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RESEARCH ARTICLE

Out of shape: Ocean acidification simplifies coral reef architecture and reshuffles fish assemblages

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Abstract

1. Climate change stressors are progressively simplifying biogenic habitats in the terrestrial and marine realms, and consequently altering the structure of associated species communities.
2. Here, we used a volcanic CO_2 seep in Papua New Guinea to test in situ if altered reef architecture due to ocean acidification reshuffles associated fish assemblages.
3. We observed replacement of branching corals by massive corals at the seep, with simplified coral architectural complexity driving abundance declines between 60% and 86% for an assemblage of damselfishes associated with branching corals. An experimental test of habitat preference for a focal species indicated that acidification does not directly affect habitat selection behaviour, with changes in habitat structural complexity consequently appearing to be the stronger driver of assemblage reshuffling. Habitat health affected anti-predator behaviour, with *P. moluccensis* becoming less bold on dead branching corals relative to live branching corals, irrespective of ocean acidification.
4. We conclude that coral reef fish assemblages are likely to be more sensitive to changes in habitat structure induced by increasing $p\text{CO}_2$ than any direct effects on behaviour, indicating that changes in coral architecture and live cover may act as important mediators of reef fish community structures in a future ocean.

KEYWORDS
coral reef fishes, coral structural complexity, habitat association, habitat simplification, indirect effects, ocean acidification

1 | INTRODUCTION

Habitat loss has been implicated as a major contributor to the current global biodiversity crisis, in which nearly half a million species face the threat of extinction over coming decades (Banks-Leite et al., 2020; Ceballos et al., 2015). However, habitat 'loss' can encompass more than merely diminishing spatial coverage. Degradation of habitat quality—when a habitat no longer meets the various needs of associated species populations—can also contribute profoundly to biodiversity declines (Fischer & Lindenmayer, 2007). Habitat quality is often more strongly dictated by the diversity of functional habitat traits than by the species richness of habitat-builders (Milanović et al., 2021; Tews et al., 2004). The physical characteristics of habitats can mediate the provision of diverse ecological services, ranging from nesting sites (Fan et al., 2003) and settlement substrate (Chase et al., 2016) to refugia from predation (Almany, 2004; Boström-Einarsson et al., 2018). In the face of environmental stress and disturbance, different sensitivities among habitat-forming species could see a shift in competitive dynamics within existing assemblages (Fabricius et al., 2011), potentially altering the distribution and abundance of functional traits without necessarily reducing the absolute spatial extent of habitat (Alvarez-Filip et al., 2013; García-Valdés et al., 2020). In this context, determining which habitat traits contribute most strongly to the provision of ecosystem services in a given system, and how these traits are likely to respond to disturbance, may offer valuable insight into how ecological communities may change in response to mounting environmental stress (Chase et al., 2016; Tews et al., 2004).

In coral reef systems, three key traits of coral species determine the bulk of their contribution to the functionality of reef communities: spatial coverage, calcification rate and structural complexity (González-Barrios et al., 2021; Graham & Nash, 2013). Changes to any one of these properties has the capacity to profoundly alter ecosystem stability (Perry & Alvarez-Filip, 2019; Wilson et al., 2019). The impacts of the loss of live corals and declining accretion rates have been well studied (González-Barrios et al., 2021; Januchowski-Hartley et al., 2017; Pratchett et al., 2008). However, while a number of studies have explored the importance of coral habitat complexity in determining the structure of reef communities (Komyakova et al., 2013; Messmer et al., 2011), the way in which climate stressors impact coral architecture and supported reef fish populations remains poorly understood. In particular, branching corals such as *Acropora* spp. typically support a higher diversity and abundance of coral-associated invertebrates than their flatter, encrusting and mound-forming counterparts, such as *Porites* spp. (Stella et al., 2010, 2011), and they are major providers of habitat, foraging opportunity, and predation refugia for coral reef fishes (Coker et al., 2009; Graham & Nash, 2013). Consequently, spatial and temporal variation in the cover of branching corals as a result of climate change may be a key determinant of trophodynamics of coral reefs (Wilson et al., 2008, 2019), with this effect potentially greatest in high diversity systems and therefore an important mediator of extinction risk in biodiversity hotspots (Holbrook et al., 2015).

Despite the integral contribution of benthic architectural characteristics to reef health, architectural diversity continues to be obscured by a ubiquitous reliance on the metric of total living coral cover in assessments of the condition of shallow reefs facing environmental stress (Richards, 2013). While the health and structure of corals are intimately linked, with mortality often leading to loss of structural integrity (Morais et al., 2022), the two are not inseparable aspects of the same metric. Living corals exhibit a range of morphologies that support distinct ecological functions (Pratchett et al., 2008; Wilson et al., 2008); conversely, dead corals that retain their structural attributes may continue to support a range of ecosystem services prior to their eventual degradation to rubble (Nelson et al., 2016), with some key functions, such as the provision of surface for microbes and encrusting biofilms that are important food resources, continuing even beyond this point (Wolfe et al., 2021). Although there are degrees of overlap, services offered primarily by structure can operate in the absence of living tissue, and vice versa.

Environmental stressors that alter coral structure whilst leaving living coral tissue undiminished are thus uniquely placed to disrupt the provision of a range of ecosystem services. In the case of ocean acidification, observations at naturally acidified coral reefs at CO_2 volcanic seeps indicate that differential susceptibility to elevated pH among coral taxa may drive a shift towards species with stress-tolerant life-histories (Darling et al., 2012; Fabricius et al., 2011), resulting in a change in coral assemblage composition as a response to acidification, rather than a decline in absolute benthic live coral cover (Alvarez-Filip et al., 2013; Fabricius et al., 2011). In particular, observations of these acidified assemblages point to a loss of branching corals and relative dominance of massive corals in these environments, likely as a function of their lower carbonate production (Fabricius et al., 2011). The presumed resilience of massive corals in the face of environmental change may be viewed positively, in light of their contribution to maintaining positive reef accretion (Januchowski-Hartley et al., 2017). However, as they contribute little to overall reef architectural complexity, their rising dominance can contribute to reef 'flattening'—a phenomenon more commonly associated with coral mortality, and which is linked to substantial reef biodiversity loss (Darling et al., 2012). The displacement of branching corals by competitively superior massive corals under acidification has consequently been projected to represent a significant ecological shift, even if absolute live coral cover is maintained (Sunday et al., 2017).

Here, we investigate how pH-driven changes in the dominant structural forms of corals link to population-level responses of five species of an ecologically important family of reef-dwelling fishes. Using a naturally acidified reef system (volcanic CO_2 vent in Papua New Guinea) we teased apart the contributions of both coral health (live vs. dead) and structure (massive vs. branching) to the habitat associations of these five species. This was done both through in situ observations of fish-habitat associations as well as through an in situ aquarium-based habitat choice experiment. This allowed us to test how the habitat associations of site-attached fishes could shape fish community responses to coral habitat reshuffling and simplification under future elevated CO_2 conditions.

2 | MATERIALS AND METHODS

2.1 | Study location

Data were collected in June 2018 from an acidified shallow (3–6 m) coral reef (median pH 7.77, 5th-95th percentile 7.02–7.99, median pCO_2 846 µatm, 5th-95th percentile 454–5737) at Upa-Upasina in Papua New Guinea's Milne Bay Province (9°49.45′S, 150°49.07′ E) and an adjacent (~500 m away) control reef with ambient pCO_2 (median pH 8.01, 5th-95th percentile 7.99–8.02, median pCO_2 443 µatm, 5th-95th percentile 415–456). Seawater carbonate chemistry at these sites has been comprehensively documented during previous studies (Comeau et al., 2022; Fabricius et al., 2011; Uthicke et al., 2016), employing gas chromatography, boat-deployable pCO_2 monitoring systems and portable conductivity, salinity and temperature meters. These assessments have shown that the gas bubbles emitted at the seep site consist predominantly (>99%) of CO_2 (Fabricius et al., 2011), and have revealed no longer-term difference in temperature and salinity between the CO_2 seep and the adjacent control site. During our study the average (±SD) temperature (27.2 ± 0.3°C and 27.1 ± 0.3°C) and salinity (35.4 ± 0.04 and 35.5 ± 0.6) were consistent between seep and control reef, respectively.

2.2 | Fish species studied

Pomacentrids (damselfishes) are an ideal test group for examining the indirect effects of ocean acidification. As one of the most abundant and ecologically diverse families of coral reef fishes, fish from this family exhibit substantial variation in habitat preference, with species ranging across the spectrum from habitat generalists to extreme specialists (Gibson et al., 2001; Komyakova et al., 2013). Furthermore, damselfishes are commonly targeted as prey by larger reef-dwelling predators, placing them as a key trophic link between benthic coral assemblages and higher-order consumers (Casey et al., 2017; Gibson et al., 2001). As such, changes to their abundances may subsequently affect broader reef trophodynamics and functioning. This study selected five focal damselfish species: *Acanthochromis polyacanthus* (spiny chromis), *Amblyglyphidodon curacao* (staghorn damsel), *Dascyllus aruanus* (banded humbug), *Pomacentrus adelus* (obscure damsel) and *Pomacentrus moluccensis* (lemon damsel). Each were selected for their relatively high abundances at both the control reef and CO_2 seep, and their strong site fidelity (mean territory size 1–1.5 m^2 per individual) (Booth, 2016; Emslie et al., 2019; Nash et al., 2015), ensuring that estimates of distribution and density were unlikely to be confounded by individuals transiting between control and seep sites. They associate with corals to different degrees, and encompass both highly sedentary benthic species and more mobile epibenthic species that often feed higher in the water column (Chase et al., 2020; Emslie et al., 2019; Table S1).

2.3 | Benthic habitat cover

Randomly distributed photo quadrats were taken at a distance of approximately 1 m off the substratum of all benthic coral cover (40 control and 31 seep quadrats). A 60 cm ruler was included as a reference in all photo quadrats to ensure that a consistent area of a similar size was analysed.

Coral cover and the proportion of living, dead, and different morphologies of coral were analysed by overlaying each digital photo quadrat with 20 randomly distributed points (stratified random distribution, with 5 randomly laid points in each of four equal quadrants) using the computer program CoralPointCount (CPCe 4.1). The substrate under each point was then classified into one of three categories: two levels of coral health (live or dead), and 'other', and three levels of coral morphology (branching, massive, or rubble). The percent cover of each category was calculated for each quadrat.

2.4 | Fish assemblage structure

Fish abundance and size-estimation surveys were visually performed on SCUBA in randomly distributed belt transects, spaced a minimum of 15 m apart. For *A. polyacanthus* and *A. curacao* transect sizes were 10 × 4 m (10 replicate transects at both control and seep sites) because these species had a larger home range (Table S1). For all other species transects of 10 × 2 m were used (10 replicate transects at both control and seep sites), as these species were more site attached (Table S1).

2.5 | In situ fish habitat use

In situ GoPro footage of target fish species was collected by placing the cameras in front of specific areas of the reef chosen as broadly representative of available habitats (Figure S1) and recording all individuals interacting with these habitats (individuals recorded: *A. polyacanthus*—46 control, 22 seep; *A. curacao*—30 control, 10 seep; *D. aruanus*—26 control, 33 seep; *P. adelus*—44 control, 28 seep; *P. moluccensis*—38 control, 35 seep).

Habitat use was quantified on a computer screen using the software VLC 3.0.18 media player. Video recordings, which ranged from a minimum of 2 min to a maximum of 13 min with an average duration of 4 min, were analysed separately for each individual recorded fish. Recordings of individuals were divided into 15-s intervals, commencing at the moment the target individual appeared in frame and ceasing when the individual was no longer associating with the available habitat. At each interval, the habitat closest to the focal individual was identified, and characterised according to two levels of health (live or dead) and three levels of morphology (branching, massive, rubble). These values were then expressed as a percentage of the total number of observations made for the individual, yielding the proportional use of each habitat type for each observed fish.

2.6 | Experimental fish habitat preference

To investigate preferential habitat use in the absence of other environmental influences (e.g. food, differential habitat availability, competition, etc.) an in situ habitat preference experiment was undertaken using a single damselfish species, *Pomacentrus moluccensis*, which was chosen due to its high abundance and ease of collection at both control and seep sites. Fish were collected from the respective reefs (seep vs. control) and individually placed within a plastic aquarium (36 × 21 × 21 cm) placed up-side down onto the sandy substratum (Figure S2). The aquaria were positioned at least 10 m away from adjacent corals to minimise interactions with other fishes, in-between the control and seep sites. Fish were collected using a hand-net from reef areas adjacent to the experimental aquaria, within a distance of no more than a 20-m radius. Upon capture, they were promptly transferred to a plastic bag to minimise potential damage and reduce handling stress. Subsequently, the fish were swiftly transported to the vicinity of the aquaria and allowed to rest for 5 min before being released into the aquaria. Fish were introduced to the upper part of the aquarium at a point approximately equidistant from both coral habitats in order to reduce initial habitat selection bias. Prior to the experiment, fish were given time to acclimatise to conditions of the experimental tank, with data collection commencing between 30 and 90 s after the fish was introduced to the tank. Experiments consisted of a simple dual choice setup, comprising an arena with only two representative habitat types offered at any time out of a possible four (live branching, dead branching coral from *Acropora* spp., and live massive and dead massive from *Porites* spp.). All selected branching corals (dead and alive), although not measured, had similar size, shape, and intra-branch spacing, and all selected massive corals (dead and alive) were individual juvenile colonies of approximately equal size. Four paired combinations of these habitat types were tested throughout the experiment, using new individual fish for each trial (dead branching vs. live massive: 11 control, 11 seep; live branching vs. dead branching: 9 control, 9 seep; live branching vs. live massive: 10 control, 10 seep; live massive vs. dead massive: 4 seep). Percentage time spent in each microhabitat was recorded via a GoPro positioned in front of the experiment arena (minimum recording time 7 min, maximum 21 min, mean 13 min).

2.7 | Flight initiation distance (FID)

Predator avoidance is a key behavioural determinant of both predation risk and resource access, and is strongly affected by altered access to appropriate shelter (Almany, 2004). The FID of each species was used as a proxy measure of this behaviour, and was recorded as the distance at which an individual fled the approach of an artificial startle cue designed to mimic a potential threat (e.g. predator attack), using methodology shown to elicit similar responses as those in genuine predator escapes (Nagelkerken et al., 2017). The startle cue consisted of PVC frame connected to a 60 cm iron rod, which supported a 30 cm metal ruler at its distal end and a GoPro camera, positioned to film the ruler, at the end proximal to the carrying diver (see fig. S2 in Coni et al., 2022). Individual fish were carefully approached, and once within range the end of the ruler was moved from above the fish towards its head at a constant speed. The camera recorded the entire process, and using VLC 3.0.18 we measured the distance at which each fish initiated a flee response from the approaching threat (distance from tip of ruler to eye of fish, with the ruler acting as a measurement reference). A total of 255 individual fish were analysed (*A. polyacanthus*—21 control, 29 seep; *A. curacao*—24 control, 21 seep; *D. aruanus*—21 control, 21 seep; *P. adelus*—27 control, 26 seep; *P. moluccensis*—30 control, 35 seep).

All experiments were performed under animal ethics approval numbers S-2018-031 of the University of Adelaide Animal Ethics Committee and A2534 of James Cook University, in accordance with the South Australian Animal Welfare Act 1985 and in compliance with the Australian Code for the care and use of animals for scientific purposes (8th Edition 2013). Research was conducted under National Research Permit (AA869803) and permit # CO1-056058 to RR-M.

2.8 | Statistical analyses

To visualise the influence of acidification on benthic coral characteristics, a non-metric multi-dimensional (nMDS) scaling plot based on a Bray–Curtis similarity matrix was generated, comparing percentage cover of the five identified coral habitat categories (live branching, live massive, dead branching, dead massive, rubble) between sites. A three-way permutational non-parametric ANOVA was then performed to assess differences in the cover of live corals and coral architecture between control and seep sites. Two treatment levels (control, seep), two levels of coral health (live, dead) and three levels of coral structure (branching, massive, rubble) were tested.

A two-way permutational ANOVA was performed to assess differences in observed abundances of each fish species between control and seep sites. Two treatment levels (control, seep) and five fish species levels were tested.

To visualise the influence of acidification on patterns of habitat association of resident damselfish, a non-metric multi-dimensional (nMDS) scaling plot based on a Bray–Curtis similarity matrix was generated, comparing percentage time spent in each habitat between sites. The habitat use of each damselfish species was further investigated by contrasting the proportional use of each habitat category against the availability of that habitat at each site. In the absence of any habitat selectivity, random habitat use would be expected to mirror the availability of the habitat at each location. To assess whether observed habitat use deviated significantly from the random habitat use model for each species and each habitat, a two-way permutational ANOVA was performed for each habitat category (live, massive, branching, rubble) at each site, with six usage levels (i.e. observed usage of each of the five fish species and an additional random usage derived from the habitat availability data) and two treatment levels (control, seep) tested. Additional two-way permutational ANOVAs with two treatment levels (control, seep) and five species levels were undertaken for each habitat type to assess if proportional use by each species differed between control and seep sites.

Differences in patterns of habitat preference between control- and seep-resident *P. moluccensis*, derived from the in situ aquarium experiments, were assessed using a separate MANOVA for each habitat pairing (dead branching vs. live massive; live branching vs. dead branching; live branching vs. live massive), with two dependent variables (each of the two available habitats in the trial, i.e. habitat 1 and habitat 2) and two treatment levels (control, seep). As there were no CO_2 effects on habitat choice, differences in habitat use within each habitat pairing were consecutively assessed for each treatment level through permutational ANOVAs with two habitat levels (Habitat 1 vs. Habitat 2).

Differences in the FID of each of the five fish species between control and seep sites were assessed through a permutational ANOVA with two treatment levels (control, seep). An additional two-way permutational ANOVA with two treatment levels (control, seep) and two habitat levels (live branching, dead branching) was performed to assess differences in FID of *P. moluccensis* at live and dead branching habitats under control and acidified conditions.

All nMDS analyses and ANOVAs were performed in PRIMER 7. For all significant ANOVA results ($p < 0.05$), pairwise tests were used to compare the respective means.

3 | RESULTS

3.1 | Benthic habitat cover

Benthic coral communities differed between control and seep sites (Figure 1a, Figure S3). Total live coral cover was 9% higher at the CO_2 seep compared with the control reef (30% vs. 21%, respectively; $p = 0.0001$, Table S2), which was mainly due to a 16% higher cover of live massive corals but a 7% lower cover of live branching corals at the seep (Figure S3). Total cover of massive corals was 27% higher at the CO_2 seep ($p = 0.0214$), comprising an increase of 16% in live and 11% in dead coral cover, respectively. Total cover of branching corals was 18% lower at the seep ($p = 0.0001$), comprising only 2% of live branching coral cover. Cover of coral rubble was similar between the control (13%) and seep (11%) ($p = 0.0524$).

3.2 | Fish assemblage structure

Distributions of the five focal damselfishes differed markedly between control and seep sites (Figure 2, Figure S4). The three most abundant focal damselfish species at the control reef exhibited 60% (*A. polyacanthus*, $p = 0.0275$), 86% (*A. curacao*, $p = 0.0231$), and 80% (*P. moluccensis*, $p = 0.0003$) lower densities at the seep, respectively (Figure 2, Table S3). Densities of the other two species (*D. aruanus* and *P. adelus*) were similar at the CO_2 seep and control reef. The most abundant focal damselfishes at the seep were *A. polyacanthus*, *P. adelus* and *P. moluccensis*.

3.3 | In situ fish habitat use

The relative importance of coral morphology and health in fish habitat associations varied across the five focal species and between control and seep sites (Figure 1b, Figure S5, Tables S4 and S5). *D.*

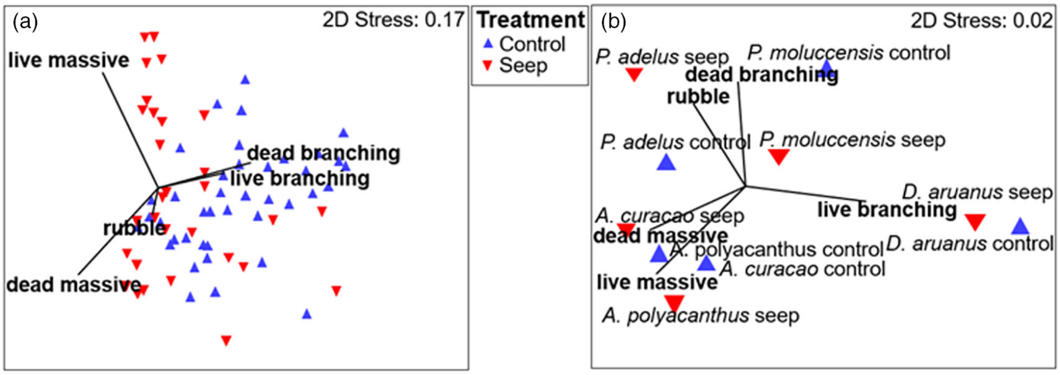

FIGURE 1 Non-metric multidimensional scaling (nMDS) plots based on Bray–Curtis similarity matrices derived from (a) percent cover of various benthic coral habitat types obtained from photo quadrats at control (40 images) and seep (31 images) sites at Upa-Upasina, Papua New Guinea, and (b) mean percent habitat use of each of five damselfish species at control and seep sites at Upa-Upasina, Papua New Guinea. Lines represent the direction of strongest change, with length of the line showing the magnitude of change. Data are colour coded by site (control and seep).

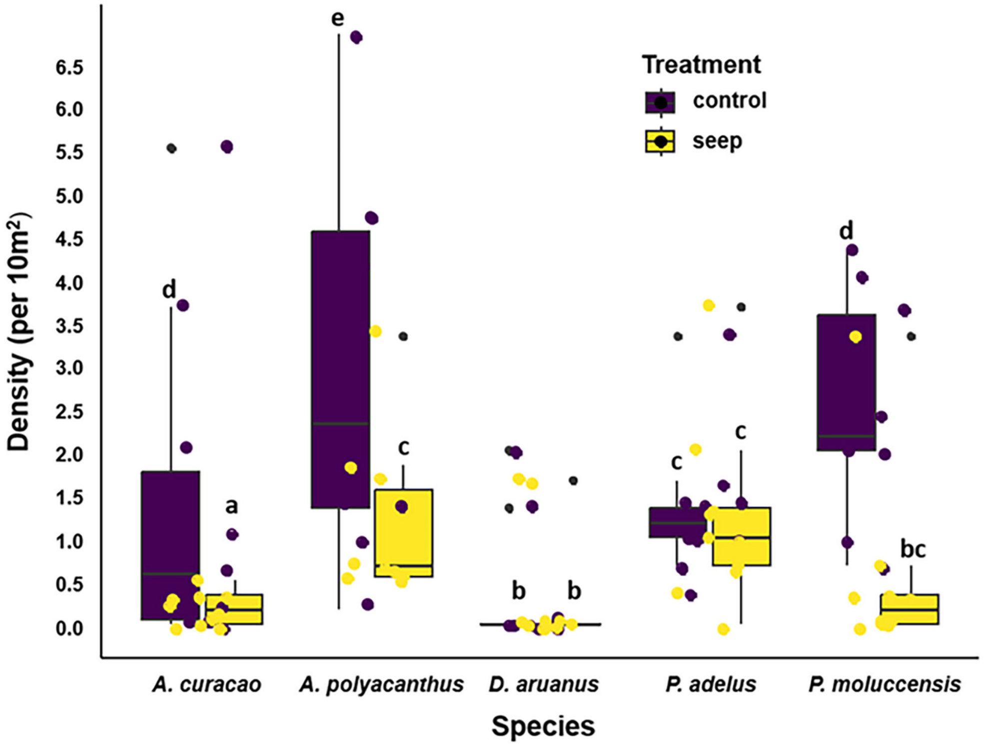

FIGURE 2 Boxplots of in situ densities of focal damselfish species at control and seep sites. Boxes represent the interquartile range, with whiskers extending to the most extreme data points with 1.5× the interquartile range, and the median indicated by a bisecting bar. Boxes are overlaid with individual data points. Significant differences between groups (across treatments and species) are indicated by different letters above bars. See Table S3 for details of statistical tests.

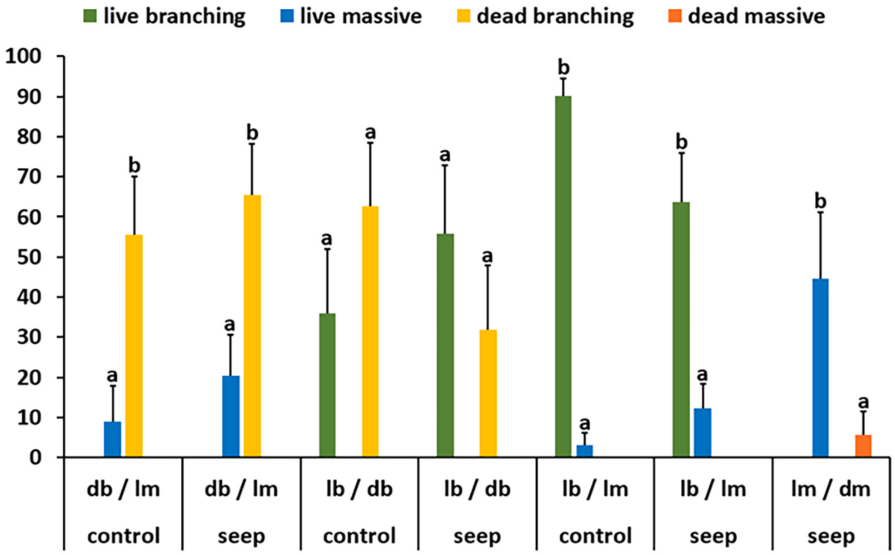

FIGURE 3 Habitat use by *Pomacentrus moluccensis* in a controlled dual-choice in situ aquarium experiment. Error bars represent standard error. Habitats offered to the fish are shown on the *x*-axis. Control and seep designations represent the location from which each individual fish was sourced. Significant differences between habitats within pairings are indicated by different letters above bars; no significant differences existed between control and seep habitat use. See Tables S6 and S7 for details of statistical tests.

aruanus selected branching corals (97% control, 98% seep) to the near exclusion of massive corals (3% control, 2% seep), irrespective of CO_2 treatment ($p = 0.8834$, Table S5). *P. moluccensis* also showed high (91%) use of branching corals at the control reef, but reduced use at the seep (72%, $p = 0.0119$) following a concurrent reduction in availability of this habitat at the seep. Contrastingly, *P. moluccensis* increased its use of massive corals from 10% at the control to 28% at the seep ($p = 0.0168$) following a concurrent increase of this habitat at the seep, though this increased use was still less than availability at both sites ($p < 0.0001$ at both sites).

The two epibenthic damselfishes, *A. polyacanthus* and *A. curacao*, showed no significant change in the use of coral structure between control and seep sites ($p > 0.05$ for all structural categories). Both spent proportionally more time associated with massive corals (63% control, 72% seep; and 62% control, 59% seep, respectively) than branching corals (35% control, 28% seep; and 36% control, 41% seep, respectively), irrespective of CO_2 treatment, and irrespective of a higher availability of massive corals at the seep. Despite this apparent preference for massive over branching corals, the maintenance of proportional use of branching corals in the face of changing availability by both species resulted in preferential selection of this habitat relative to its availability at the seep ($p = 0.0036$ *A. polyacanthus*, $p = 0.0008$ *A. curacao*).

Pomacentrus adelus was the only focal species displaying preferential use of rubble habitat relative to availability ($p = 0.0074$ control, $p < 0.0001$ seep), being higher (41%) at the seep than at the control reef (25%, $p = 0.0337$).

All species displayed a higher use of live corals relative to availability at the control reef (Figure S5, Table S5), with this preference most pronounced for *D. aruanus* (98% live coral use, $p < 0.0001$), *A. curacao* (79%, $p < 0.0001$) and *A. polyacanthus* (77%, $p < 0.0001$). This preference for live coral remained significant at the seep for all species other than *P. adelus* ($p = 0.9102$), which significantly reduced use of live corals at the seep ($p = 0.0388$). No species showed a significant increase in use of live corals at the seep (Table S5) despite the 9% higher live coral cover at this site.

3.4 | Direct effects of chronic exposure to elevated CO_2 on experimental fish habitat preference

Control and seep *P. moluccensis* individuals did not differ significantly in their proportional use of available coral habitats in any of the experimental habitat pairings ($p \geq 0.1471$ for each habitat pairing, Figure 3, Table S6). Fishes instead prioritised coral architecture over tissue health across the different habitat types, and irrespective of CO_2. Fishes from both control and seep preferred branching corals above live massive corals, irrespective of whether the branching corals were alive or dead ($p < 0.0001$ live branching vs. live massive control, $p = 0.0022$ live branching vs. live massive seep; $p = 0.0171$ dead branching vs. live massive control, $p = 0.0128$ dead branching vs. live massive seep, Table S7). Contrastingly, when offered equal portions of live and dead branching habitat, both control and seep *P. moluccensis* showed no significant discrimination between either ($p \geq 0.4841$ in both instances, Table S7).

3.5 | Flight initiation distance

Of the five damselfish species, only *D. aruanus* showed a lower FID at the seep than at the control reef (Figure 4A; $p = 0.0003$, Table S8). Habitat-specific tests for *P. moluccensis* showed that FID was higher in dead branching compared to live branching corals, irrespective of CO_2 levels (Figure 4B, $p = 0.0001$, Table S9).

4 | DISCUSSION

We show that ocean acidification can indirectly reshuffle fish assemblages through a change in the dominant architectural characteristics of a coral reef ecosystem. Mediated by the process of fish habitat selectivity, the constraint imposed by ocean acidification on coral architecture significantly altered the abundance of a suite of small-bodied reef fishes on an acidified coral reef. The magnitude of change in overall damselfish density at the seep (60% lower), where

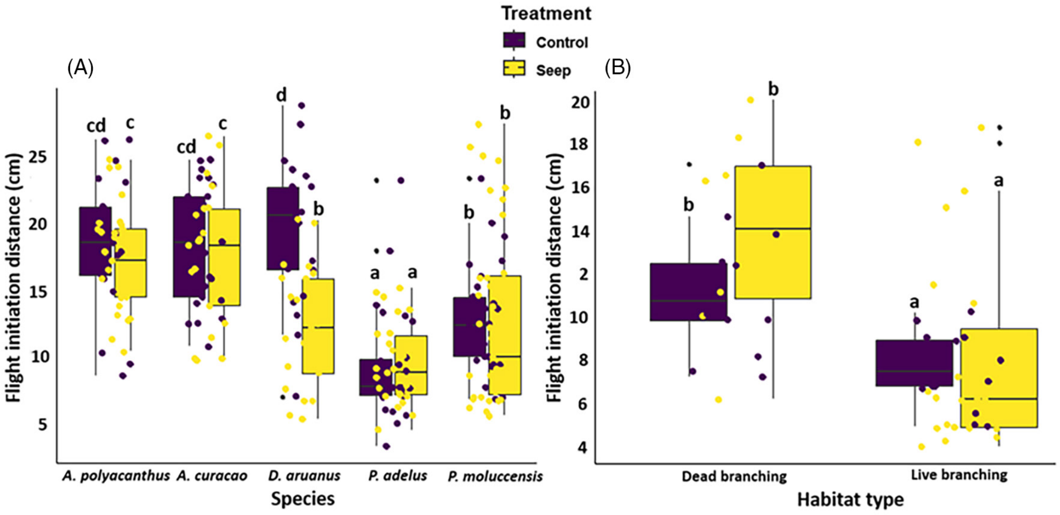

FIGURE 4 Boxplots of flight initiation distance of (A) all focal damselfishes irrespective of habitat type at control and seep sites, and (B) *Pomacentrus moluccensis* at live and dead branching habitats at control and seep sites. Boxes represent the interquartile range, with whiskers extending to the most extreme data points with 1.5× the interquartile range, and the median indicated by a bisecting bar. Boxes are overlaid with individual data points. Significant differences between groups are indicated by different letters above bars. See Tables S8 and S9 for details of statistical tests.

branching structures were nearly absent (<2% cover), is indicative of the power of this indirect effect, and foreshadows potentially significant alterations to reef fish communities under future ocean acidification scenarios.

Availability of branching structure, rather than live tissue, emerged as a dominant driver of damselfish abundance in this study. Damselfishes were associated with branching corals in one of two distinct ways: (1) displaying clear preference for branching over massive coral structures (benthic species *P. moluccensis* and *D. aruanus*), (2) maintaining rigid proportional use of branching structures at the seep irrespective of reduced availability, and despite a higher preference for massive corals (epibenthic species *A. polyacanthus* and *A. curacao*) or a roughly similar preference for branching, massive and rubble habitats (*P. adelus*). Of the two species that distinctly favoured branching over massive corals, only *P. moluccensis* showed a significant decrease (80%) in abundance at the seep. This decline occurred despite evidence of some degree of plasticity in habitat use, with seep individuals increasing their relative use of massive coral forms by 18%. The other branching coral specialist, *D. aruanus*, was restricted in its habitat niche due to preference for both branching structures and live tissues, and as a result their population abundances were very low at both sites (i.e. due to reduced branching coral at vents vs. reduced live coral at controls). Contrastingly, as the only damselfish to associate with rubble habitats, the availability of which were unchanged at the seep, densities of *P. adelus* were insulated from the negative effects of reduced branching coral availability at the seep through their increased use of rubble. Consequently, densities of this species remained unchanged between sites. The two epibenthic damselfishes (*A. polyacanthus* and *A. curacao*) showed preference for massive over branching corals at both the control and seep sites. Both species used branching corals in line with their availability at the control site but significantly more than their availability at the seep, implying active selection of these complex structures. It is the maintenance of this association with branching corals that likely drove their reduced abundance at the seep. In summary, it is the availability of branching habitats that may thus act as a limiting or driving factor of the abundance of those damselfish species (and possibly also other fish species) that display a significant association with branching corals. Accordingly, the simplification of coral architecture associated with ocean acidification represents an ecological disturbance on reef fish communities. This finding mirrors that of previous studies of habitat shifts at CO_2 seeps that revealed similar patterns of both simplification and community reshuffling, with scleractinian corals and canopy-forming macroalgae in tropical regions (Cattano et al., 2020) and kelp-dominated mosaics in temperate systems (Nagelkerken et al., 2016) both giving way to low-profile turf algae in acidified areas and with this habitat simplification driving significant shifts in associated fish assemblages. Nonetheless, such effects are not universally observed. A previous study of fish assemblages at Upa-Upasina revealed little difference between control and seep sites (Munday et al., 2014). However, the similarities in assemblages between sites were primarily attributable to highly mobile species, which were able to freely transit in and out of acidified areas, and the study did note substantially reduced abundances of small-bodied, site-attached species. Although the effects of habitat simplification and community reshuffling were tested at the relatively small spatial scales of naturally acidified CO_2 seeps, these results collectively presage effects on a more diverse suite of species under future acidification scenarios, which will manifest globally.

Increasing live coral cover as observed at the CO_2 seep did little to ameliorate the negative effects of loss of branching structure. None of the five species of damselfish showed a positive change in density at the seep despite a 9% increase in live coral cover, even those species (*D. aruanus*, *A. polyacanthus* and *A. curacao*) that associated most strongly with live coral (98%, 77% and 79%, respectively, at the control, and 93%, 80% and 60%, respectively, at the seep). For *D. aruanus*, the nearly exclusive association with live tissues was matched by equally strong association with branching structure (97% control, 98% seep), with this species hence found almost exclusively in live branching corals. Yet, even for the two epibenthic species, *A. polyacanthus* and *A. curacao*, whose dominant habitat preferences were for live massive corals, the increasing cover of live massive habitats at the seep was not matched by either increased densities or increased proportional use. Significant negative effects on the populations of live coral specialists in response to architectural simplification points to the unique and vital ecosystem services contributed by structurally complex habitats, and heralds broad-scale ecological shifts if projected dominance-transitions towards massive corals are realised under future acidification scenarios. Furthermore, as acidification may promote shifts in biogenic habitat (Milazzo et al., 2019) and food web simplification (Fabricius et al., 2014; Vizzini et al., 2017), the burden of indirect effects on those fish species with highly specialised habitat and resource use is likely to compound. Taken together, the results of this and related studies highlight the vulnerability of site-attached specialist species to acidification.

Ocean acidification did not appear to directly influence habitat association through behaviour. Habitat preference in an in situ choice experiment did not differ significantly between seep-resident *P. moluccensis* and their control counterparts under controlled conditions of equal habitat availability. Instead, fishes consistently displayed an affinity for branching corals, with the importance of structure over health underscored by significant selection of dead branching corals over live massive corals. This result aligns with previous habitat selection experiments involving larval damselfishes, including *P. moluccensis*, which have found that larvae exposed to elevated CO_2 retain species-specific habitat preferences despite impairment of olfactory discrimination (Devine et al., 2012). In the absence of evidence of a direct effect of ocean acidification on habitat selection behaviour, the plasticity displayed by *P. moluccensis* in the wild (increasing proportional use of massive corals at the seep relative to the control site) is more likely to be induced by changing habitat availability. Furthermore, as *P. moluccensis* was the only species to show a significant increase in the use of massive corals at the seep (and decrease in use of branching habitat) and as this flexibility in habitat use was nonetheless insufficient to insulate the species abundance from the negative effects of architectural simplification at the seep, we conclude that changes to dominant habitat characteristics outweigh the direct effects of acidification on damselfish habitat association.

The effect of altered habitat availability and subsequent changes to fish–habitat associations also appeared to be more influential than the direct effects of ocean acidification on other types of damselfish behaviour. Aside from an isolated increase in boldness at seep sites by a single species (*D. aruanus*), previously shown to be susceptible to the direct effects of acidification (Munday et al., 2014), the impact of elevated CO_2 at the seep did not directly alter anti-predator behaviour in the other fishes. Considering an adaptive capacity to acidification has been documented in some reef fish species, ranging from the cellular to behavioural (Rodriguez-Dominguez et al., 2019; Suresh et al., 2023), this behavioural tolerance may reflect an acclimation to chronic exposure to elevated CO_2. In contrast, our investigation of the influence of coral health on boldness for *P. moluccensis* revealed that individuals associating with dead branching corals at both the control and seep displayed heightened anti-predator behaviours relative to those found on live branching corals, becoming more fearful. This accords well with other studies that have identified live tissue cover as a key determinant of sheltering behaviour for this species, with sheltering cues lost immediately following coral mortality and long preceding any loss of structural integrity of habitats (Boström-Einarsson et al., 2018). Although individuals may retain the benefits of branching structure in this case, the cost of associating with dead corals results in the disruption of boldness behaviours, which might have ensuing implications for other behaviours such as foraging, mating and predation avoidance.

In conclusion, our findings demonstrate that assemblages of small-bodied, site-attached coral reef fishes (Pomacentridae) that are one of the more common benthic taxa on shallow reefs across the world, are responsive to changes in habitat structure induced by ocean acidification, and that this indirect effect of habitat modification seems stronger than the direct effect of elevated CO_2 on behaviour. Whether as a primary or secondary driver of habitat use, coral structure can exert a significant influence over the abundances of associated damselfish populations, with three out of five damselfishes in this study displaying significantly lower population densities in line with a diminished cover of branching structure under elevated CO_2 and the population density of the whole damselfish assemblage nearly 60% lower at the seep. In light of the ongoing, global nature of ocean acidification and its capacity to impose a considerable constraint on reef architectural complexity, this study demonstrates the power of indirect impacts associated with this environmental stressor and foreshadows broader ecological change in future oceans.

AUTHOR CONTRIBUTIONS

Ivan Nagelkerken, Philip L. Munday and Timothy Ravasi conceived the ideas and designed the methodology; Ivan Nagelkerken and Camilo M. Ferreira collected the data. Jamie Priest and Amelia Roberts analysed the data. Jamie Priest led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.np5hqc02d (Priest et al., 2024).

STATEMENT ON INCLUSION

We are grateful to the residents of Normanby Island for allowing us to conduct the study on their reefs, and to the National Research Institute, the Milne Bay Provincial Research Committee, and the Conservation and Environment Protection Authority of Papua New Guinea for relevant permits. We are indebted to Prof. Ralph Mana (University of UPNG) and to Prof. Katharina Fabricius (AIMS) for their help in realising the fieldwork. We thank the crew of the M/B Chertan for their support during the cruise.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Video stills taken from recordings of in situ fish habitat association at a seep site (a, b) and control site (c, d) in Upa Upasina, Papua New Guinea.

Figure S2. Experimental habitat choice arena consisting of a plastic aquarium tank equipped with two distinct habitat types (pictured: live massive, dead branching).

Figure S3. Stacked percentage benthic cover of coral structural categories at control and seep sites.

Figure S4. Non-metric multidimensional scaling (nMDS) plot based on a Bray-Curtis similarity matrix derived from damselfish abundance data obtained by visual census at control (10 transects) and seep (10 transects) sites at Upa-Upasina, Papua New Guinea.

Figure S5. Proportional use of (a) branching corals, (b) massive corals, (c) rubble and (d) live corals as habitat by five focal damselfish species at control and seep sites.

Table S1. Characteristic summaries for the five focal species of damselfish.

Table S2. Permutational ANOVA results showing the effects of treatment (control, seep), structure (branching, massive, rubble), health (live, dead) and their interactions on benthic cover, and their pair-wise comparisons.

Table S3. Permutational ANOVA results showing the effects of treatment (control, seep) on observed population densities of five species of damselfish, and their pair-wise comparisons.

Table S4. Permutational ANOVA results showing differences between proportional use of habitat categories by each damselfish species and random use (derived from proportional availability).

Table S5. Permutational ANOVA results showing differences between proportional use of habitat categories by each damselfish species at control versus seep sites.

Table S6. Permutational MANOVA results showing the effects of treatment (control, seep) on the proportional use of equally available habitats in a controlled in situ aquarium experiment.

Table S7. Permutational ANOVA results showing differences in proportional time spent in available habitats in a controlled experimental aquarium.

Table S8. Permutational ANOVA results showing the effects of treatment (control, seep) on observed flight initiation distance of five species of damselfish, and their pair-wise comparisons.

Table S9. Permutational ANOVA results showing the effects of treatment (control, seep) and habitat type (live branching, dead branching) on observed flight initiation distance of *Pomacentrus moluccensis*.

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