosystems (a), ocean-warming-driven tropicalized ecosystem (b) and simplified ecosystem under combined ocean warming and acidification (c)

or community structure within each location (Figures S2 and S3), we selected those sites that were previously studied the most (see e.g. Agostini et al., 2015, 2018; Cattano et al., 2020; Harvey et al., 2020; Harvey, Kon, et al., 2021; Higuchi et al., 2018).

2.2 | SST historical data from remote sensing data

Daily SST satellite data GHR SST Level 4 G1SST Global Foundation Sea Surface Temperature Analysis (GHR SST; JPL OurOcean, 2010) were used to determine the climatology, and low temperature and high temperature events at the three locations. GHR SST has a spatial resolution of 0.01° (Latitude) \times 0.01° (Longitude). A frequency distribution of SST falling below 15°C and rising above 28°C for the Izu peninsula and the Izu Islands was produced by counting the number of days below 15°C between 1st January 2011 and 31st December 2018. This analysis and the map production were conducted in MATLAB (version 2020a). Finally, GHR SST was used to calculate the median seasonal climatology of each location over the year from 2011 to 2018.

2.3 | Carbonate chemistry

The seawater chemistry of the "OW" and "OAW" locations has been extensively described across multiple years and seasons (Agostini et al., 2015, 2018; Cattano et al., 2020; Harvey et al., 2018; Harvey, Kon, et al., 2021). Measurements for carbonate chemistry at these sites at the same time of the transplantation experiments (26th May to the 5th July 2016) were previously published (Table S1; Harvey et al., 2018). The carbonate chemistry at the "Present" was monitored using a combination of continuous measurements (from the 10th April 2014 to the 24th May 2014) for pH, temperature (SP-11, Kimoto) and salinity (Infinity-CT, JFE Advantech), and discrete samples were taken for measurement of total alkalinity (TA, $n = 5$) and dissolved inorganic carbon (DIC, $n = 5$). Salinity and pH sensors were calibrated according to the manufacturer's instructions. TA and DIC were measured simultaneously using an automated DIC and TA analyzer equipped with a coulometer (Nippon ANS, Co.) and spectrophotometer (Ocean Optics, TM-VIS/NIR; Kosugi et al., 2017), these measurements were used to validate pH measurements and to calculate the carbonate chemistry using CO2SYS (Pierrot et al., 2006). Seawater temperature at each was monitored for 1 year using Hobo temperature loggers (Onset Inc.) deployed at 4–6 m depth. Due to a malfunction with one of the loggers, data from the "Present" between 2015/10/16 and 2015/12/10 were replaced with the daily record of the Shimoda Marine Research Center, University of Tsukuba (available at <http://www.shimoda.tsukuba.ac.jp/kansoku.html>).

2.4 | Benthic communities

Each location was surveyed by scuba divers for coral and kelp abundances using 25×1 m belt transects. These transects were

conducted at three sites within each location ($n = 2$ –6 belt transects per site, with site nested within location). Scleractinian coral colonies greater than 5 cm in diameter were identified in situ following Nishihara and Veron (1995) and Sugihara et al., (2015). The diameter of each colony within the belt was recorded in situ and area coverage ($\text{cm}^2 \text{ m}^{-2}$) was calculated assuming a circular shape. The number of kelp thalli (*Eisenia bicyclis* and *Ecklonia cava*) that were greater than 10 cm in length was counted within each transect belt. These surveys were carried out between June and July 2016.

2.5 | Transplantation experiments

Two kelp transplantation experiments were conducted in September 2015 and February 2016, hereafter referred to as "warm period transplantation" and "cold period transplantation", using *E. bicyclis* thalli (10–50 cm long) collected from 3 to 10 m depth at the "Present" location (using scuba) with care taken to not damage the holdfast. Each transplant experiment was carried out at one site in each of the three locations with the "Present" location serving as a procedural control for transplant stress. In September 2015, thalli were attached by their holdfast using cyanoacrylate instant glue (Toagosei Co. Ltd.) to individual concrete blocks (one thalli per block, $n = 15$ at each of the "Present", "OW" and "OAW" locations; Serisawa et al., 2002). In February 2016, four thalli were attached to individual sand bags using cable ties by their holdfasts ($n = 5$ bags at each of the "Present", "OW" and "OAW" locations). Transplants were haphazardly transplanted at 4–6 m depth within 100 m^2 and were assessed for survival 2 months after transplantation. The two transplantation experiments (warm and cold periods) were used to assess for any seasonal differences in survival. Time lapse videos of transplanted kelp were recorded in September 2016 using a video camera mounted on a frame at the "OAW" location, since those transplanted previously seemed to have been grazed intensively in the warm-water locations.

The transplantation experiment of two species of scleractinian corals was conducted between September 2015 and July 2016. Large colonies of the corals *P. heronensis* ($n = 9$, from the "Present" location) and *A. solitaryensis* ($n = 9$, from the "OW" location) were sampled by scuba at 4–6 m depth in August 2015 with permits obtained from the relevant prefectures (*P. heronensis*: Shizuoka (2015), permit: 27–9; *A. solitaryensis*: Tokyo (2015) permit: 27–18). The colonies were fragmented into individual pieces (20–30 cm^2 in size) and attached using epoxy glue to a 6×6 cm PVC tile (one fragment per tile). The tiles were placed in outdoor aquaria at the Shimoda Marine Research Center, University of Tsukuba, with running seawater for 1 month to allow coral recovery. Tiles with corals that appeared healthy were then placed at 4–6 m depth in one site at each study location, in September 2015 ($n = 15$, 15, 14 for *P. heronensis* and 15, 16, 19 for *A. solitaryensis* at the "Present", "OW" and "OAW" locations, respectively). Coral transplants were attached to three separate bars (1 m length) which were fixed 30 cm above the seafloor using concrete blocks at each end. The "Present" location and

"OW" location served as procedural controls for transplant stress, for *P. heronensis* and *A. solitaryensis*, respectively. Transplants were randomly assigned to each bar (5–7 tiles per species per bar) when deployed and after each set of measurements.

Coral fragments were retrieved after 85 (December), 210 (April) and 293 (July) days to take measurements, being returned to their respective locations within 24 h. Coral growth was measured using the buoyant weight technique (Jokiel, 1978). Photosystem efficiency, maximum yield of the photosystem II (Fv/Fm), was measured using a Junior PAM (Walz) after 30 min of dark incubation. In April and July 2016, the metabolic rates of haphazardly selected fragments were measured ($n = 3$ per location). These coral fragments were incubated in a 500 ml vessel filled with seawater from the respective locations and at the temperature recorded on that day. Incubation conditions and associated carbonate chemistry are reported in Table S2. Illumination was provided by metal halide lamps ($200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) with water movement from magnetic stirrers. Corals were incubated for 2 h under light conditions, held for 30 min in the dark and then incubated for a further 2 h in the dark. Net photosynthesis and respiration rates were determined by the change in dissolved oxygen concentrations during the incubations. Calcification rates in the light and dark were determined using the alkalinity anomaly method (Cohen et al., 2017). Total alkalinity was measured by titration against 0.1 N HCl using an automatic titrator (Ti-Touch 916, Metrohm) and calculated by the Gran plot method. Dissolved oxygen, pH_{NBS} and temperature were measured using a multimeter (Orion 4-star, Thermo Fisher) equipped with a RDO probe and a ROSS pH electrode. Metabolic rates were normalized using the buoyant weight of the corals.

2.6 | Statistical analysis

Statistical analysis was performed with the R statistical software (R Core Team, 2020). Mixed-effect nonparametric ANOVA (Type III Wald F test) as an aligned rank transform procedure with Kenward-Roger approximation for the degrees of freedom in the "ARTool" package (Kay & Wobbrock, 2020) was used to assess changes in the abundance of corals and kelp, with location (fixed effect, 3 levels) and sites (random effect on intercept).

Linear mixed models, using the R package lme4 (Bates et al., 2015), were used to assess changes in coral growth and photosystem efficiency, with location (three levels) and season (three levels) as fixed effects, and mother coral colony nested within "Season" which is nested within "Location" as a random effect on the intercept. Pairwise comparisons were made using Bonferroni-corrected contrasts of the least square means, using the "diffsmeans" function in the "lmerTest" package (Kuznetsova et al., 2017).

Changes in the physiological parameters during the incubation experiments (gross primary production) were assessed using nonparametric ANOVA (Type III Wald F test) as an aligned rank transform procedure with Kenward-Roger approximation for the degrees of freedom in the "ARTool" package (Kay & Wobbrock, 2020) with

pairwise comparisons made using estimated marginal means computed using the package "emmeans" (Lenth, 2021).

Graphs were made using R and ggplot2 (Wickham, 2016) and ggpubr (Kassambara, 2018). The code and raw data are available at <https://gitlab.com/agoremix/tropicalization-under-ocean-warming-and-acidification.git> and the data are deposited on the Pangaea environmental data repository.

3 | RESULTS

3.1 | Environmental context

Remote sensing data show that from 2011 to 2018, the "Ocean Warming" ("OW") and "Ocean Warming and Acidification" ("OAW") locations had the same sea surface temperature regime. They were both slightly warmer than the "Present" location (Figure 2a; "OW": $+0.81^\circ\text{C} \pm 0.28 \text{ SD}$; "OAW": $+0.84^\circ\text{C} \pm 0.29 \text{ SD}$). Between January 2011 and December 2018, the "Present" location had a total of 241 days (averaging 30 days per year) in which the average sea surface temperature fell below 15°C , compared to just 99 days (averaging 12 days per year) at our "OW" location (Figure 2b). This temperature triggers cold bleaching in *P. heronensis* (Higuchi et al., 2018) and *A. solitaryensis* (Higuchi et al., 2015) which are two common scleractinian species in warm-temperate areas of Japan. Over the same period, our two warmer locations had 72 and 74 days ("OW" and "OAW", respectively) where average sea surface temperature was above 28°C (averaging 9 days per year), 2.5-fold higher than that of the "Present" location (30 days total, averaging 4 days per year; Figure 2c). This is the upper thermal limit for kelp survival in Japan (Bolton, 2010; Komazawa et al., 2015). During the transplant experiment (October 2015–July 2016), the "Present" location had 42 days in which the in situ daily mean seawater temperature (next to the experimental setup at 4–6 m depth) fell below 15°C , whereas our other locations only had 13 and 15 days below this temperature (Figure S1). Daily mean seawater temperatures above 28°C were never recorded in situ during our transplant experiments (October 2015–July 2016).

3.2 | Biological communities

Benthic communities differed greatly between our three study locations with a clear degradation in the aesthetic value of the seascape at the "OAW" location (Figure 1). A temperate community dominated by kelp forests and other large macrophytes with few hard corals characterized the "Present" location, a subtropical community with no kelp and a greater abundance of hard corals occurred at the "OW" location and an algal turf-dominated community with few corals and very low habitat complexity characterized the "OAW" location. Kelp forests (*E. cava* Kjellman 1885 and *E. bicyclis* (Kjellman) Setchell 1905) were only found at the "Present" location where they formed dense forests on rocky substrata at all three sites with a

mean of 93.5 ± 65.63 thalli per 25 m^2 (mean \pm SE, $n = 15$, Figures 3a and S2). This resulted in their abundance being significantly greater compared to the other two locations (LMM: $p < .001$; Table S3).

The abundance of hard corals differed among locations albeit non-significantly (LMM: $p = .059$; Figures 3b and S2, and Table S4). At the "Present" location, corals had a patchy distribution with generally low coverage ($70.7 \pm 26.2 \text{ cm}^2 \text{ m}^{-2}$, mean \pm SE; Figure S3, Table S5). The "OW" location had large and diverse coral colonies ranging from 3 to 211 colonies found within each belt transect at the different sites and abundant Acroporid colonies (Figure S3 and Table S6). At this location, the coral coverage was $916.3 \pm 248.9 \text{ cm}^2 \text{ m}^{-2}$ (mean \pm SE). Only a few coral colonies were found at the "OAW" location representing a mean (\pm SE) coverage of $27.8 \pm 16.6 \text{ cm}^2 \text{ m}^{-2}$ (Figures 3b, S2 and S3). In contrast to the "OW" location, only a few scleractinian coral species inhabited the "Present" and "OAW"

locations with only three and six species, respectively, compared to the 14 species found at the "OW" location (Table S7). Only the encrusting coral *P. heronensis* was found in all locations, whereas Acroporid corals were only found at the sites within the "OW" location (Figures S2 and S3, Table S7).

3.3 | Transplantation experiment

The survival rates of the kelp thalli transplanted at the "Present" location were 60% and 100% for the experiment during the warm period (September–October) and the cold period (February–March), respectively (Figure 4a,b). All the transplanted kelp thalli died in both warm-water locations ("OW" and "OAW"; Figure 4a) with only the holdfasts remaining (Figure 4c). Subsequent monitoring

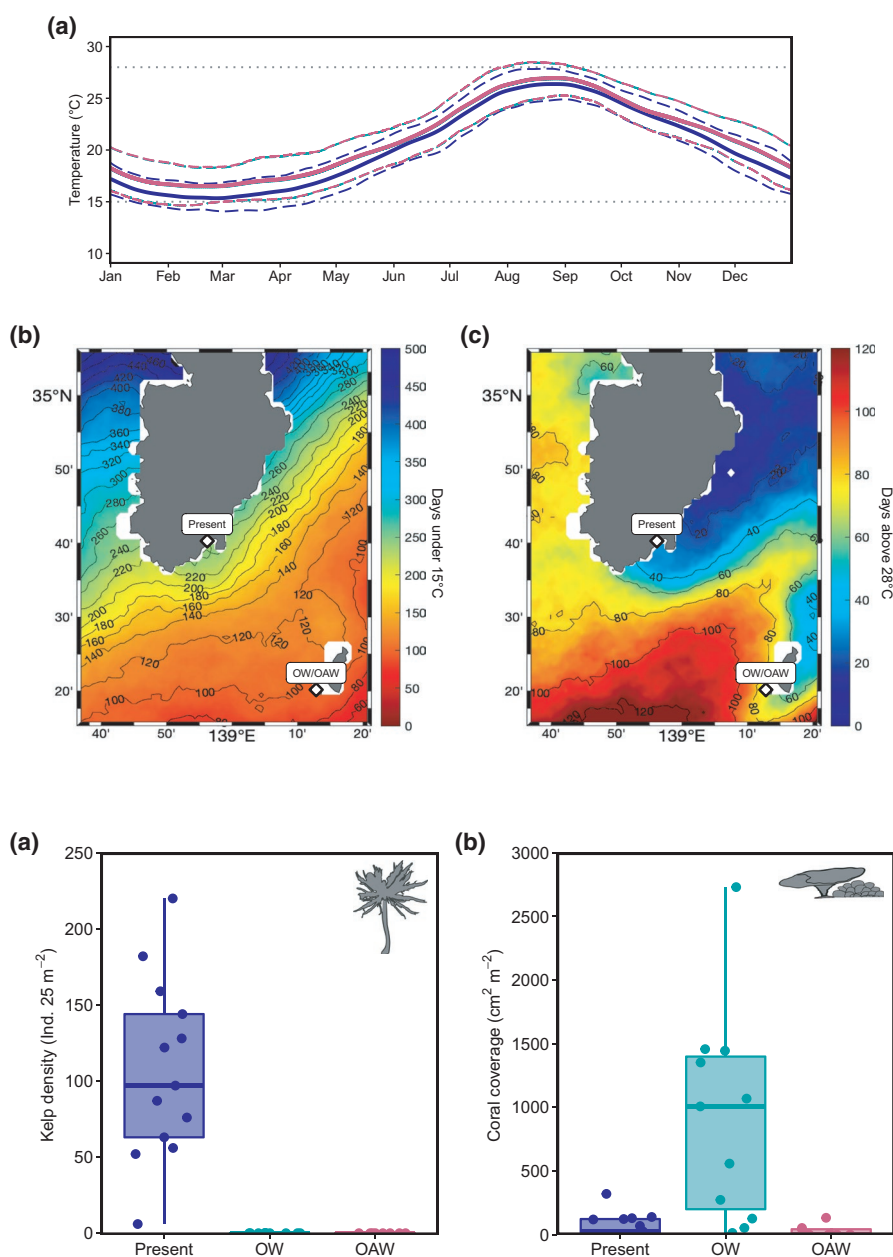


FIGURE 2 Seasonal climatology (median and interquartile) at the three study locations (a): "Present" (blue), "OW" (green) and "OAW" (red). Maps of Izu Peninsula and Izu Islands, Japan, showing the "Present" and the "Ocean Warming" ("OW") and "Ocean Acidification and Warming" ("OAW") study locations and a contour plot of the number of days under 15°C (b) and above 28°C (c) between 2011 and 2018 at the three study locations.

Note: As the seasonal climatology of the "OW" and "OAW" locations is similar, the green line representing the climatology at the "OW" location is covered by the red line of the "OAW" location

FIGURE 3 Kelp densities (a) and coral coverages (b) at the three study locations "Present" (blue), "OW" (green) and "OAW" (red). For the boxplots, the line indicates the median, the upper and lower hinges correspond to the interquartile range and the upper and lower whiskers extend to the highest and lowest values that are within 1.5 times the interquartile range. Points show the raw values

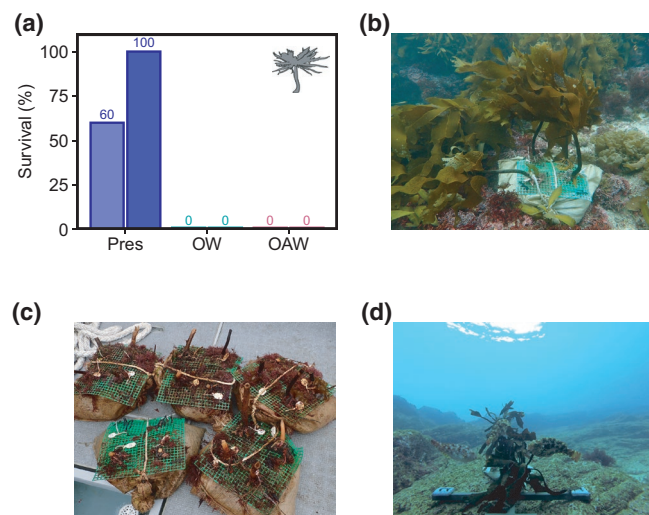


FIGURE 4 Percentage of thalli of *Eisenia bicyclis* transplanted that remained alive after 2 months during warm (September–November 2015) and the cold period (February–April 2016) and transplantation trial (a). All thalli survived at the “Present” location thalli (b) while those transplanted at the Acidified location were heavily grazed by the subtropical parrotfish *Calotomus japonicus* within a few hours (c and d)

by time-lapse video showed intense grazing by the subtropical parrotfish *Calotomus japonicus* Valenciennes (1840) fish at the warm-water locations with near-total consumption of the transplanted kelp within a few hours of transplant deployment, but no fish herbivory of kelp transplants at the “Present” location (Figure 4c,d; Video S1).

In our coral transplant experiments, all transplanted colonies of *A. solitaryensis* ($n = 15$) and 13 out of the 15 *P. heronensis* colonies survived at our cooler “Present” location over the 9 months studied. Some coral transplants were lost due to bad weather damage to our attachment frames between September and December 2015 at our warmer locations, but of those that remained in situ all survived (14 and 8 *P. heronensis* colonies; 17 and 12 *A. solitaryensis* colonies at the “OW” and “OAW” locations, respectively).

Coral did not show any signs of bleaching at the time of transplantation in September. During the coldest period (December–April), the in situ daily mean seawater temperature fell to 13.5°C at the “Present” location, and both species demonstrated cold bleaching (F_v/F_m : 0.278 ± 0.014 for *A. solitaryensis* and 0.238 ± 0.015 for *P. heronensis*; Tables 1, S8 and S9; Figure 5a,b). During the same period (December–April), the coral colonies in the “OW” and “OAW” locations only displayed minimal cold bleaching (Figure 5a,b) with significantly higher F_v/F_m values compared to the “Present” location (Tables 1, S8 and S9; Figure 5c,d; Pairwise within December–April: Present vs. OW and Present vs. OAW: $p < .001$), suggesting that the warmer conditions in these locations prevented the minimum temperature threshold from being exceeded. Following the warmer period between April and July, the corals in the “Present” location started to recover from the cold bleaching with their photosystem

efficiency increasing to a mean of 0.565 ± 0.014 for *A. solitaryensis* and 0.458 ± 0.014 for *P. heronensis* (Tables S8 and S9; Figure 5c,d; Pairwise within Present: December–April vs. April–July; $p < .001$ for both species).

The mean growth rate of *A. solitaryensis* across all seasons and locations ($1.23 \pm 0.05 \text{ mg g}^{-1} \text{ day}^{-1}$) was more than twofold greater than *P. heronensis* ($0.49 \pm 0.03 \text{ mg g}^{-1} \text{ day}^{-1}$; Figure 5e,f). During the colder periods (December–April and April–July), growth rates of *A. solitaryensis* were significantly promoted by the warmer conditions in the “OW” location compared to the “Present” location (Tables 1 and S10; Pairwise within December–April and April–July: Present vs. OW: $p < .001$). These increases in growth rates were negated when combined with ocean acidification, resulting in the “Present” and “OAW” locations having similar growth rates (Tables 1 and S10; Pairwise within December–April and April–July: Present vs. OAW: $p > .1$). During the warmest period (September–December), growth rates of *A. solitaryensis* were similar between the “Present” and “OW” locations, although the “OAW” remained at a lower growth rate (Tables 1 and S10; Figure 5e; Pairwise within September–December: Present vs. OW: $p > .512$; Present vs. OAW: $p = .001$). The growth of *P. heronensis* (Figure 5f) was less variable than *A. solitaryensis*, and although a significant interaction between Season and Location was observed (LMM: $p = .0123$), it did not result in significant post-hoc comparisons in growth rate (Tables 1 and S11).

During the colder periods (December–April and April–July), laboratory measurements of coral metabolism showed a strong decrease in metabolic rates accompanying the bleaching of corals at the “Present” location (Figure 6). For both species, gross photosynthesis was lowest in the “Present” location compared to both the “OW” and “OAW” locations (which themselves were similar) (Tables 1, S12 and S13; Figure 6a,b; Pairwise Present vs. OW and Present vs. OAW: $p < .01$; OW vs. OAW: $p > .7$). Dark respiration rates of *A. solitaryensis* were significantly higher in the “OW” and “OAW” locations compared to those at the “Present” location regardless of the season (Tables 1 and S14; Figure S4; Pairwise Present vs. OW and Present vs. OAW: $p < .05$). No differences in dark respiration were observed for *P. heronensis* (Tables 1 and S15; Figure S4, ANOVA, all: $p > .2$).

Following the same pattern as the growth rates, the laboratory measurements of the light calcification of *A. solitaryensis* were significantly promoted by the warmer conditions in the “OW” location compared to the “Present” location regardless of the season (Figure 6; Tables 1 and S16; Pairwise: Present vs. OW: $p < .001$). These increases in light calcification were largely negated by ocean acidification resulting in calcification rates in the “OAW” location being between those of the “Present” and “OW” locations for both seasons (Figure 6c,d); being significantly higher than the “Present” location (Tables 1 and S16; Pairwise Present vs. OAW: $p = .045$) and significantly lower than the “OW” location (OW vs. OAW: $p = .028$). The lowest calcification rates were observed in the “Present” location where net dissolution was observed ($-0.149 \pm 0.065 \mu\text{mol CaCO}_3 \text{ g}^{-1} \text{ h}^{-1}$) corresponding with the most pronounced bleaching (Figure 5a,b). For *P. heronensis*, net dissolution was observed at almost all locations (overall mean calcification rate of *P. heronensis* across

	Location		Season		Location: season	
	Chi sq.	p	Chi sq.	p	Chi sq.	p
Photosynthetic efficiency (Fv/Fm)						
<i>Acropora solitaryensis</i>	<u>78.6</u>	<u><.001</u>	<u>22.2</u>	<u><.001</u>	<u>22.9</u>	<u><.001</u>
<i>Porites heronensis</i>	<u>20.1</u>	<u><.001</u>	<u>290.0</u>	<u><.001</u>	<u>172.0</u>	<u><.001</u>
Growth (mg g ⁻¹ day ⁻¹)						
<i>Acropora solitaryensis</i>	<u>78.6</u>	<u><.001</u>	<u>22.2</u>	<u><.001</u>	<u>22.9</u>	<u><.001</u>
<i>Porites heronensis</i>	0.623	.733	<u>13.600</u>	<u>.00109</u>	<u>12.80</u>	<u>.0123</u>
	F	p	F	p	F	p
Gross photosynthesis (mg DO g ⁻¹ h ⁻¹)						
<i>Acropora solitaryensis</i>	<u>13.18</u>	<u>.001</u>	<u>15.16</u>	<u>.002</u>	0.29	.754
<i>Porites heronensis</i>	<u>12.23</u>	<u>.001</u>	2.01	.182	1.35	.296
Dark respiration (mg DO g ⁻¹ h ⁻¹)						
<i>Acropora solitaryensis</i>	<u>9.19</u>	<u>.004</u>	1.53	.240	2.85	.097
<i>Porites heronensis</i>	1.71	.221	1.10	.314	0.96	.411
Light calcification (μmol CaCO ₃ g ⁻¹ h ⁻¹)						
<i>Acropora solitaryensis</i>	<u>16.43</u>	<u><.001</u>	0.03	.856	0.07	.930
<i>Porites heronensis</i>	0.94	.417	<u>17.20</u>	<u>.001</u>	<u>10.93</u>	<u>.002</u>
Dark calcification (μmol CaCO ₃ g ⁻¹ h ⁻¹)						
<i>Acropora solitaryensis</i>	4.66	.030	<u>4.25</u>	<u>.060</u>	0.49	.620
<i>Porites heronensis</i>	0.19	.830	<u>37.92</u>	<u><.001</u>	<u>4.73</u>	<u>.030</u>

Note: Linear mixed models were used for the photosystem II efficiency and growth, and ANOVA for the gross photosynthesis, dark respiration, light calcification and dark calcification. Underlined values indicate a significant effect.

TABLE 1 Summary of the statistical analysis of the physiological parameters tested for the transplants of *Acropora solitaryensis* and *Porites heronensis*

all locations and months: $-0.169 \pm 0.055 \mu\text{mol CaCO}_3 \text{ g}^{-1} \text{ h}^{-1}$; Table S17). The only positive net calcification observed for this species was in July at the "OW" location ($0.205 \pm 0.061 \mu\text{mol CaCO}_3 \text{ g}^{-1} \text{ h}^{-1}$) when the corals started to recover from mild bleaching. The only net dark calcification (i.e., positive rate) was observed for *A. solitaryensis* in July at the "OW" location with all other measurements showing net dissolution (Figure S4; Tables 1, S18 and S19).

4 | DISCUSSION

Marine biogeographical boundaries are changing rapidly across the ocean as the impacts of the Anthropocene ratchet-up (Pecl et al., 2017). In this paper, we assessed the impacts of ocean warming alone, as well as the more realistic scenario of ocean warming combined with ocean acidification. We examined present-day coastal marine ecosystems near the warm-water limit of kelp forests and the cold-water limit of hermatypic corals. Through a combination of field surveys and transplantation experiments at natural analogues for these scenarios, we found that although ocean warming facilitates the growth and colonization of hermatypic corals in warm-temperate latitudes, ocean acidification could hinder some coral species, especially the fast-growing Acroporids that are now colonizing higher latitudes. Moreover, the loss of kelp in warm-temperate areas, driven by increased herbivory by warm-water fish,

is not countered by ocean acidification. As a result, marine ecosystems in warm-temperate areas face major simplification, first driven through habitat simplification due to the loss of foundation species and then through its cascading effects on associated biodiversity (Cattano et al., 2020; Sunday et al., 2017). If carbon emissions are not brought under control, we suggest that a shift from kelp towards turf-dominated ecosystems (simplification) is far more likely than a shift from kelp to coral-dominated (tropicalization) as projected solely from ocean warming (Nakamura et al., 2013; Pecl et al., 2017; Figure 7).

At the southern limit of kelp forests in Japan, local fishermen, seaweed gatherers and local diving guides all agree that the ecosystem is clearly changing. At Shikine Island, kelp forests (*Ecklonia radicata* (Kjellman) Okamura, 1892) and abalone fisheries were common 10–20 years ago but have since disappeared (Mr Onuma, Shikine Island Fisheries Agency, pers. comm., Biodiversity Center of Japan, 2019). Our diving surveys demonstrate that hermatypic corals now play an important role in shaping the sublittoral community, and although true reefs have not formed (as the corals grow attached to rock) they increase habitat complexity with a variety of table, branching and boulder forms present (Agostini et al., 2018). There are now also abundant warm-water fish in this habitat (Cattano et al., 2020), far more than are observed in the slightly cooler waters off Shimoda. The rocky shore communities change markedly in areas acidified by CO₂ seeps where a typical diverse fauna and flora that include corals

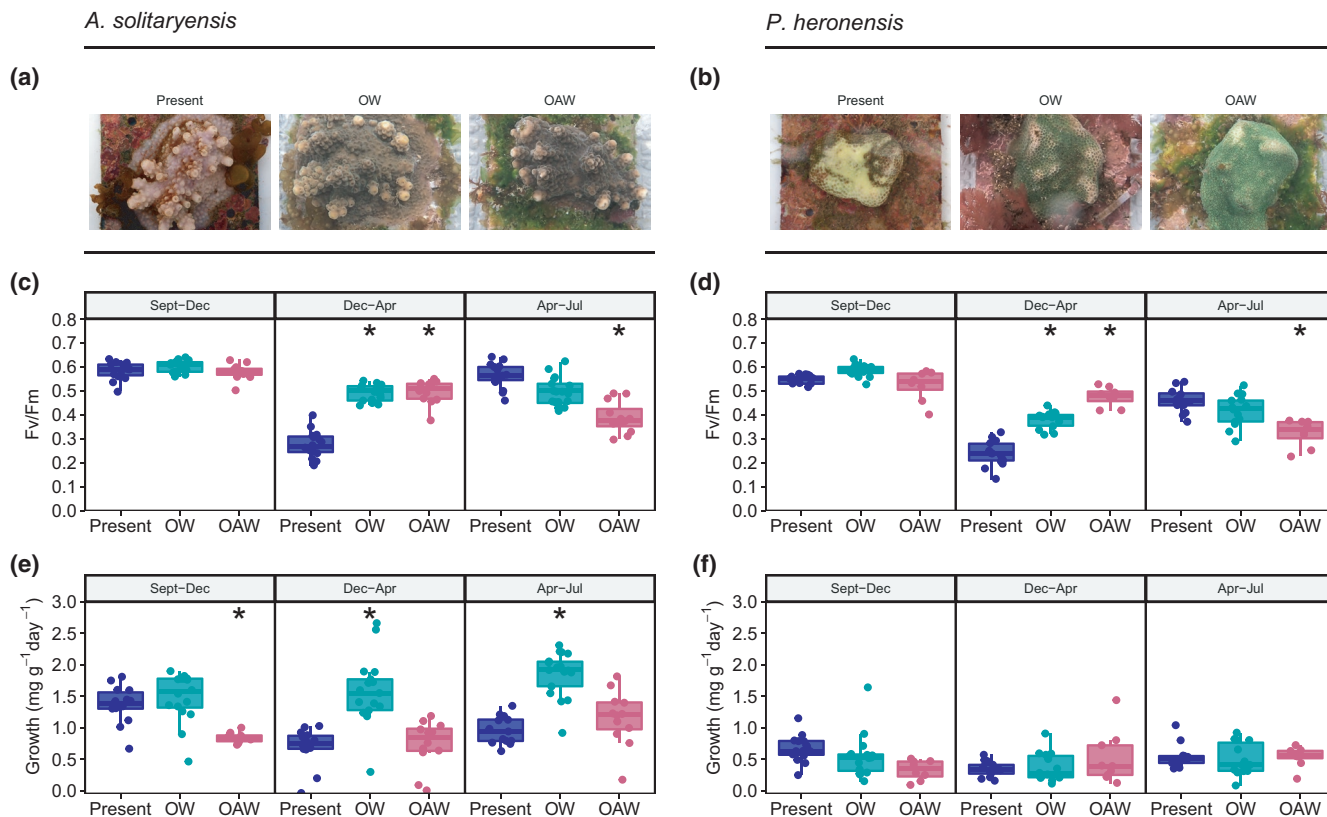
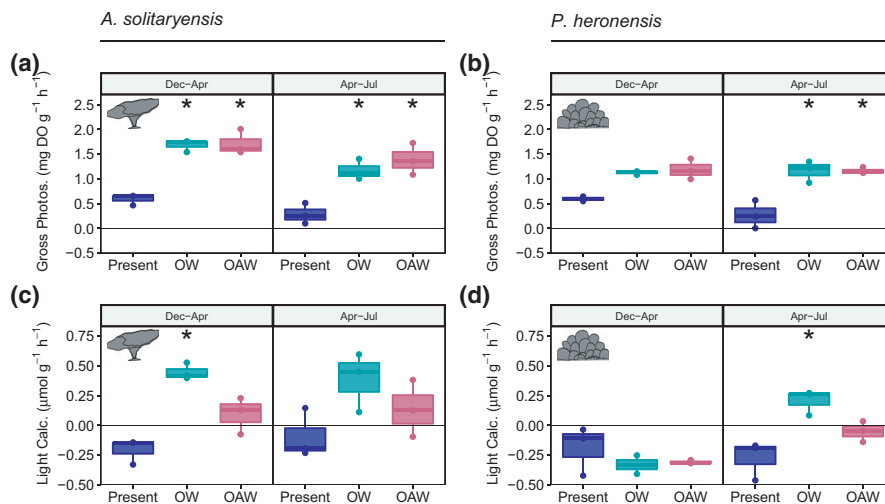


FIGURE 5 Example of scleractinian coral transplants, *Acropora solitaryensis* (a) and *Porites heronensis* (b) in April 2016 at the following locations: "Present" temperate conditions, "OW" for an analogue of ocean warming conditions and "OAW" for an analogue of ocean acidification and warming. Photosystem efficiency (Fv/Fm) (mean \pm SE) measured after dark adaptation with a PAM fluorimeter for *Acropora solitaryensis* (c) and *Porites heronensis* (d) and seasonal growth rates (mean \pm SE) for *A. solitaryensis* (e) and *P. heronensis* (f)

FIGURE 6 Gross Photosynthesis (a, b) and Light Calcification (c, d) measured in the laboratory in April and July (mean \pm SE) for three transplants of *Acropora solitaryensis* (a, c) and *Porites heronensis* (b, d)



and macroalgae are replaced by a carpet of turf algae with much lower habitat and species complexity (Harvey, Allen, et al., 2021).

In tropical and subtropical regions, coral reefs are some of the most diverse and complex marine ecosystems. Recent and ongoing anthropogenic warming is pushing corals over their upper temperature thresholds causing an increasing frequency of widespread bleaching events and associated mortality worldwide (Hughes et al.,

2018; Nakamura, 2017), thereby threatening the existence of tropical coral reefs (IPCC, 2018). Some hope that hermatypic corals will simply spread poleward to track suitable water temperature conditions and it is true that the biogeographical limits of tropical corals are already changing, with some species spreading poleward, such as into the southernmost regions of Honshu in Japan (Yamano et al., 2011). Colonization by tropical corals is underway where kelp

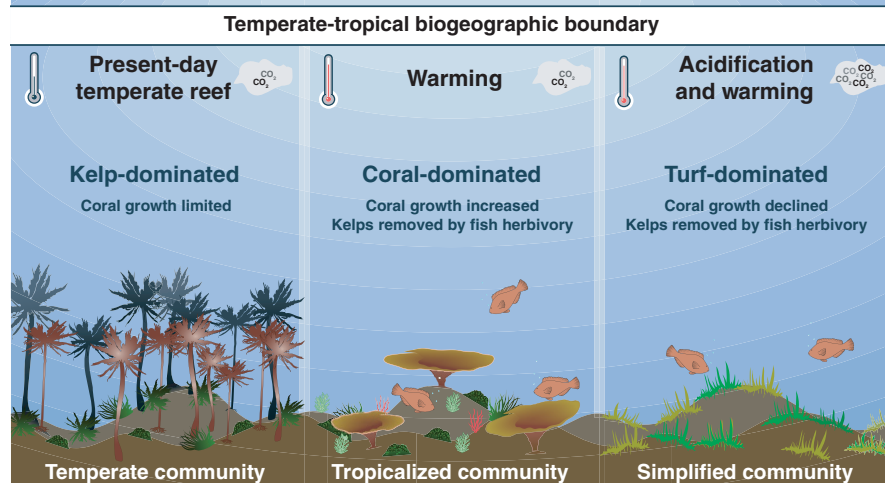


FIGURE 7 Schematic summary of the expected tropicalization trajectories from kelp-dominated temperate marine ecosystems towards coral-dominated under ocean warming scenario (tropicalized), and the more realistic shift towards turf-dominated ecosystem under ocean acidification and warming scenario (simplified community)

forests have already been lost due to sea surface warming in recent decades (Kumagai et al., 2018; Nakabayashi et al., 2019). The main limiting factor for colonization by these tropical corals in higher latitudes is cold stress during winter months (Higuchi et al., 2015, 2018). Like high temperature stress, cold stress can cause bleaching which is accompanied by severely reduced growth rates and metabolic activities. We can therefore expect that only the more cold-resilient coral species will be able to colonize the highest latitudes in the near future (Higuchi et al., 2015) and these communities would not be associated with the productivity, diversity and functions typical of coral reefs.

While corals benefited from the increase in temperature at our analogue for ocean warming, especially the poleward expanding *Acropora* species, this benefit was negated when warming was combined with acidification. These opposing effects of ocean warming and acidification have been predicted by models based on the known threshold of corals regarding temperature and ocean acidification (Guinotte et al., 2003; Takao et al., 2015; Yara et al., 2012). However, these thresholds are not well constrained, especially for warm-temperate coral species (such as *P. heronensis* in this study) or coral species which have shown a poleward shift in their distribution (such as *A. solitaryensis* in this study; Yamano et al., 2011). Using the combination of analogues for warming and ocean acidification plus warming, we show direct evidence that the latitudinal shift of corals will be limited by ocean acidification. Although the drastic decline in calcification rates observed in the laboratory for the fast-growing coral *A. solitaryensis* may be overestimated due to the high $p\text{CO}_2$ used in the OAW treatment during the incubation experiment performed in July 2016, the results obtained in the laboratory and field surveys both support the fact that colonization by fast-growing species such as Acroporids will be limited by ocean acidification and only the slow-growing coral species, such as Poritids which are already established at these latitudes, could persist under future ocean acidification. These results are similar to observations made under laboratory conditions (Brown & Edmunds, 2016) and at the tropical natural analogues for ocean acidification in Papua New Guinea, where Poritid corals are some of the few corals remaining in acidified

areas (Fabricius et al., 2011) demonstrating physiological traits that could contribute to their resistance to OA (Agostini et al., 2021). No difference in the photosynthetic rates was observed for both species of corals between colonies transplanted at the ocean warming alone and the combined warming and acidification analogues. This suggests that these coral species would not benefit from increased availability in inorganic carbon (Agostini et al., 2013; Takahashi & Kurihara, 2013). As the time scales at which ocean acidification and warming affect the distribution of marine organisms differ (Couce et al., 2013), whether ocean acidification will limit the poleward shift of corals will depend on the specific greenhouse gas emission rates (Makino et al., 2015), the geographical area in question (influence of ocean current, local stressors, etc.) and the effort put into the conservation of the newly established coral communities (Makino et al., 2014).

Ocean acidification is a stressor for many organisms, especially calcified organisms such as coralline algae or corals, but the additional inorganic carbon is also a resource for those algae that have suitable physiological mechanisms (Koch et al., 2013). Some algae grow better at high CO_2 and this alters seaweed communities, favouring low profile, fast-growing turf algae (Connell et al., 2013, 2018) that can inhibit the recruitment of other organisms including kelp, reef-forming vermetids and corals (Alessi et al., 2019; Filbee-Dexter & Wernberg, 2018; Harvey et al., 2019; Kennelly, 1987). Large kelp forests support an extensive range of fauna and provisioning of ecosystem services on temperate rocky reefs (Teagle et al., 2017). These forests have been declining around the world due to the effects of climate change (Filbee-Dexter & Wernberg, 2018). Temperature is not the only factor driving and stabilizing these shifts (Krumhansl et al., 2016). Over-grazing by herbivorous fishes and sea urchins has been documented in Japan and other parts of the world and is thought to play an important role in the decline of kelp forests (Vergés et al., 2014). While kelp forests are still abundant at the "Present" location, they have been continuously declining over the last decade (Biodiversity Center of Japan, 2019). Kelp forests were abundant at the ocean warming analogue 10–20 years ago (Biodiversity Center of Japan, 2008), but no thalli

were observed during our surveys and the hundreds of hours spent diving at these locations. Sea surface temperature of the studied region has increased by around 1.5°C over the last century (Takatsuki et al., 2007). The temperature at the analogue for ocean warming may have already exceeded the threshold for local kelp species. As shown by the important grazing that affected the transplanted kelps at this location, any increase in the abundance or feeding rates of the subtropical parrotfish *Calotomus japonicus* will surely have played a role in the recent loss of kelp forests in the area (Vergés et al., 2014). Whether kelp forests could benefit or not from the inorganic carbon available (Falkenberg et al., 2013) could not be shown in our study due to the lack of an ocean acidification (alone) location and because of the overwhelming effect of warming through the changes in fish grazing pressure. Fish communities are affected by ocean acidification through changes in their habitats and food availability. The communities of fish found at the acidified location in Shikine Island were shown to include more temperate and herbivorous fishes than the surrounding non-acidified areas (Cattano et al., 2020). Moreover, ocean acidification-driven habitat shifts were suggested to slow down the tropicalization of fish communities (Coni et al., 2021). Regardless, while additional dissolved inorganic carbon could act as a resource for kelp forests, the combined increase in temperature and grazing pressure likely negates any potential benefit.

Our results show that ocean acidification can prevent the tropicalization trajectory of coastal marine ecosystems, halting the poleward redistribution of warm-water corals. Our results suggest that declining kelp forests will instead be replaced by turf algae under an ocean acidification and warming scenario. Consequently, warm-temperate regions are likely to experience major losses in ecosystem services caused by simplification of the ecosystem (Cattano et al., 2020; Hall-Spencer & Harvey, 2019; Pecl et al., 2017; Sunday et al., 2017). Overall, these results show the benefits to be gained from reducing carbon dioxide emissions to the atmosphere that would limit both the warming and the acidification of the ocean. Such reductions would help prevent biodiversity loss and a simplification of coastal ecosystems that otherwise would become dominated by the few resistant species, such as Poritid corals and turf algae. These species provide low habitat complexity and do not support the diversity of organisms that inhabit present-day marine ecosystems and associated services. It has been suggested that the tropicalization trajectory towards a coral-dominated ecosystem would be associated with a shift from fisheries to tourism-based economies (Nakamura et al., 2013). However, the degradation of the aesthetic qualities of the seascape observed under combined warming and ocean acidification shows that “simplification” rather than a “tropicalization” of the ecosystem would lead to a decrease in the economic value of coastal systems.

ACKNOWLEDGEMENTS

We thank Yasutaka Tsuchiya and the technical staff at Shimoda Marine Research Center and aboard RV Tsukuba II, University of Tsukuba for their assistance and the fisheries agencies of Izu/Shimoda (Shizuoka prefecture) and Nijima/Shikine Island (Tokyo

prefecture) for their support. Prof. Hama kindly provided the chemistry data for the “Present” location.

CONFLICT OF INTERESTS

The authors declare no conflict of interests.









AUTHORS' CONTRIBUTIONS

Conceptualization and Methodology: S.A., J.M.H.-S., M.M. and K. Kom.; Investigation: S.A., J.M.H.-S., M.M., S.W., K. Kon., B.H., M.K., K. Kom. and N.F. Formal Analysis and Software: S.A., K. Kom. and M.K. Writing—Original Draft: S.A., B.H. and J.M.H.-S. and Writing—Review and Editing: all authors.

DATA AVAILABILITY STATEMENT

The code and raw data are available at [https://urldefense.com/v3/https://gitlab.com/agoremix/tropicalization-under-ocean-warming-and-acidification.git_!!N11eV2iwtfs6catvxP9YTnm6m-qwsRAM07WPHV7g8x_bSV-8HAYfspteVRmwnFeUlmDek\\$](https://urldefense.com/v3/https://gitlab.com/agoremix/tropicalization-under-ocean-warming-and-acidification.git_!!N11eV2iwtfs6catvxP9YTnm6m-qwsRAM07WPHV7g8x_bSV-8HAYfspteVRmwnFeUlmDek$) and the data is deposited on the Pangaea environmental data repository.

ORCID

Sylvain Agostini  <https://orcid.org/0000-0001-9040-9296>
Ben P. Harvey  <https://orcid.org/0000-0002-4971-1634>
Marco Milazzo  <https://orcid.org/0000-0002-2202-0542>
Shigeki Wada  <https://orcid.org/0000-0001-6893-7498>
Koetsu Kon  <https://orcid.org/0000-0003-1379-0702>
Kosei Komatsu  <https://orcid.org/0000-0002-4731-7035>
Mayumi Kuroyama  <https://orcid.org/0000-0001-7060-7623>
Jason M. Hall-Spencer  <https://orcid.org/0000-0002-6915-2518>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Agostini, S., Harvey, B. P., Milazzo, M., Wada, S., Kon, K., Floc'h, N., Komatsu, K., Kuroyama, M., & Hall-Spencer, J. M. (2021). Simplification, not “tropicalization”, of temperate marine ecosystems under ocean warming and acidification. *Global Change Biology*, 27, 4771–4784. <https://doi.org/10.1111/gcb.15749>