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ORIGINAL PAPER

The vertical distribution of *Alveopora japonica* provides insight into the characteristics and factors controlling population expansion at Jeju Island off the south coast of Korea

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Abstract

Populations of the subtropical coral *Alveopora japonica* Eguchi, 1965 are expanding, likely in response to changes in coastal water conditions caused by human activities and climatic factors. To uncover the causes of population increase, we propose the establishment of a long-term monitoring station to comprehensively assess the drivers of population dynamics. Therefore, the aim of this study was to obtain baseline information on *A. japonica* in Oedo at Jeju Island (Korea) by documenting benthic composition and characteristics of *A. japonica* populations at different depths. In Oedo, the distribution of *A. japonica* is mainly restricted to 15-m depth where a high density of colonies was observed (410 ± 123 colonies m^{-2}). These colonies consist predominantly of small colonies with individual or few polyps and are associated with a vertical shift in benthic composition and interactions. Indeed, comparing results with shallower waters where *A. japonica* is absent and geniculate coralline algae dominate (66.5 ± 2.2% at 5-m and 60.5 ± 2.7% at 10-m depth), a contrasting pattern emerges at 15-m depth. Here, crustose coralline algae make up the majority of the substrate at 56.1 ± 3.4%. These possible biotic drivers are discussed in conjunction with other abiotic factors such as temperature to explain the benthic community composition in Oedo. Given the current benthic structure and accessibility of the study area, Oedo proves to be an ideal sentinel site for monitoring the effects of anthropogenic disturbances, especially global warming, on temperate marine ecosystems.

Keywords Scleractinian coral · High latitude · Temperate · Tropicalization · Monitoring · Climate change

Introduction

Surrounded by the East China Sea, the Sea of Japan, and the Yellow Sea, the waters around Jeju Island, off the south coast of Korea, are among the fastest warming in the world (Takatsuki 2007). Over the past 40 years, seawater temperatures at Jeju have increased by ~ 0.1 °C per year with a more pronounced increase in winter months than in summer months (Ribas-Deulofeu et al. 2023). Warming of the ocean around the island results in the loss of seasonality, which dramatically affects the number of "cold" days, i.e., days when temperatures fall below thresholds established for coral survival and reef development (Ribas-Deulofeu et al. 2023). Several independent events and observations indicate that a reconfiguration of shallow benthic habitats at Jeju is underway, involving several key taxa for the productivity of these ecosystems (e.g., Kim et al. 2016b; Samanta et al. 2019). Thus, an increasing contribution of cosmopolitan, tropical, and subtropical algae has been observed, while

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temperate algae have declined (Kang 1966; Lee and Lee 1982; Ribas-Deulofeu et al. 2023). *Ecklonia cava* Kjellman, 1885 (Kjellman and Petersen 1885) is being replaced by barren grounds "getnoguem" on which crustose coralline algae can now thrive (Lee et al. 2022). Coral populations are thought to be expanding (Denis et al. 2015), and some reef fishes have been recorded for the first time in waters around the island (Kwun et al. 2017; Myoung et al. 2014). In addition to temperature, other factors such as modifications in nutrient concentrations (Kwon et al. 2020) and overfishing (Chang et al. 2010; Kim et al. 2016a) have also been suspected as additional causes of these changes but they remain untested to date. Actually, it is likely that various biotic and abiotic factors interact synergistically and contribute to the emergence of new ecosystem states (Vergés et al. 2019) in which energy fluxes and functionality are altered (Pessarrodona et al. 2022). Understanding the interplay between changes in temperature regimes and the tropicalization of temperate communities required detailed and prolonged demographic data on the population of interest.

Alveopora japonica Eguchi 1965 (Eguchi 1965) is a scleractinian coral that occurs from tropical to temperate latitudes (Veron et al. 2016). It is particularly common in subtropical shallow coastal areas in northeast Asia, where it is native (Harii et al. 2001; Kang et al. 2020). Appearance and phylogenetic relationships of *A. japonica*, along with its Symbiodiniaceae endosymbiont distinguished tropical populations from those in Japan and Korea, suggesting distinct species (Kang et al. 2020). At high latitudes, small hemispherical colonies of *A. japonica* are found in rocky foreshores, usually nested among algae and soft corals (Veron et al. 2016). Typically, *A. japonica* inhabits kelp forests residing beneath the canopy formed by the regionally endemic brown algae, *Ecklonia cava* (Denis et al. 2013). While *A. japonica* is a species recognized for its cold temperature tolerance, its colonies stress and bleach when exposed to prolonged periods below 15 °C (Higuchi et al. 2020). On the other hand, colonies were also observed to bleach following summer heat waves while also quickly recovering (Kim et al. 2022). The survival of bleached colonies of *A. japonica* for months (~ 3 mo) in winter has however suggested that this species can decrease its metabolic demand to some extent or use alternative sources of energy (Higuchi et al. 2020). Known populations are reproductively active and *A. japonica* is described as a hermaphroditic brooding coral with planulae released in late summer to early fall according to spawning estimation and observation in 2015 at Jeju (August–September; Park et al. 2020) and in 1994/95 at Tokyo, Japan (September–October 1994/1995; Harii et al. 2001), respectively. At Jeju, *A. japonica* has long been described as sympatric with other photosymbiotic scleractinians (National Species List of Korea, https://www.kbr.go.kr - last accessed 07/2023), whose diversity, physiology, and ecology have attracted increasing interest in recent years (Denis et al. 2014; De Palmas et al. 2015; Vieira et al. 2015). There, *A. japonica* is characterized by a slow growth rate (4.8 mm year^{-1}) and a short life span (12–13 years) (Vieira et al. 2015). However, the density of *A. japonica* populations can reach exceptionally high densities of up to 58–155 colonies m^{-2} depending on water depth (Noseworthy et al. 2016; Vieira et al. 2015). The recruitment rate is estimated to be 10.4 colonies m^{-2} year^{-1} at 10-m depth (Hong et al. 2015; Park et al. 2020), but the density of recruits can reach up to 7590 ± 660 (SE) recruits per m^2 at 15-m depth (Denis et al. 2015). Those exceptional densities have been associated with contemporary changes in the habitability of marine environments in Jeju, causing a reconfiguration of benthic assemblages.

Alveopora japonica is observed as an opportunistic species, capable of rapidly colonizing newly available habitats and aggressively competing with other local taxa (Vieira et al. 2015). Populations have been documented to be exploding and dominate some sites in the 10–15-m depth zone (Denis et al. 2014, 2015; Vieira et al. 2015), while being almost absent at shallower depths (Ribas-Deulofeu et al. 2023). In the northern part of Jeju, the distribution of *A. japonica* is patchy. In some sites, this species is not or rarely observed (De Palmas et al. 2015; Ribas-Deulofeu et al. 2023), contributing only slightly to an already insignificant coral cover (Ribas-Deulofeu et al. 2023). In contrast, at some others sites to the east, this species is described as abundant at 10–15-m depth, but to have already abundantly colonized depth up to 5 m (Lee et al. 2022). The vertical (bathymetric) and horizontal (spatial) distribution of *A. japonica* is though to depend on the temperature which tends to be higher and less chilled at − 15 m than at the surface, and has increased over past > 40 years (Ribas-Deulofeu et al. 2023). However, as previously emphasized (Ribas-Deulofeu et al. 2023), the root causes of the recent expansion of the *A. japonica* population remain unclear in the absence of long-term data on population status and habitats. To determine the reasons for the expansion of *A. japonica*, we urgently need to identify sites that could serve as sentinels of the changes and from which we can quantify the drivers of population dynamics. Thus, this study aimed to get baseline data on *A. japonica* by first documenting the overall benthic composition at a selected site located on the north coast of Jeju Island, and then by examining the status and characteristics of the coral populations across three depths. Using detailed information on the communities and depth distribution, we hope to gain further insight into possible factors driving the expansion of *A. japonica*.

Materials and methods

Study site and benthic surveys

Located on the northern coast of Jeju Island off the south coast of Korea (Fig. 1a, b), Oedo (33°29.79′N, 126°25.77′E) was selected as the study site because preliminary investigations indicated that the shallow waters were still free of *Alveopora japonica*. In contrast, this species has been observed at other nearby sites expanding its depth distribution (Lee et al. 2022). This site is also close to a harbor (< 1 km; Fig. 1c) and therefore readily accessible all year round for scientific research and monitoring. The adjacent Jeju Port surface buoy (33°31.65′N, 126°32.58′E; Fig. 1b) further allows the temperature context at the study site to be characterized. Hourly sea surface temperature (SST) data were obtained from the Korea Ocean Observing and Forecasting System website (www.khoa.go.kr/koofs, accessed in January 2024) for the period 2000/01/01–2023/12/31. Underwater investigations were performed by SCUBA diving at three depths (5-, 10-, and 15-m deep; Fig. 1c) following the methodology adopted in a similar study in the area (Lee et al. 2022). At each depth, a 20-m line transect was deployed. Photographs (~ 1.5 × 1.5 m) were taken every meter using a high-resolution camera (Nikon D800, maximum resolution of 7360 × 4912 pixels) while maintaining a relatively constant distance (~ 1 m) from the substrate to avoid geometric distortion. This method allows the reconstruction of the entire area (30 m^2) after merging photographs.

Benthic composition and *A. japonica* densities

Using photoQuad® software (Trygonis and Sini 2012), the resulting orthomosaic image was calibrated and 20 virtual 1 m^2 photo quadrats were delineated along the transect for the benthic composition and coral density analyses. Within each

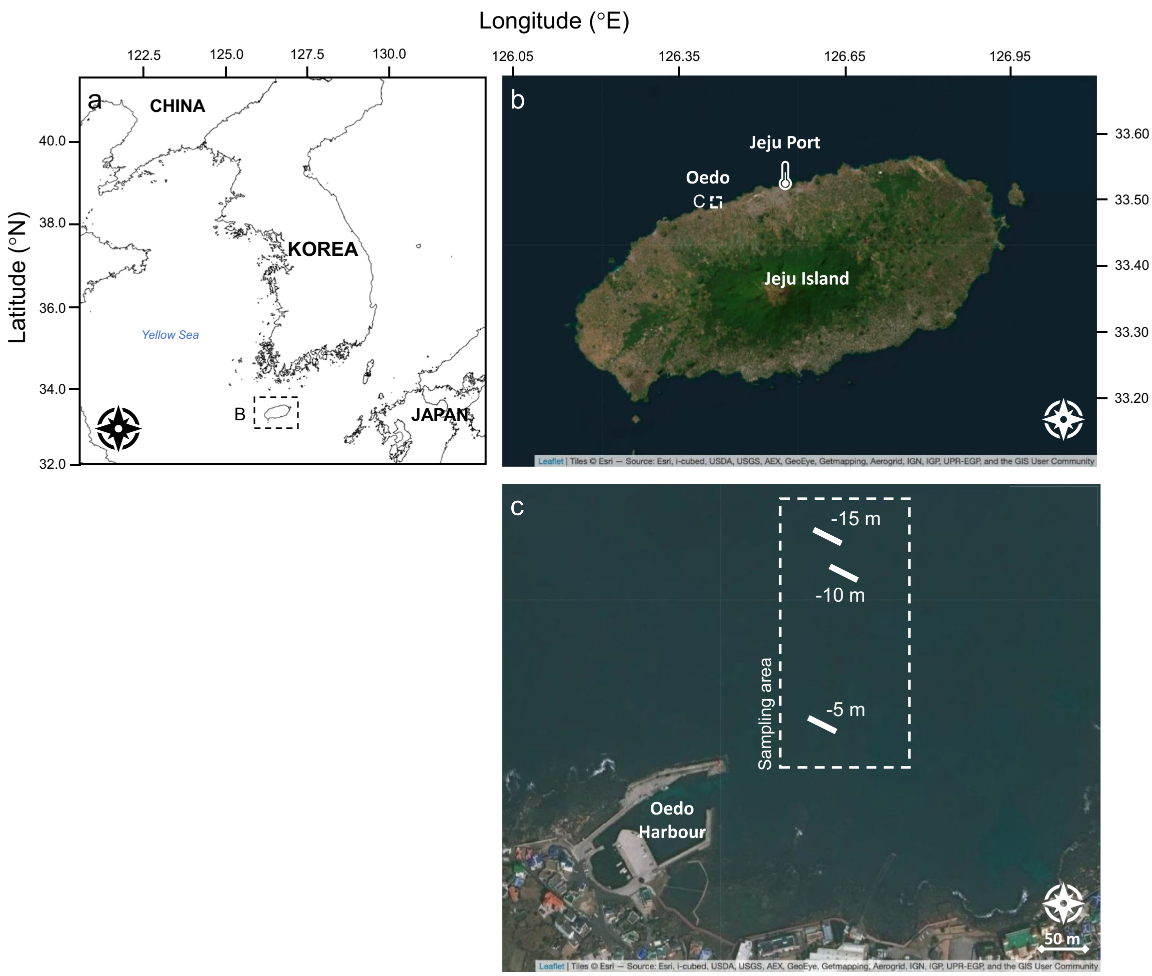

Fig. 1 Location and details of the sampling site Oedo on the north coast of Jeju Island, Korea. **a** Location of Jeju Island off the south of the Korean Peninsula in northeast Asia; **b** Jeju Island with the location of Oedo and Jeju Port (sea surface buoy) to the north; **c** Details of the sampling area off Oedo Harbour, with the positioning of the three 20-m-long underwater photo transects at 5-, 10-, and 15-m deep. Maps were made in R using the packages "rgdal" (Bivand et al. 2023) with spatial data from the Database of Global Administrative Areas (panel **a**) and "leaflet" (Cheng et al. 2023) with world imagery from the Environmental Systems Research Institute based on the following sources: Esri, i-cubed, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, UPPR-EGP, and the GIS User Community (panels **b** and **c**)

quadrat, 100 random points were overlaid, and organisms beneath were identified as accurately as feasible. *Alveopora japonica* colonies were counted in each virtual quadrat and categorized according to their size and general appearance (live or recently dead). The smallest *A. japonica* colony visible on the benthic images was 0.5 cm in diameter, and we use a threshold of 1 cm in diameter to distinguish small (presumably juvenile) from large (presumably adult) colonies.

Data analyses

For temperature, the hourly SST data were summarized as daily averages and decomposed into seasonal, trend, and irregular components (Ribas-Deulofeu et al. 2023). The data were then aggregated monthly or annually to test the significance of temperature changes using modified Mann-Kendall tests and Sen's slope (Rao et al. 2003). Due to the large amount of missing data, the period 2000–2001 was visualized but excluded from subsequent decomposition, trend, and statistical analyses which were all performed in R (V4.3.1) with the packages "tidyverse" (v2.0.0; Wickham et al. 2019) and "modifiedmk" (v1.6; Patakamuri and O'Brien 2021). For the benthic data, 2.9% (n = 176) of the 6000 benthic identifications could not be assigned to any taxa and were removed from further analysis. To summarize the composition of the benthos at a given depth, the taxa that contributed to > 5% in each quadrat were categorized as geniculate coralline algae, crustose coralline algae, *Ecklonia cava*, *Sargassum macrocarpum*, and *Alveopora japonica*. All other organisms (diverse representatives of Chlorophyta, Rhodophyta, and Porifera) were grouped under "Other life" because they contribute only a little to the benthic cover (< 3%). At each depth, the benthic composition was presented using the average benthic cover along with the standard error of the mean (mean ± SE). For large algae, such as *E. cava*, the cover actually corresponded to the measurement at the canopy, and underlying organisms were not visible on the benthic images. Densities of large, small, and recently dead *A. japonica* colonies were also calculated as mean ± SE from individual count data on the quadrats at a given depth. The errors in the means provided information on the spatial heterogeneity of cover or density. The complete benthic dataset is available as Supplementary file 1 to repeat the analyses.

Results

Temperature pattern

Daily SST (Fig. 2a) were decomposed (2002–2023 period) from their seasonal cycle to extract SST trends (Fig. 2b) and irregular component (Fig. 2c). The daily trend was significant with a slope of 0.00013 °C d^{-1}. Modified Mann-Kendall and Sen's slope further confirmed a significant warming concentrated in the winter and spring months (January, March, April, May, November), giving an overall temperature increase (annual mean) of 0.07 °C yr^{-1} (Table 1).

Benthic composition

The orthomosaics of the 20-m-long phototransects are provided in Supplementary file 2 with a schematic view of the benthic cover across depths. At 5- and 10-m depths, the geniculate coralline algae largely dominated the substrate with covers of 66.5 ± 2.2 and 60.5 ± 2.7%, respectively (Fig. 3). The crustose coralline algae were the second dominant benthic group at those depths with respective covers of 33.3 ± 2.1% and 30.1 ± 2.3% at 5 and 10 m in depths, respectively (Fig. 4). No *Alveopora japonica* colonies were observed at both 5 and 10 m in depth. While *Ecklonia cava* was absent at 5-m depth, its contribution to the benthic cover averaged 4.4 ± 1.4% at − 10 m. "Other life" contributed between 0.2 ± 0.1% at − 5 m and 2.6 ± 0.6% at − 10 m. At 15 m in depth (Fig. 3), the crustose coralline algae dominated the substrate accounting for 56.1 ± 3.4% of the benthic cover. There, geniculate coralline algae occupied 17.4 ± 3.5% of the substrate, approximately one-third of the cover reported at 10-m depth. The cover of *E. cava* rose to 13.3 ± 3.6% while the scleractinian coral *A. japonica* took up to 12.1 ± 4.1% of the substrate. "Other life" contributed to 1.1 ± 0.4% of the benthic cover at − 15 m.

Vertical distribution of *A. japonica*

While absent at shallow depths (− 5 and − 10 m), a total of 8203 *Alveopora japonica* colonies were counted within the 20 m^2 area examined at 15-m deep for a density estimated at 410 ± 123 colonies m^{-2}. Most consisted of small colonies (n = 8009) with individual or few polyps (Fig. 4a, b, Fig. 5), and reached a density of 400 colonies m^{-2}. Density in small colonies is patchy as revealed by a standard error reaching 121 colonies m^{-2} at this depth. Large colonies (n = 164) were far less abundant (density up to 8 ± 2 colonies m^{-2}), and the presence of a few recently dead colonies was noted (2 ± 0 colonies m^{-2}). Interestingly, dead skeletons were observed to be used as settling ground for youngsters.

Discussion

The results confirm the previously reported warming trend and loss of seasonality around Jeju with an overall increase of 1.54 °C (annual mean, Sen's slope) concentrated in the winter months over the last 22 years. In Oedo, the population of *Alveopora japonica* is limited to 15-m

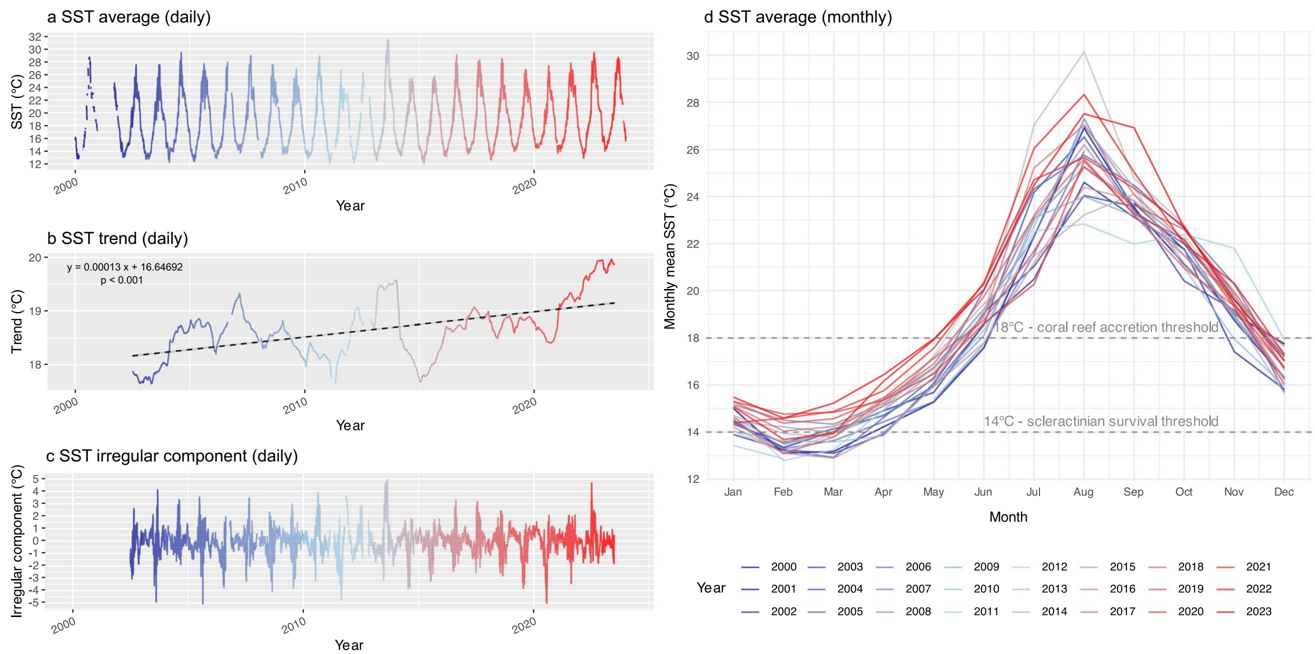

Fig. 2 Sea surface temperatures (SSTs) recorded at Jeju Port. **a** Daily SST average (2000–2023) decomposed into **b** daily SST trend (2002–2023), and **c** daily irregular SST component (2002–2023). **d** Monthly SST average with thresholds for scleractinian survival and coral reef accretion (see Ribas-Deulofeu et al. 2023). The years are displayed by colors shown in **d**

Table 1 Statistical results of sea surface temperature (SST) trend analyses (period 2002–2023)

Time period	tau statistic	Sen's slope	*p*-value
January	0.44	0.06	< 0.05
February	0.28	0.06	n.s.
March	0.36	0.07	< 0.05
April	0.63	0.09	< 0.001
May	0.58	0.11	< 0.001
June	0.19	0.05	n.s.
July	0.23	0.12	n.s.
August	0.20	0.10	n.s.
September	0.24	0.06	n.s.
October	0.25	0.05	n.s.
November	0.39	0.06	< 0.05
December	0.32	0.06	n.s.
Year	0.45	0.07	< 0.05

depth to date. The high density of coral colonies at this depth is associated with a change in benthic community structure. Small *A. japonica* colonies, consisting mainly of individual polyps, are abundant at 15-m depth, where crustose coralline algae dominate the community. This is in contrast to the abundance of geniculate coralline algae in shallow water. The current composition of the benthic communities and the accessibility of this site make it an ideal sentinel site to monitor the long-term consequences of anthropogenic disturbances such as global warming on temperate marine ecosystems.

Benthic composition

In Jeju, benthic communities have historically been dominated by geniculate coralline algae at shallow depths and large fleshy brown algae at greater depths (Kang 1966; Lee and Lee 1982). In the recent past, the brown algae *Ecklonia cava* and *Sargassum* spp. were abundant around the island and were even described as locally dominant (Ko et al. 2008; Kim et al. 2016b). Since then, however, a sharp decline in their populations has been observed, which is not limited to Jeju Island but affects their entire distributional ranges (Vergés et al. 2014). In addition, whitening events of barren grounds colonized by CCA have seen an increase of their occurrence in fast-warming areas around Jeju Island (Hwang et al. 2017; Serisawa et al. 2004; Song 2022). Alongside, previous studies have observed that the populations of subtropical corals seem expanding, probably related to increasingly favorable conditions around the island (Denis et al. 2015). The corals could indeed benefit from the substrate provided by CCA (Denis et al. 2015) which is also known to stimulate coral settlement (e.g., Negri et al. 2001). On the other hand, the increase in seawater temperature (e.g., Kim et al. 2022; Ribas-Deulofeu et al. 2023) and changes in nutrient concentrations (e.g., Kwon et al. 2020) are thought to also enhance the habitability of Jeju waters for tropical

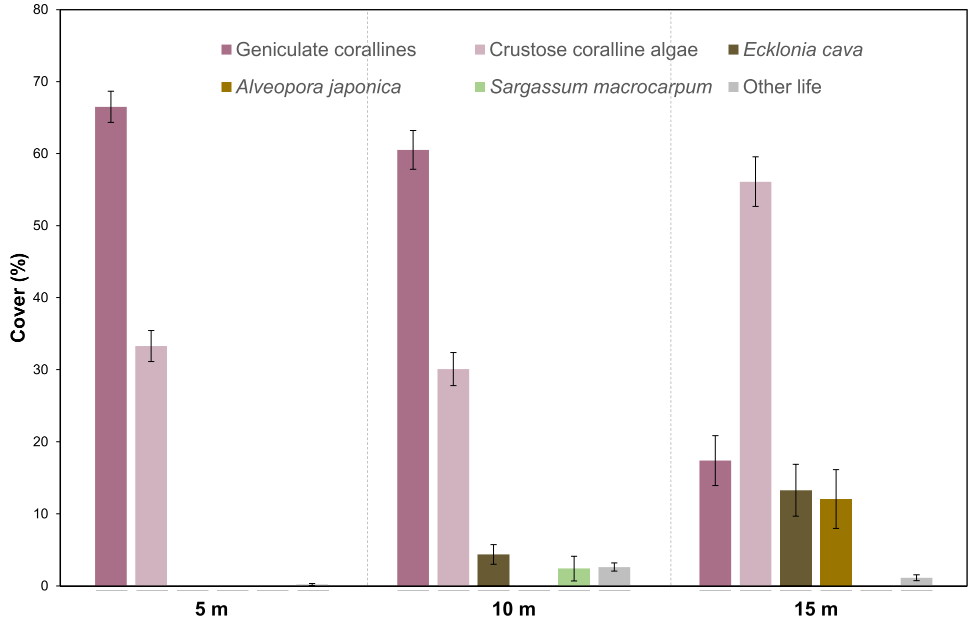

Fig. 3 Cover (± SE) of major benthic categories at the study depths

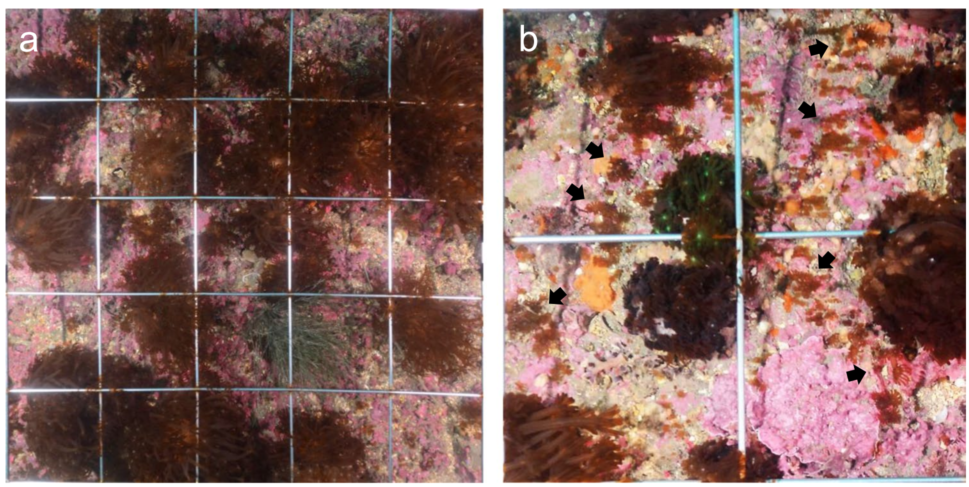

Fig. 4 Examples of benthic images illustrating benthic composition and *Alveopora japonica* colonies' density at − 15 m in Oedo. **a** A 1 m^2 quadrat illustrating the high density of *Alveopora japonica* large colonies. **b** Close-up image showing aggregation of small colonies (black arrows) in-between large colonies and recruiting on crustose coralline algae

taxa and contribute to the recent expansion of coral populations (Lee et al. 2022).

Benthic communities in shallow waters (− 5 and − 10 m) in Oedo are dominated by geniculate coralline algae, consistent with previous observations in northern Jeju (Ribas-Deulofeu et al. 2023). CCA is the second most abundant benthic group at these depths while a few *Ecklonia cava* thallus appear at − 10 m. While wave exposure is paramount for algal distribution and biodiversity (Nishihara and Terada 2010), a number of parameters such as desiccation, precipitation, low salinity, low light intensity, turbidity, suspended sediment accumulation, epiphytes, and grazing pressure are also known to influence the distribution of macrophytes such as *E. cava* (Terawaki et al. 2001). In addition, kelp can benefit from the abundance of geniculate coralline algae, which provide protection from grazing for recruits in the early stages of development (Lee et al. 2023). At 15 m in depth, the decrease in the contribution of geniculate coralline algae (17.4 ± 3.5%) appears to benefit CCA (56.1 ± 3.4%). This latter cover far exceeds the average value (21.7%) obtained from an island-scale survey in 2012–2014 as well as cover reported from northern Jeju (28.3%) at the same depth (Ribas-Deulofeu et al. 2023). *E. cava* cover (13.3 ± 3.6%) is in the same range as the island-wide average (12.0%), but lower than the cover observed in 2012–2014 for the same sector (22.0%) (Ribas-Deulofeu et al. 2023). Importantly as our survey was conducted in winter, it can be assumed that many tropical and subtropical species were rare or absent. Seasonality is seldom considered in reef monitoring, yet it is an important element to take into consideration in subtropical and temperate regions where algal biomass can fluctuate greatly throughout the year (Kang et al. 2011).

Coral cover (12.1 ± 4.1%) almost equaled the contribution *Ecklonia cava*'s canopy at − 15 m and largely exceeds

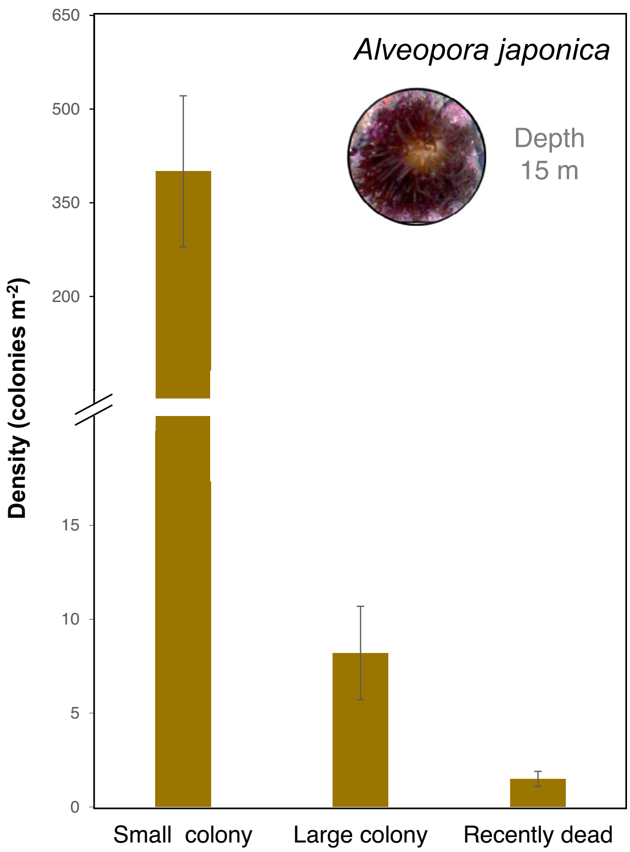

Fig. 5 Density of small, large, and recently dead *A. japonica* colonies at 15 m in depth. Error bars are standard errors

the island average (5.8%; Ribas-Deulofeu et al. 2023). From the previous survey in 2012–2014, no corals were reported at a nearby site less than 7 km away (Ribas-Deulofeu et al. 2023) and only rare *Alveopora japonica* colonies were found to the north around Gwantaldo islet (De Palmas et al. 2015). Extensive populations of *A. japonica* were observed at sites located westward and eastward of Oedo (up to 75% of the benthic cover, Viera et al. 2015) with *A. japonica* occuring sporadically (0.4–10.0%) in the shallow waters (Lee et al. 2022; Ribas-Deulofeu et al. 2023).

A coral population in expansion?

In Oedo, the coral cover consists exclusively of the coral *Alveopora japonica*, which is limited to 15-m depth. Photosymbiotic scleractinians are preferentially found at mid-depths in Jeju and rarely below − 20 m (Sugihara et al. 2014). At shallow depths (~ 5m deep), there are generally few coral species, with the notable exception of Seogwipo in southern Jeju, where four coral taxa (*Montipora millepora*, *Oulastrea crispata*, *Psammocora profundacella*, and *Psammorora* spp.) contribute to a coral cover of up to 11.0% (Ribas-Deulofeu et al. 2023). *A. japonica* in Oedo has an average density of 410 ± 123 colonies m^{-2}, mostly consisting of individual or few polyps, indicating relatively recent settlement and expansion. Similar observations in Biyangdo (northwestern tip of Jeju) in 2014 also suggested a recent population explosion (Denis et al. 2015), with numerous *A. japonica* recruits described near kelp holdfasts (Denis et al. 2013). Typhoons easily uproot kelp (Lee et al. 2023), creating barren ground for the coral colonization (Hong et al. 2015). While *A. japonica* is restricted to − 15 m in Oedo, rapid colonization of shallower depths (as already seen at nearby sites) would support an opportunistic ecological strategy in response to ocean warming and its indirect consequences.

The age of coral recruits cannot be estimated in our study, but considering the known reproductive season *Alveopora japonica*'s in Jeju (August–September) and the timing of our survey (December), it is likely that most recruits did not experience winter yet. Low temperatures in the past might have led to high mortality (see Higuchi et al. 2020), but the "loss of winter" (Ribas-Deulofeu et al. 2023) at Jeju may explain the current population burst and expanded distribution. The distribution of *A. japonica* in Oedo is patchy, as indicated by high errors in mean density estimates. This patchiness appears to be consistent with the distribution of *A. japonica* around the island. *A. japonica* is a brooder coral that releases planula larvae during the day, a behavior that is stimulated by light (Nojima and Tokeshi 2001). While larvae are not necessarily restricted in their dispersal, they routinely recruit over much shorter distances in brooder corals compared with the broadcast spawner (Underwood et al. 2020). Therefore, we hypothesize that the patchiness is due to planulae recruiting close to where they are released and that the population is primarily composed of clones. On the other hand, polyp bail-out (Schweinsberg et al. 2021) could also be an effective way for *A. japonica* to increase its populations, akin to observed invasive potential (e.g., *Tubastraea coccinea* in the Atlantic; Capel et al. 2014). In both cases, the modalities of population expansion should be further investigated.

Insights into the drivers of expansion

From the composition of the benthic community and the characteristics of the population, two types of non-mutually exclusive factors for the expansion of *Alveopora japonica* can be deduced: abiotic and biotic factors. Regarding the abiotic factors, the changing temperature pattern around Jeju (this study; Ribas-Deulofeu et al. 2023), with a more significant increase in the winter months, reduces the cold days that are crucial for controlling the demography of certain species. This, together with wave exposure and light, is thought to influence the distribution of *A. japonica*. Rapid warming could alter the competitive ability of some species, possibly freeing them from a factor that limits populations. In this scenario, *A. japonica* could colonize shallow waters in places where wave action and light are not limiting. On the biotic side, however, warming will see emerging novel ecosystems characterized by original biotic interactions in temperate zones (Vergés et al. 2019). While not necessarily leading toward novelty, the effects of climate change in Jeju cause the decline of some formerly dominant species and the emergence of others, which could have a cascading effect on trophic pathways in the original ecological system (Pessarrodona et al. 2022). Although possibly not solely controlled by water temperature, the increase in CCA could favor *A. japonica* through a change in the benthic habitability (Lee et al. 2024).

Regardless of the reasons for the emergence of *Alveopora japonica*, its rapid proliferation and tremendous changes in benthic structure and diversity can have catastrophic consequences for the original ecosystem functions (Vergés et al. 2019). This ecological shift may further have ramifications on social and economic services that affect the livelihoods of local communities (Lee and Iwasa 2014). In Jeju, the seaweed forests not only provide fishing grounds for traditional women divers "Haenyo" (Ko et al. 2010), but are also the source of important economic resources (Hwang et al. 2020) which are threatened by climate change and anthropogenic impacts. Therefore, there is an urgent need to understand the reasons for this shift and the full range of its consequences. To this end, a monitoring approach that enables the capture of subtle demographic changes is important for interpreting the transformation of the benthic assemblages caused by the changes in thermal environment. As part of a long-term monitoring network, Oedo would represent an ideal location to test for the tropicalization of temperate latitudes and where emerging technology such as three-dimensional photogrammetry could be deployed to acquire robust quantitative and demographic data (Denis et al. 2020).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-024-01418-8.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No animal testing was performed during this study.

Sampling and field studies No permits were required to conduct the field survey.

Data availability The benthic dataset generated during this study is available as a supplementary material. The temperature data are available at www.khoa.go.kr/koofs, acknowledged in the text of the manuscript as the source of our dataset.

Author contribution K-SC and C-KK conceived and designed the research. SS and TS carried out fieldwork. SS, LR-D, K-TL, and VD analyzed the data. SS, LR-D, VD, and K-SC wrote the manuscript. All authors read and approved the manuscript.

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