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RESEARCH ARTICLE

Marine invertebrates and fishes exhibit inconsistent body size responses to ocean acidification

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Abstract

Body size is a fundamental characteristic of all living organisms that determines physiological functions and life-history traits. Ecological theory predicts that ocean acidification can cause body size reductions, confirmed by several studies reporting miniaturization in ectotherms. Based on this prediction, we would expect a broad suite of species to show similar plastic body-size responses to elevated CO_2. Using four natural climate change analogues of ocean acidification across the northern and southern hemispheres, we quantified body size alterations across 18 marine invertebrate and fish taxa to test for climate-driven miniaturization. Only three species consistently showed body-size reductions under ocean acidification: one urchin and two fish species. In contrast, 15 other species, ranging from highly calcified to non-calcified, displayed unchanged or increased body sizes or inconsistent miniaturization. If body-size miniaturization responses were consistently reproducible across taxa we would have observed it more frequently, suggesting that species responses to ocean acidification are more variable than previously thought and likely vary depending on a species' physiology and life history. Thus, rather than entire communities undergoing miniaturization, species are likely to display a spectrum of responses, with some exhibiting size reductions, others demonstrating physiological resistance to elevated CO_2, and others potentially benefiting from the indirect effects of ocean acidification.

Theory predicts that the body size of many marine ectotherms will reduce in response to the chemical stresses of increasing oceanic CO_2 concentrations (Kroeker et al. 2013a; Harvey et al. 2016; Leung et al. 2020). Ocean acidification can cause decreased growth rates in marine calcifiers—like gastropods, urchins, and bivalves—that struggle to maintain their calcareous skeletons and shells under reduced pH conditions (Connell and Leung 2023). While ocean acidification can directly affect calcification, reproduction, growth, and survival of many calcifying species (Connell and Leung 2023), it is evident through laboratory and in situ studies that some calcifiers are able to adjust shell building to withstand acidified conditions (Leung et al. 2019, 2020; Langer et al. 2014), and even expand their population size (Connell et al. 2017). Additionally, some species of corals (Teixidó et al. 2020), polychaetes (Calosi et al. 2013), and bryozoans (Figuerola et al. 2025) can acclimatize (meaning non-genetic adjustment within an individual's lifetime) to a new or changing environment, while other species including some polychaetes (Calosi et al. 2013) and urchins (Pespeni et al. 2013) have shown to undergo genetic adaptation over multiple generations to withstand ocean acidification and minimize physiological harm (Foo and Byrne 2016). Other organisms—including some corals and crabs—buffer their response to low pH by exploiting bicarbonate as an alternative carbon source to sustain calcification processes (Comeau et al. 2013; Maus et al. 2018).

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Thus, ocean acidification appears to have a species-specific effect on organism body size and skeletal mass (Watson et al. 2012; Carey et al. 2016); however, there is no consensus on their physiological outcomes, and thus requires further assessment. Additionally, there remains a paucity of studies utilizing natural CO_2 vents to examine the longer-term exposure effects of ocean acidification on marine organism body size. Natural vent systems serve as valuable analogues for ocean acidification because they expose entire marine communities to sustained low pH over multiple generations, allowing us to observe realistic biological and ecological responses under naturally varying environmental conditions (Agostini et al. 2018; Nagelkerken and Connell 2022; Hayes et al. 2026). Thus far, the limited existing research at natural analogues has yielded inconsistent findings with respect to patterns of miniaturization (Table 1). Non-calcifying species such as fishes are known to exhibit behavioral and physiological changes in response to ocean acidification (Nagelkerken et al. 2021), however, evidence for direct effects on growth rates and body size remains inconsistent. While elevated CO_2 has been shown to accelerate somatic growth in some species (Di Franco et al. 2019), it can also slow growth and alter skeletal development in others (Mirasole et al. 2021; Rodríguez et al. 2026). Other studies report no measurable effect of ocean acidification on fish body size (Nagelkerken et al. 2023), which may be because highly active fishes have more efficient gill-based ion regulation than less energetic species, which allows them to better manage CO_2 excretion and pH balance (Fabry et al. 2008; Melzner et al. 2009). Thus, these apparently pre-adapted (meaning the possession of an advantageous trait) fishes may compensate any negative effects of ocean acidification and ultimately be more tolerant than others. Nagelkerken et al. (2021) also showed that generalist fish species that were able to capitalize on the positive indirect effects of ocean acidification—including boosted primary production and prey availability and enhanced reproductive behavior—may have competitive dominance over more specialized fishes. Therefore, such habitat generalists are likely to have dominance over resource allocation in ecosystems and thus be able to maintain or even increase body size (Brown and Maurer 1986). Not only do these findings reveal the species-specific nature of body size responses to ocean acidification, but also highlight the importance of in situ studies in incorporating both direct and indirect stressors to better predict how different species will respond to climate change.

Here, we aimed to understand whether ocean acidification leads to consistent body size changes in benthic marine species. We compared the body sizes of 11 invertebrate and 7 fish species at natural analogues of climate change and adjacent controls. The analogues were two volcanic CO_2 vents at White Island (New Zealand) and two CO_2 vents at Shikine Island (Japan). If miniaturization under ocean acidification is a general ecological phenomenon, we would anticipate observational and experimental trials to reproduce smaller body sizes across species more frequently than not.

Table 1. Studies that have used natural CO_2 vents to assess the body size or growth rates of different invertebrate species under ocean acidification. Red downward-facing arrows indicate a reduction in the given variable, a green upward-facing arrow denotes an increase in the given variable, and a blue equal sign (=) denotes no significant change. Variables include body size and growth rate.

Species	Taxon	Study region	Variable	Result	References
Pinna nobilis	Bivalve	Ischia (Naples, Italy)	Growth rate	Decrease	(Basso et al. 2015)
Septifer bilocularis	Bivalve	Shikine Island (Japan)	Growth rate	Decrease	(Zhao et al. 2023)
Ervilia castanea	Bivalve	São Miguel and Faial (Portugal)	Size	Decrease	(Martins et al. 2021)
Pentapora ottomuelleriana	Bryozoan	Ischia (Naples, Italy)	Growth rate	Decrease	(Figuerola et al. 2025)
Platynereis dumerilii	Polychaete	Ischia (Naples, Italy)	Size	Decrease	(Calosi et al. 2013)
Arbacia lixula	Sea urchin	Levante Bay, Vulcano Island (Italy)	Size	Decrease	(Di Giglio et al. 2020)
Astroides calycularis	Coral	Ischia (Naples, Italy)	Size	Decrease	(Teixidó et al. 2020)
Nassarius corniculus	Gastropod	Vulcano Island (Italy)	Size	Decrease	(Garilli et al. 2015)
Cyclope neritea	Gastropod	Vulcano Island (Italy)	Size	Decrease	(Garilli et al. 2015)
Charonia lampas	Gastropod	Shikine Island (Japan)	Size	Decrease	(Harvey et al. 2018)
Hexaplex trunculus	Gastropod	Isola Vulcano (Sicily, Italy)	Size	Decrease	(Harvey et al. 2016)
Echinometra sp. *C*	Sea urchin	Milne Bay (Papua New Guinea)	Size and growth rate	Increase	(Uthicke et al. 2016)
Anemonia viridis	Sea anemone	Vulcano Island (Italy)	Size and growth rate	Increase	(Suggett et al. 2012)
Symphodus ocellatus	Fish	Levante Bay, Vulcano Island (Italy)	Growth rate	Increase	(Di Franco et al. 2019)
Amphiglena mediterranea	Polychaete	Ischia (Naples, Italy)	Size	No change	(Calosi et al. 2013)
Paracentrotus lividus	Sea urchin	Levante Bay, Vulcano Island (Italy)	Size	No change	(Di Giglio et al. 2020)
Forsterygion lapillum	Fish	White Island (New Zealand)	Size and growth rate	No change	(Nagelkerken et al. 2016)
Gobius bucchichi	Fish	Vulcano Island (Italy)	Size and growth rate	No change	(Nagelkerken et al. 2016)
Pocillopora damicornis	Coral	Milne Bay (Papua New Guinea)	Growth rate	No change	(Fabricius et al. 2011)

Materials and methods

Study locations

Shikine Island, Japan

Three reefs, situated off the shore of Shikine Island, Japan (34°19′9″N, 139°12′18″E), were chosen for observation and experimentation at 5–8 m depth (Supporting Information Fig. S1). The island has several shallow water CO_2 vents that present varying levels of $p\mathrm{CO}_2$ concentrations. Therefore, one reef was sampled as a control for elevated CO_2 concentrations (hereafter: "Control": pH range 8.18–8.30; temperature range 20.5–27.1°C; Supporting Information Table S1). The other two reefs had additional acidification effects and were chosen to represent two different end of the century projections for reductions in pH, the SSP3 (pH range 8.12–8.13; temperature range 22.0–27.0°C) and SSP5 scenarios (pH range 7.80–8.09; temperature range 22.3–27.6°C; Supporting Information Table S1), respectively (IPCC 2021; hereafter, "OA(SSP3)" and "OA(SSP5)"). While these study reefs were previously temperate rocky reef ecosystems, the Kuroshio Current is transporting warm waters past Shikine Island causing habitat simplification, with corals dominating the Control reef, and brown algae and diatoms forming thick turf mats at the OA(SSP3) and OA(SSP5) reefs (Agostini et al. 2021). Biological surveys of the benthos at each of the three reefs show a reduction in floral and faunal biodiversity with decreasing pH, which aligns with known effects of pH on benthic communities (Agostini et al. 2018; Hall-Spencer et al. 2022). Therefore, while the community composition between reefs is likely to differ, the carbonate chemistry and nutrients within the water of these treatments have previously been well characterized (Agostini et al. 2015, 2018; Harvey et al. 2019; Cattano et al. 2020; Supporting Information Table S1) and are not confounded by other geochemical factors, including temperature, total alkalinity, nutrients, and dissolved oxygen. Natural fluctuations in pH at the reefs were likely caused by variation in the amount of gas released from the vents or water circulations, which may explain the variation in the pH values recorded at these reefs (Agostini et al. 2015; Supporting Information Table S1). While similar fluctuations have been recorded at other comparable, well-studied CO_2 vents (Hall-Spencer et al. 2008; Barry et al. 2010; Fabricius et al. 2011), we do recognize that these vents do not isolate the effects of CO_2 but may provide valuable contributions to the field of climate change research when considered with similar in situ and laboratory-based literature.

White Island, New Zealand

Te Puia o Whakaari (White Island) is a volcanic island located within the Bay of Plenty, New Zealand (37°31.013′S, 177°11.649′E). Our study site represents a temperate rocky reef ecosystem, characterized by kelp, *Ecklonia radiata*, and turf-forming macroalgae (Connell et al. 2018). Around the north-eastern coast of the island are two natural CO_2 vents at ~ 6–8 m depth, which exhibit $p\mathrm{CO}_2$ levels that correspond with SSP2 (south vent) and SSP3 (north vent) scenarios for 2100 (IPCC 2021; Nagelkerken et al. 2021). These two independent vent sites (hereafter, "Vent South": pH range 7.90–8.02; temperature range 20.2–23.2°C and "Vent North": pH range 7.76–7.85; temperature range 20.5–23.1°C) and two corresponding control sites representing ambient oceanic conditions (hereafter, "Control South": pH range 8.03–8.10; temperature range 20.2–23.2°C and "Control North": pH range 7.92–8.09; temperature range 20.2–23.2°C) were sampled (Supporting Information Fig. S2). The vent sites are characterized by extensive carpets of turf algae, whereas all other features of the sites including light and wave exposure, current, rock formations and topography are like that of the control sites (Nagelkerken et al. 2016; Connell et al. 2018). While CO_2 enrichment has shown to boost the nutritional value of the turfs from the vents (Leung et al. 2019), extensive seawater testing has shown no significant differences in the nutrient or mineral content at vents compared to controls (Leung et al. 2019, 2020). Details on the carbonate chemistry and biology of this location have previously been intensely studied, allowing us to select sites that do not have confounding effects of temperature or dissolved seawater elements (Brinkman and Smith 2014; Connell et al. 2017, 2018; Leung et al. 2019, 2020; Supporting Information Table S2).

Community sampling

Shikine Island, Japan

Sampling jars (surface area = 16 cm^2; Supporting Information Fig. S3) were used to core and collect the benthic macroinvertebrate community ($n = 50$ cores per reef, except present-day reef which was $n = 60$ cores) during July 2023, on rocky substratum at a depth of ~ 6–8 m. A 4.5 cm wide paint scraper was then slid underneath the jar to trap the contents inside and the lid quickly screwed on. All samples were placed in 70% ethanol solution for storage. A stereomicroscope was used to inspect the contents of each jar, separate the invertebrates from any algae present, and classify the invertebrates to the lowest taxonomic groups possible using several sources to aid identification (Hall-Spencer et al. 2022; JAMBIO 2025).

For the size measurements, we only included invertebrates whose species identity was known or could be differentiated from other species so that the same species was compared across treatments. This included bivalve Lucinidae sp. (Fleming, 1828), ostracod Myodocopida sp. (Sars, 1866), brittle star *Ophiura* sp. (Lamarck, 1801), amphipod *Monocorophium insidiosum* (Crawford, 1937), and tanaid *Zeuxo normani* (Richardson, 1905). A Zeiss Axiocam 208 and Labscope technology stereomicroscope was used to take images and measure total length of the invertebrates. Invertebrates with natural curvature—including amphipods, isopods, and tanaids—were straightened in order to measure lengthwise growth.

Additionally, two urchins *Diadema setosum* (Leske, 1778; $n = 14$ specimens total) and *Echinometra* sp. A (Gray, 1825; $n = 10$ specimens total) whose species identity has been confirmed at these reefs (Hall-Spencer et al. 2022) were randomly sampled at each location for test size measurements using calipers during May 2024. Some taxonomic confusion surrounds urchins formerly identified as *Echinometra mathaei* in the Indo-Pacific, as they are now recognized as a species complex comprising at least five distinct species, currently designated as types A through E (Arakaki et al. 1998). We investigated *Echinometra* sp. A, as identified by B.P.H.

Visual surveys across two years of sampling (July 2023 and May 2024) were used to estimate total fish length. Divers swam along 10 m belt transects with a sampling area of 2 m either side (40 m^2 total per transect), and all surveys were performed during the day at depths of ~ 5–8 m (Hayes et al. 2024). While visual surveys do not provide exact measurements for true fish length (Bower et al. 2011), precautions were taken to limit the bias (the same diver conducted all surveys) and thus any observational bias would be consistent across all measurements. Reef-attached species with small home ranges (*Chromis notata* (Temminck & Schlegel, 1843), *Chromis yamakawai* (Iwatsubo & Motomura, 2013), and *Plectroglyphidodon altus* (Okada & Ikeda, 1937)) were targeted as to ensure long-term exposure to elevated CO_2 (Ochi 1986; Fishelson 1998). Supporting Information Table S3 contains details on the number of replicates for each sample type, and Supporting Information Table S4 contains details of the sample size for each species per year.

White Island, New Zealand

The benthic macroinvertebrate community was sampled for each of nine predominant habitat types (as categorized by Blain et al. 2021) at each reef: "coralline turf," "crustose coralline algae," "red turfing algae (fleshy; < 10 cm height)," "red foliose algae (> 10 cm height)," "cyanobacteria," "other encrusting algae (including *Codium cranwelliae*)," "green foliose algae (including *Ulva* sp.)" and "barrens," during April 2022. Sampling jars (surface area = 16 cm^2; $n = 5$ per habitat type) were randomly placed within each habitat type and the same sampling method was used as of that in Japan 2023. To sample the final predominant habitat type, "sand and cobbles," a 1.75-l pitcher was used (surface area = 0.0147 m^2) at each reef ($n = 5$). Additionally, starfish (*Coscinasterias calamaria* [Gray, 1840]) were sampled separately to account for their high abundance, by collecting them from a 0.25 m^2 quadrat in each habitat type ($n = 2$) at each reef. All sampling was conducted on the rocky reef substratum at a depth of ~ 6–8 m. All benthic and starfish samples were placed within 70% ethanol for storage and underwent the same laboratory analysis as the Japan samples using several sources to aid identification (Blain et al. 2021; WoRMS Editorial Board 2025). The invertebrate species measured included brittle star *Ophionereis fasciata* (Hutton, 1872) and a tanaid species from the family Tanaidae (Dana, 1849). Additionally, the test size of urchin *Evechinus chloroticus* (Valenciennes, 1846) was estimated at controls and vents within randomly sampled 1 m^2 quadrats ($n = 10$) using calipers, like in Japan.

To assess the effect of ocean acidification, fish body size data from different surveys across multiple years (February 2017, February 2018, January 2019, April 2022) were aggregated. During 2017 and 2022, 0.5 m^2 quadrats ($n = 10$ at vent reefs and $n = 6$ at control reefs, and $n = 3$ per habitat type per reef, respectively) were used to estimate the total length of the benthic fish community. All surveys were performed during the day at depths of ~ 6–8 m. Finally, in 2018 and 2019, fishes from each reef were caught using clove oil and handheld nets and then measured for total length using calipers. Only one sampling method was used for a species; hence, any effect of the sampling method on fish length was consistent across the species. Highly reef-attached species (*Forsterygion lapillum* (Hardy 1989), *Notoclinops yaldwyni* (Hardy 1987), *Notoclinops segmentatus* (McCulloch & Phillipps, 1923), and *Parablennius laticlavius* (Griffin, 1926)) were observed because of their long-term, continuous exposure to elevated CO_2 (Wellenreuther and Clements 2007). Supporting Information Table S5 contains details on the number of replicates for each sample type, and Supporting Information Table S6 contains details of the sample size for each species per year.

Statistical analyses

Size-frequency distribution plots were constructed to visualize how the populations of various invertebrate and fish species were distributed across size classes. As per Rodriguez-Dominguez et al. (2022), a two-sample Kolmogorov–Smirnov test was used to examine whether population distributions from Control South and Control North at White Island differed from populations at Vent South and Vent North, respectively, for each invertebrate and fish species. Similarly, for species from Japan, we used a two-sample Kolmogorov–Smirnov test with multiple pairwise comparisons (due to there being more than two reefs) to determine whether population distributions changed shape across Control, OA(SSP3), and OA(SSP5) reefs, applying Bonferroni corrections to control for type I error. We used R (v.4.2.0) and the "KS-test" function for non-parametric statistical tests and the "ggplot" package for graphical outputs (R Core Team 2021; Supporting Information Tables S7 and S8).

Results

Effects of ocean acidification on body size

At the southern- and northern-hemisphere volcanic CO_2 vents, 75% and 60% of species respectively showed significant differences in body size distributions at the natural CO_2 vents compared to their respective controls (Figs. 1 and 2; $p < 0.043$; Supporting Information Tables S7 and S8). Fish *Parablennius laticlavius* showed miniaturization at Vent South ($p = 0.011$), but not at Vent North ($p = 0.417$), and fish *Notoclinops segmentatus* showed miniaturization at Vent North ($p < 0.001$), but not Vent South ($p = 0.536$), at the southern-hemisphere vents (Fig. 2; Supporting Information Table S8). Similarly, highly calcified

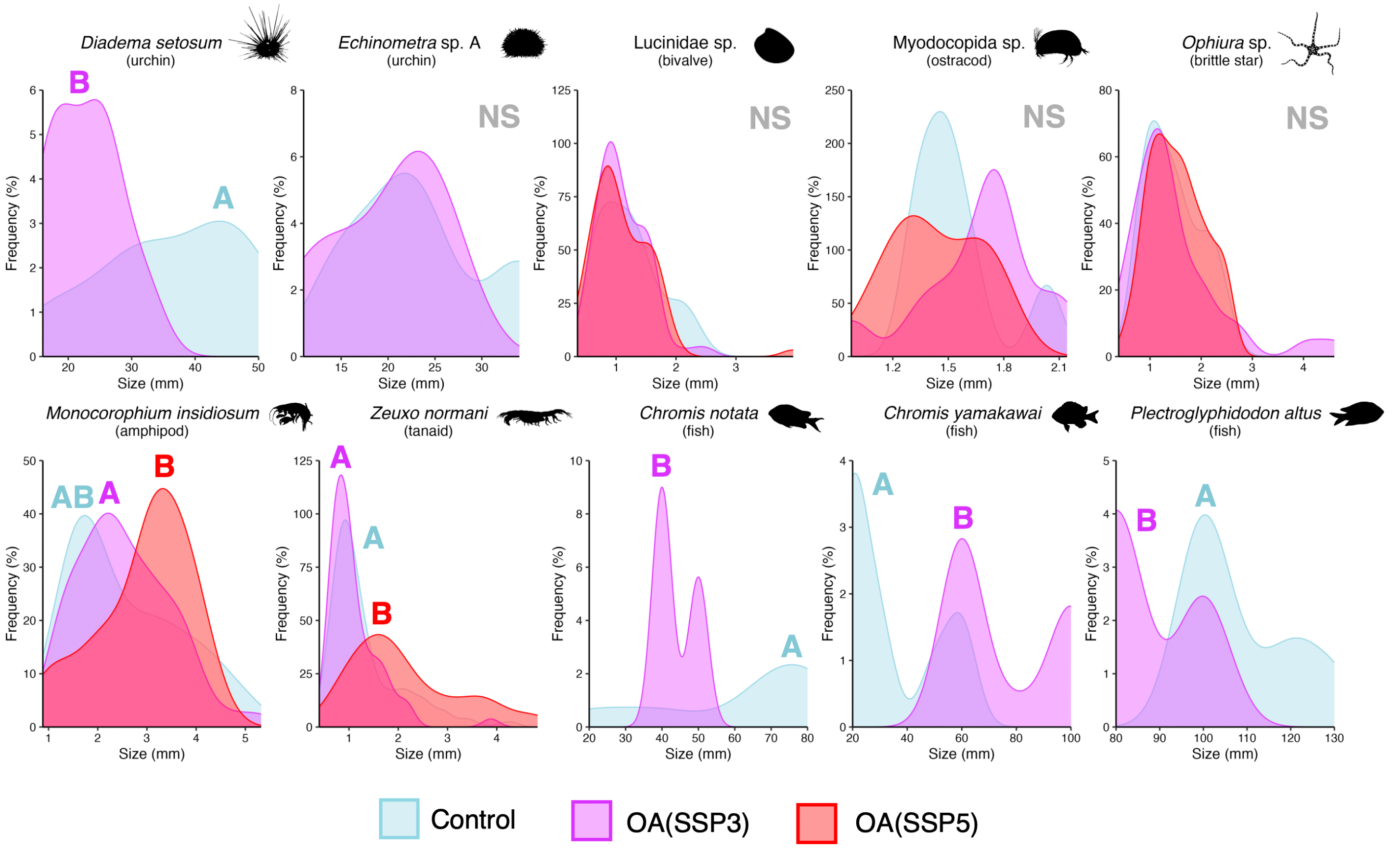

Fig. 1. Size-frequency distributions of various invertebrate and fish species at the Control reef (light blue), and reefs exposed to mild acidification (OA (SSP3); purple) and severe acidification (OA(SSP5); red) in Shikine Island, Japan. The *x*-axis represents body size (mm), and the *y*-axis shows the relative frequency of occurrence of individuals within each size class (expressed as %). The area under each curve sums to 100%, allowing comparison of the shape and spread of size distributions independent of sample size. Peaks indicate the most common body sizes within each treatment, and differences in curve width reflect variation in size structure. Overlapping curves indicate similarity in population size distributions between treatments, whereas separated peaks suggest shifts in population size structure under different ocean acidification scenarios. Common names are shown in parentheses below each species name. Letters are used to indicate significant differences between treatments ($p < 0.05$; Supporting Information Table S7), and NS = no significance.

urchin (*Diadema setosum*) and fishes (*Chromis notata* and *Plectroglyphidodon altus*) showed miniaturization under OA(SSP3) compared to Control at the northern-hemisphere vent ($p < 0.043$; Fig. 1; Supporting Information Table S7).

Several species also showed increased body sizes: the urchin *Evechinus chloroticus* was significantly larger at both southern-hemisphere vents compared to their respective controls ($p < 0.001$; Fig. 2; Supporting Information Table S8). The starfish *Coscinasterias calamaria*, brittle star *Ophionereis fasciata*, and fish *Forsterygion lapillum* were all significantly larger at Vent North than Control North ($p < 0.041$), but were unchanged at Vent South ($p > 0.102$) compared to Control South (Fig. 2; Supporting Information Table S8). Similarly, the fish *Chromis yamakawai* was significantly larger under OA(SSP3) compared to Control ($p < 0.001$), and tanaid (*Zeuxo normani*) was larger under OA(SSP5; $p < 0.001$), but unchanged under OA(SSP3; $p = 1.000$; Fig. 1; Supporting Information Table S7).

Some exceptions to these findings were that 25% (Southern Hemisphere) and 40% (Northern Hemisphere) of species, ranging from highly-calcified urchin (*Echinometra* sp. A), bivalve (*Lucinidae* sp.) and brittle star (*Ophiura* sp.) to lightly-calcified tanaid (*Tanaidae* sp.) and ostracod (*Myodocopida* sp.) and to fish (*Notoclinops yaldwyni*) showed no differences in body size distributions at any of the natural CO_2 vents compared to their respective controls (Figs. 1 and 2; $p > 0.055$; Supporting Information Tables S7 and S8). While the body size distribution of amphipod *Monocorophium insidiosum* differed between the OA(SSP3) and OA(SSP5) reefs ($p = 0.011$) at the northern hemisphere vents, neither differed from the Control reef (Fig. 1; $p > 0.109$; Supporting Information Table S7).

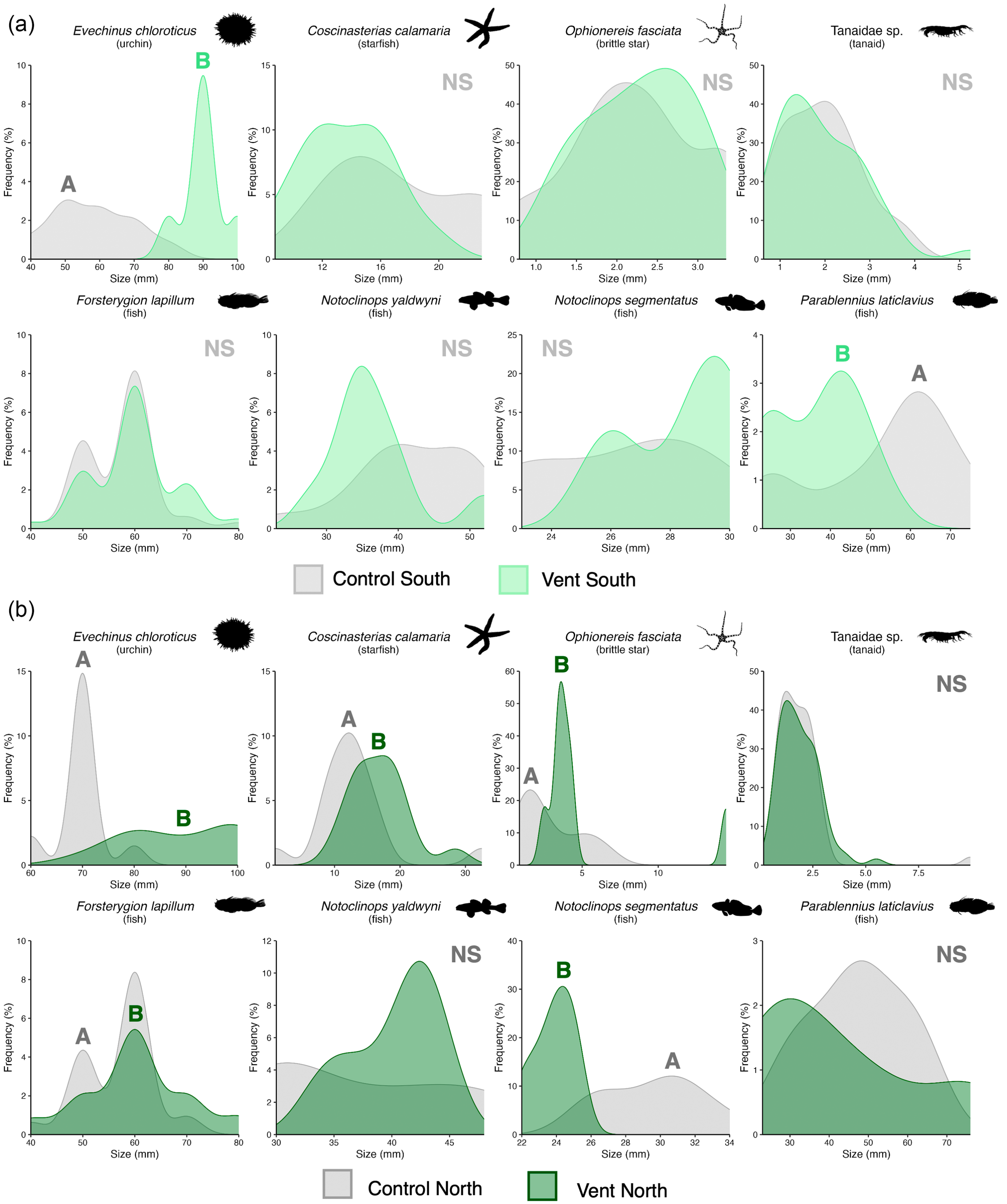

Fig. 2. Legend on next page.

Additional analyses of mean body size for each species at the southern- and northern-hemisphere vents revealed slight body-size differences for several species (*Coscinasterias calamaria, Ophionereis fasciata, Forsterygion lapillum, Notoclinops segmentatus, Parablennius laticlavius*, and *Zeuxo normani*). However, there were no differences in the number of species that exhibited consistent miniaturization across the southern- and northern-hemisphere vents between the two analytical methods (body size means and size-frequency distributions; Supporting Information Figs. S4 and S5; Supporting Information Tables S9–S14). Therefore, we refer to the results of the size-frequency distributions for the remainder of this study, because they capture the full spread and shape of body-size variation within populations rather than reducing patterns to a single average. A comparison of results for both statistical methods can be found in Supporting Information Tables S13 and S14.

Discussion

Various laboratory studies have observed that climate-change stressors can reduce the growth and size of marine ectotherms (Wood et al. 2008; Ries et al. 2009; deVries et al. 2024), particularly calcifying species (Connell and Leung 2023). However, using four natural CO_2 vents across a combined 18 species, we show that only 3 species (2 of which are fishes) consistently miniaturized, 7 showed no change, and 2 increased in size under ocean acidification. The remaining 6 species show inconsistent body size responses across vents. This suggests that responses to ocean acidification are much more variable than previously predicted and are likely mediated by a species' physiology and life history.

Effects of ocean acidification on body size

Body miniaturization

Miniaturization caused by ocean acidification was recorded in only one out of eight calcifying species: urchin *Diadema setosum*. Sea urchins are known to show divergent responses to elevated CO_2, whereby urchin species with higher acid–base regulation capacity are generally more tolerant, whereas those with low capacity are more vulnerable to decreased skeletal integrity and reduced calcification (Di Giglio et al. 2020). The effects of ocean acidification on urchin body size therefore seem highly species-specific, which is consistent with our findings, as one species increased its body size (*Evechinus chloroticus*), one did not demonstrate significant size change (*Echinometra* sp. A), and one miniaturized (*D. setosum*) under ocean acidification. Unpublished data (from B.P.H.) indicate that *Echinometra* sp. A experiences miniaturization under more extreme pCO_2 conditions, suggesting the existence of a physiological tipping point when pH levels become too low. The lowest pH values examined within this study were around 7.8 (representing SSP2-4.5 ocean acidification forecasts); however, many laboratory experiments show different urchin species having reduced calcification and growth rates when exposed to pH values less than 7.7 (Byrne and Hernández 2020; Bednaršek et al. 2021; deVries et al. 2024). Therefore, it is possible that *Echinometra* sp. A and *E. chloroticus* could also experience body miniaturization if exposed to more extreme acidification levels.

A similar threshold effect may also explain patterns observed in fish. *Notoclinops segmentatus* maintained body size at the relatively CO_2-benign southern White Island vent but miniaturized under the more extreme northern vent. This suggests that, like urchins, some fish species may only exhibit body size reductions when environmental stress exceeds a physiological limit, highlighting that responses to ocean acidification may depend on the severity of exposure. Two fish species (*Plectroglyphidodon altus* and *Chromis notata*) did display consistent miniaturization under ocean acidification, which was surprising as many fishes have shown to have a higher tolerance for low pH (Fabry et al. 2008; Melzner et al. 2009; Nagelkerken et al. 2023). *P. altus* is primarily herbivorous and might be expected to benefit from enhanced primary productivity under ocean acidification (Doubleday et al. 2019). However, studies on damselfishes indicate that these species can exhibit strong dietary selectivity for particular algal taxa (Montgomery 1980; Gobler et al. 2006). As a result, the proliferation of turf algae in acidified environments (Connell et al. 2018; Harvey et al. 2021) may not constitute a suitable food source, potentially constraining nutritional intake and contributing to reduced body size. Ultimately, the cause of miniaturization in these species is unclear, as it could reflect a physiological sensitivity to low pH or behavioral traits that limit performance under ocean acidification. This highlights the species-specific nature of body-size responses to ocean acidification.

Interestingly, fish *Parablennius laticlavius* exhibited reduced body size at the southern White Island vent, while individuals at the northern vent showed no change. This suggests that

Fig. 2. Size-frequency distributions of various invertebrate and fish species at (**a**) Control South (light gray) compared to Vent South (light green) and (**b**) Control North (dark gray) compared to Vent North (dark green) in White Island, New Zealand, which represent SSP2 and SSP3 climate projections, respectively. The *x*-axis represents body size (mm), and the *y*-axis shows the relative frequency of occurrence of individuals within each size class (expressed as %). The area under each curve sums to 100%, allowing comparison of the shape and spread of size distributions independent of sample size. Peaks indicate the most common body sizes within each treatment, and differences in curve width reflect variation in size structure. Overlapping curves indicate similarity in population size distributions between treatments, whereas separated peaks suggest shifts in population size structure under different ocean acidification scenarios. Common names are shown in parentheses below each species name. Letters are used to indicate significant differences between treatments ($p < 0.05$; Supporting Information Table S8), and NS = no significance.

the smaller sizes at the southern, more CO_2-benign vent likely reflect natural variability rather than true miniaturization, underscoring how localized sampling can give a misleading impression of broader trends. If sampling had only occurred at one (south) vent, miniaturization would have been inferred as a response to climatic stress, thereby prematurely positing that miniaturization might be a general response. Furthermore, the cryptic nature of several species included in this study resulted in small or uneven sample sizes, which may have limited statistical power. Additionally, differences in the proportion of juveniles and mature individuals sampled from vent and control sites may have influenced the observed patterns, although analyzing size-frequency distributions rather than relying solely on mean body sizes was used as an approach to minimize this potential bias. Therefore, while these findings should be interpreted with caution, they nonetheless provide valuable insights into the body-size responses of taxa rarely examined in vent studies and underscore the species-specific variability in responses to ocean acidification.

Body size enlargement

Four calcifying invertebrates showed increased body size under ocean acidification, including urchin *Evechinus chloroticus*, starfish *Coscinasterias calamaria*, brittle star *Ophionereis fasciata* and tanaid *Zeuxo normani*. Reduced pH directly affects some calcifying species by reducing calcification and growth rates (Doney et al. 2009), so this observed increase in body size might be a result of the beneficial indirect effects of ocean acidification. Elevated CO_2 is known to boost primary productivity (particularly turf algae; Connell et al. 2018) and increase its nutritional quality, which may carry through to its consumers, ultimately reducing the energetic burden of growth (Doubleday et al. 2019; Leung et al. 2019). Therefore, this may explain how opportunist grazers (*E. chloroticus*), detritivores (*O. fasciata* (Pentreath 1970) and *Z. normani* (Jóźwiak et al. 2022)) and carnivores (*C. calamaria* [Day et al. 1995]), which have also been found at other CO_2 vent reefs in Italy (Kroeker et al. 2011; Vizzini et al. 2017), may be increasing their body size under ocean acidification.

These indirect benefits appear to extend beyond invertebrates, as fishes *Forsterygion lapillum* and *Chromis yamakawai* also exhibited increased body sizes. Generalist species, such as *F. lapillum*, and potentially *C. yamakawai*—for which limited ecological information is available but whose close relatives are generally considered habitat generalists (Lin et al. 2022)—can capitalize on enhanced algal growth, increased prey availability and resource enrichment at CO_2 vents (Nagelkerken et al. 2021), which may lead to greater body size. Interestingly, *C. calamaria*, *O. fasciata*, *Z. normani* and *F. lapillum* all had unchanged body sizes at the more CO_2-benign southern White Island vent but exhibited increased body size at the northern vent which represents a more extreme CO_2 scenario. This pattern suggests that a higher concentration of CO_2 may be necessary before invertebrates and fishes derive benefits from CO_2 enrichment. However, whether a tipping point exists— beyond which excessive CO_2 exposure ceases to be beneficial and instead induces physiological stress and body-size reduction—remains to be determined. Overall, however, while ocean acidification imposes physiological and indirect stress on some invertebrate and fish species, other species—particularly generalists—may instead benefit from indirect effects, resulting in unexpected increases in body size.

Lack of body size change

The other six invertebrate species, ranging from highly-calcified (urchins, bivalves and brittle stars) to lightly-calcified (amphipods, tanaids and ostracods), showed no change in body size under elevated CO_2 in the field. While this result is unexpected for the highly-calcified species which, in previous mesocosm and in situ studies have shown reduced calcification and growth rates under ocean acidification (Riebesell et al. 2000; Gazeau et al. 2007; Doney et al. 2009; Ries et al. 2009; Figuerola et al. 2021), it is less surprising for the crustacean and fish species which have generally shown variable responses (Whiteley 2011; Siegel et al. 2022) or no response, respectively (Harvey et al. 2013; Kroeker et al. 2013b). The predominance of crustaceans and fish within the sampling may have contributed to the lack of observed effects in the in situ experiments. Inclusion of a broader range of calcifying species (like gastropods) may have yielded different outcomes. The species examined within this study may also be inherently more resilient to ocean acidification as a result of long-term, multigenerational exposure to low pH conditions. As a result, more sensitive species that cannot persist in vent environments may not have been captured in our study. Additionally, categorizing taxa by other developmental traits rather than calcification may also produce different outcomes. Species with fixed developmental durations or a set number of larval stages may be more likely to exhibit reduced adult body size under environmental stress, as slower growth cannot be offset by prolonging development (Dupont et al. 2010; Ross et al. 2011). Future research could help disentangle the role of developmental strategy in body size responses to ocean acidification. However, many species can adjust their physiological or developmental processes to mitigate the effects of ocean acidification, so the absence of detectable changes in body size may reflect such compensatory responses. The gastropod *E. mortoni* adaptively modifies the structural properties of its shell when exposed to elevated CO_2 by reducing porosity, increasing organic matter content, and adjusting the calcium carbonate crystals to become stronger and more durable (Leung et al. 2020). A species of sea urchin (*Paracentrotus lividus*) was able to maintain test integrity when exposed to low pH (Collard et al. 2016). However, this response was likely mediated by consumption of calcifying algae which can help increase test strength (Asnaghi et al. 2013). Sometimes these compensation processes to cope with low pH can yield trade-offs. Bryozoan species have been shown to acclimate to ocean acidification by altering their skeletal properties. However, this acclimation triggered shifts in their microbiome—likely resulting from the combined effects of acidification and warming—which ultimately reduced overall fitness (Figuerola et al. 2025). The brittle star *Amphiura filiformis* was able to upregulate calcification and metabolic rates to survive low pH, but long-term exposure led to muscle wastage (Wood et al. 2008). Similarly, the Dungeness crab (*Metacarcinus magister*) increases calcification to counteract exoskeletal dissolution, but this comes at an energetic cost that may compromise overall growth (Bednaršek et al. 2020). While these physiological and adaptive mechanisms may seemingly allow vulnerable calcifying species to maintain growth and body size under climate stressors, it is possible that these processes will not be sustainable long-term. The fish *Notoclinops yaldwyni* also showed no change in body size as a response to ocean acidification. Some other studies have observed that reduced pH has little to no effect on fish growth rate or body size, as fish generally have greater capacity for acid–base regulation than calcifying species (Fabry et al. 2008; Melzner et al. 2009; Kroeker et al. 2013b; Nagelkerken et al. 2023). The absence of a size response in *N. yaldwyni* is therefore consistent with the broader evidence that many fish species can tolerate acidification without substantial impacts on growth.

Overall, while many invertebrate and fish species from the northern- and southern-hemispheres appear to be able to cope with reduced seawater pH through adaptive mechanisms or advantageous life history traits, the extent to which these processes can be maintained long-term remains largely unknown. Given the limited number of CO_2 vents in our study ($n = 4$), we cannot rule out the possibility that some of these species may exhibit miniaturization.

Reproducibility in climate change research

Our in situ and laboratory studies tested whether early observations of miniaturization under climate stressors (e.g., Sheridan and Bickford 2011; Cheung et al. 2013; Gardner et al. 2011) could be reproduced across species and functional groups from the southern and northern Pacific Oceans. Such search for reproducibility of an ecological mechanism is essential because it allows the global research community to verify ideas, ensuring insight into the extent that their predictions can yield consistent outcomes across different studies or contexts. While we found some support for miniaturization under ocean acidification, it had limited generality. Similarly, historical examples show that early studies on corals and coccolithophores suggested strong negative effects of ocean acidification on calcification, but later research revealed more varied outcomes, particularly among tolerant taxa, leading to a reduced effect size over time (Connell and Leung 2023). This process of developing and replicating initial findings across varying locations, conditions, and taxa is essential to identifying limitations of accepted phenomena—a fundamental of theory development.

Author Contributions

Mary E. Hart: conceptualization; investigation; formal analysis; visualization; writing—original draft preparation; writing—review and editing. Sean D. Connell: conceptualization; investigation; writing—review and editing; funding acquisition. Angus Mitchell: investigation; writing—review and editing. Ben P. Harvey: resources; writing—review and editing. Sylvain Agostini: writing—review and editing; Joshua M. Heitzman: investigation; writing—review and editing. Ivan Nagelkerken: project administration; conceptualization (lead); funding acquisition; investigation; supervision; writing—review and editing.

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Conflicts of Interest

None declared.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information Data S1 of this article.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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