




RESEARCH ARTICLE

Can niche plasticity mediate species persistence under ocean acidification?

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Handling Editor: Jacob Allgeier**Abstract**

1. Global change stressors can modify ecological niches of species, thereby altering ecological interactions within communities and food webs. Yet, some species might take advantage of a fast-changing environment, allowing species with high niche plasticity to thrive under climate change.
2. We used natural CO₂ vents to test the effects of ocean acidification on niche modifications of a temperate rocky reef fish assemblage. We quantified three ecological niche traits (overlap, shift and breadth) across three key niche dimensions (trophic, habitat and behavioural).
3. Only one species increased its niche width along multiple niche dimensions (trophic and behavioural), shifted its niche in the remaining (habitat) was the only species to experience a highly increased density (i.e. doubling) at vents. The other three species that showed slightly increased or declining densities at vents only displayed a niche width increase in one (habitat niche) out of seven niche metrics considered. This niche modification was likely in response to habitat simplification (transition to a system dominated by turf algae) under ocean acidification.
4. We further showed that, at the vents, the less abundant fishes had a negligible competitive impact on the most abundant and common species. This species appeared to expand its niche space, overlapping with other species, which likely led to lower abundances of the latter under elevated CO₂.
5. We conclude that niche plasticity across multiple dimensions could be a potential adaptation in fishes to benefit from a changing environment in a high-CO₂ world.

KEYWORDS

behavioural plasticity, climate change, CO₂ vents, niche plasticity, ocean acidification, species interactions, stable isotopes, temperate rocky reefs

1 | INTRODUCTION

Ecosystems are being rapidly reshaped around the globe as they respond to climate change (Doney et al., 2012). The ecological niches

of species determine how organisms interact within their ecosystems and respond to environmental and ecological disturbances. Niche dynamics are characterised by more than just niche size. For example, a niche that shrinks, but shifts at the same time, can

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indicate an adaptive response to altered resource availability or quality. Niche modifications and shifts often affect relationships with other community members. Thus, community structure and dynamics can be evaluated through the quantification of fundamental ecological niche traits, such as the degree of competition (i.e. niche overlap), the use of the environmental resources (i.e. niche breadth) and whether these are flexible (i.e. niche shift). Such ecological traits are a key correlate of species adaptation to rapid environmental change (Broennimann et al., 2012) and can reveal which niche traits could allow species to best respond to changing environments and potentially adapt to new conditions.

A species' niche, as defined by the niche concept of Hutchinson (1957), considers a niche as an n -hyperm-dimensional volume, where n is the number of dimensions that compose the niche. Therefore, niche differentiation can occur along different dimensions, such as space, time, food or habitat. Incorporating multiple dimensions which best describe the species' niche, allows us to obtain a multidimensional representation of such space as well as explore the species' interactions with other community members (Geange et al., 2011). Niche multidimensionality has been used, for example, to explore the drivers of community shifts under invasions (Helsen et al., 2020), evolutionary radiation using morpho-functional traits (Tuset et al., 2018) and niche partitioning among co-occurring species (Gimenez et al., 2018). Similarly, it can be applied to understand the underlying mechanisms of adaptation to new environmental conditions for species experiencing impacts of climate change. This application is particularly useful for conservation planning and management, whose decisions are often founded on niche-based species distribution models. Traditional niche studies often focus only on one trait (niche overlap, shift or contraction/expansion) or dimension (with the diet niche being the most commonly studied). Thus, a multitrait, multidimensional niche approach can provide an overview on how climate change can impact an organism's ecological niche.

Under projected future climatic conditions, a simplification of the structure and function of coastal and shallow marine ecosystems has been predicted, with detrimental impacts on marine resources and ecosystem services (Agostini et al., 2021; Nagelkerken & Connell, 2015). Such simplification is forecasted to reduce energy flow to higher trophic levels (i.e. predators) and their top-down control (Nagelkerken et al., 2021). Carbon dioxide enrichment can act as resource for primary producers and their consumers, leading to altered food web interactions with ensuing feedbacks on the structure of the whole community (Connell et al., 2013). Direct and indirect effects of climate change can affect the fitness and performance of individuals (Clements & Hunt, 2015), which in turn can have consequences for species interactions and key ecological processes (Gilman et al., 2010), which translates to altered responses at the community level. The ecological niches of individuals are constantly adjusting in response to ongoing climate change, making niche

traits such as niche shift, expansion and overlap a powerful multilevel tool for understanding such adjustments (Coni et al., 2022; Gouraguine et al., 2019; Stuart-Smith et al., 2021). These traits can provide valuable insights into how species and communities are adapting to novel environments and conditions, the tendency towards generalist or specialist behaviours and the level of competition as a response to climate change. Furthermore, they are useful tools to understand the ecological and evolutionary mechanisms that underlie the response of species and ecosystems to climate change. They provide a deeper understanding of how organisms and communities are affected by climate change and how they are likely to respond in the future, which ultimately can be used to design effective conservation strategies.

Understanding how different dimensions (such as diet, behaviour and habitat) of a niche and its traits make species vulnerable to ecosystem disturbance is vital to predict species-specific responses to different disturbance types. For instance, by adjusting their trophic niche, and through behavioural niche shift and expansion, range-extending species can coexist with local species in novel mixed communities resulting from global warming (Coni et al., 2022; Kingsbury et al., 2020). Similarly, coral reef species that can adapt by expanding their thermal limits and utilising different habitats may have a competitive advantage amidst the ongoing habitat loss and warming caused by anthropogenic pressure (Stuart-Smith et al., 2021). Thus, to understand the factors that drive niche modification under climate change, it is important to disentangle niche trait processes (expansion, shift and overlap). It could be the combination of the different niche traits and dimensions that can drive successful adaptation, as focusing on just one trait or dimension is unlikely to provide a full understanding of their adaptive potential (see conceptual graph Figure S1). Hence, understanding how niches change or persist is a key determinant to predict the resilience of species and the mechanisms they use to adapt to changing conditions caused by climate change.

In this study, we test how ocean acidification might alter multiple niche traits across various niche dimensions in an assemblage of temperate rocky reef fishes. We investigate if it is the modification of a single, particular niche trait or dimension that drives the potential adaptability of species to the effects of elevated CO_2 , or if it is the ensemble of multiple niche traits and dimensions. We assessed three different niche dimensions for each of four fish species at natural volcanic CO_2 vents and adjacent control sites: trophic niches (based on stable isotopes and diet), habitat and behavioural niches. Changes in niche traits (breadth, shifts and overlap) were assessed, and a multidimensional hyper-volume approach was used to depict each species' ecological niche under current and future ocean acidification conditions. We show that multidimensional niche analysis provides a more detailed insight into, and better predictability of fish adaptability to ocean acidification, and enhances our understanding of the drivers of niche modification strategies among sympatric species under climate change.

2 | MATERIALS AND METHODS

2.1 | Study system

The shallow temperate rocky reef ecosystems of the volcanic island White Island (Bay of Plenty, New Zealand) represent a natural laboratory to investigate the ecological effects of ocean acidification. The CO₂ vents at the Island naturally enrich an entire benthic community. Hence, our in situ study integrated multiple interacting factors, such as habitat availability, species interactions, predation, competition, food resources and other biological factors that are difficult to reproduce in the laboratory. Two control sites that represented present-day conditions (average pH 8.05–8.10) were selected ~25 m away from the two vents sites (pH 7.82–7.88) on the northeast side of the island (Nagelkerken et al., 2021). The ocean pH levels at the subtidal volcanic CO₂ vents correspond to SSP projections of 2.6–4.5 for the end of the century (Kwiatkowski et al., 2020). The study sites featured rocky reefs characterised by medium-sized boulders, approximately 0.5–1 m in diameter, being the predominant feature of the hard-bottom benthic habitat (Nagelkerken et al., 2016). Control sites displayed crustose coralline algae (44%), turf (25%), erect calcareous algae (24%), fleshy algae (4%) and kelp (3%) (Nagelkerken et al., 2018), while the vent sites had a predominance of turf algae (54%) and displayed crustose coralline algae (15%), fleshy algae (12%), erect calcareous algae (10%), bare substratum (8%), cobbles (1%) and no kelp benthic cover (0%) (Nagelkerken et al., 2018).

2.2 | Study species

The fish species studied were selected based on their site attachment, small home range and territorial behaviour (Feary & Clements, 2006). Common triplefin *Forsterygion lapillum*, Yaldwyn's triplefin, *Notoclinops yaldwyni*, blue-eyed triplefin *Notoclinops segmentatus* and crested blenny *Parablennius laticlavius* are the most abundant benthic species at the study site (densities provided in Nagelkerken et al. (2017)). These fish species are mostly associated with turf, calcifying algae and crustose coralline algae. Specifically, the common triplefin is most frequently associated with turf (50%), the blue-eyed triplefin with crustose coralline algae (40%) and Yaldwyn's triplefin with calcifying algae (57%) (Nagelkerken et al., 2018). After settlement, they show little or no movement, thus resembling a perfect target species to investigate ocean acidification effects, as they have been exposed all their life to elevated CO₂.

2.3 | Stable isotopes

Stable isotopes are naturally occurring trophic tracers that provide information on the stability and change of feeding interactions (Fry, 2006). Biological processes can discriminate between heavy and light C and N isotopes. The ¹³C signature of a consumer may reflect that of the primary producer source that fuels the food web, while the

¹⁵N signal may be indicative of trophic level (Caut et al., 2009). Isotope ratios integrate fish feeding choices over weeks to months (Fry, 2006).

All four fish species were collected under water with hand nets and euthanised using *ike jime*. Muscle tissue was extracted and dried in an oven at 60°C to constant mass. The tissue was then pulverised in a ball mill and weighed into a tin capsule (0.5–1 mg). Samples were combusted in an elemental analyser (EuroVector, EuroEA) coupled to a mass spectrometer (Nu Instruments Horizon) at the University of Adelaide. After correction to internal standards, ratios of ¹³C/¹²C and ¹⁵N/¹⁴N were expressed in the conventional δ notation as parts per thousand deviation from international standards. A total of 251 fishes were analysed for stable isotopes (131 from control and 120 from vents) across 3 years of sampling. Initially, during the 2016 sampling period, only three fish species (common triplefin, Yaldwyn's triplefin and blue-eyed triplefin) were collected from both control and vent sites. To augment sample size and include another species, the crested blenny, additional specimens were collected at both sites in 2018 and 2019. See Table S1 for details of the sample size for each species for each year. Data from 2016, 2018 and 2019 were pooled for analysis.

2.4 | Fish diets

Stomach content analysis can provide detailed taxonomic information on prey but only represents a snapshot of prey consumption of a few hours shortly before fish collection. It thus complements the time-integrated stable isotope signatures, which instead are only able to resolve general dietary shifts. An accurate and comparable assessment of fish stomachs is made difficult by the large variability in prey size, prey digestibility and feeding periodicity across species. To fully capture the dietary niche of the fishes, we therefore employed and compared three measures of stomach contents: visual volume estimation, count and calculated biomass. For this, individuals of all four fish species were caught using hand nets over a period of 4 years (2015–2016 and 2018–2019, see Table S1 for number of replicates for each year). Stomach contents were assessed under a stereo microscope according to 19 (for volumetric analysis, years 2018–2019) or 10 prey categories (for biomass and prey count analysis, years 2015–2016), including ostracods, gastropods, tanaids, isopods, amphipods, bivalves, copepods, crabs, polychaetes, fishes, acarids, foraminifera, algae, bryozoans, eggs, chitons, hydrozoans and others. Digested items that were not identifiable were excluded from the analysis.

For the volumetric measure, the volume contribution of each prey category relative to the total stomach content was visually estimated. To obtain the measure of prey count and mass, all prey items in the stomach were first counted. Then, for each prey category, a subsample of well-preserved individuals was photographed and their mass calculated by employing length and width measures in geometrical formulas fitting the various body morphologies. The average per capita mass for each prey category was finally combined with the count to calculate total prey biomass. For all three measures (volume, count and mass), the relative contribution of each prey category to the total stomach content was used in the data analysis.

2.5 | Habitat choice

The relative microhabitat use was quantified for three triplefin species. Using free roaming visual surveys on SCUBA, a predetermined number of fish for each species was targeted (~60 common triplefins and Yaldwin's triplefins, and 30 blue-eyed triplefins) to determine relative habitat use. The microhabitat occupied and habitat orientation (horizontal, angle and vertical) was recorded during February 2018 (see Nagelkerken et al. (2018)). The microhabitat types recorded were bare rocky substratum, cobbles (~0.5–2cm in diameter), crustose coralline algae (CCA), encrusting fleshy green algae (*Codium* sp.), erect calcareous algae (largely *Amphiroa* sp.), sand and turf algae <10cm in height (largely *Gigartina* sp.). The resulting data matrix had a total of 17 different combinations of habitat and surface orientation.

2.6 | Fish behaviour

GoPro cameras were used to quantify fish behaviours in situ during 2017. Underwater cameras (GoPro) were placed on the substratum to record for a total of 30min over a period of 4 days with a minimum of two cameras per site per day (for a total of 11 recordings per site). Video recordings were analysed with the software VLC media player. The first minute was considered as acclimatisation time to the presence of the cameras, even if disturbance to the fishes was not observed. Individuals were closely followed for the first 5 min of the recording, then 10min was skipped and observations proceeded for another 5 min. The following behavioural variables were quantified from the footage: swimming, jumping, feeding, attacking and fleeing from an attack. Behaviours were expressed as rates per minute. Only behaviours recorded for a minimum of 10s were included in the analysis to avoid biases towards events performed during short periods of time.

In order to enhance our understanding of the behaviours observed in the field and to incorporate factors such as habitat choice and interspecific interactions in a controlled setting, we conducted on-board aquarium experiments in 2016 with the common triplefin and Yaldwin's triplefin. By simulating conditions representative of their natural environment within the controlled confines of the aquarium, we aimed to elucidate the extent of niche plasticity in the fish, both in isolation and during interactions with another species, while minimising the influence of other potential confounding variables. This experimental approach allowed us to complement our field observations and provide a more comprehensive understanding of the ecological responses to ocean acidification. Fishes were caught alive at control and vent sites and their habitat preference (turf vs. bare substratum), surface orientation (horizontal vs. vertical) and level of activity (swimming freely, resting at the bottom or on the aquarium wall and habitat switches) were measured in a test arena mimicking the natural rocky environment typical of the study site (see Nagelkerken et al., 2017). The rectangular aquarium was divided

into half to resemble bare and turf habitat, populated with a mixture of synthetic and live turf algae, freshly collected from both control and vents site in order to maintain visual and olfactory habitat cues and were regularly replaced. During the experiments, water was collected from the control and vent site, and mean seawater temperature and pH were maintained at $22.9 \pm 0.5^\circ\text{C}$ and 8.18 ± 0.03 units, respectively, for control experiments and $22.8 \pm 0.7^\circ\text{C}$ and 7.82 ± 0.02 units, respectively, for the elevated CO_2 experiments (Nagelkerken et al., 2017). Behaviours were recorded with a GoPro camera for 10min per replicate. The footage was analysed with VLC media player and behaviours were recorded as relative time spent performing a behaviour. The data collection and experiments were performed under animal ethics approval numbers S-2015-222 and S-2015-019 (Australia) and approved protocol # 977 (New Zealand), and according to the University of Adelaide's animal ethics guidelines.

2.7 | Data analyses

2.7.1 | Individual niche classes

Seven niche metrics were analysed across the following four niche classes: isotopic, dietary (prey volumetric contribution, count and biomass), habitat and behavioural (field vs. aquarium) niches, respectively. Each multidimensional data set of the niche classes was first reduced to two dimensions using ordination analysis for each niche class. Data were standardised, if recorded in different units, before calculating distance matrices.

A specific ordination method was employed for each niche class to best reflect the characteristics of the multidimensional data set in the reduced dimensions. Ordination of stomach content data was conducted with nonmetric multidimensional scaling (nMDS), following arcsine transformation for volumetric data, which were expressed as percentage (Paliy & Shankar, 2016) and Hellinger transformation for the other count and biomass. Jaccard distance was used for the volumetric measure (stress value=0.17) and Bray–Curtis distance for the count (stress value=0.19) and biomass measure (stress value=0.20). Behavioural data were first transformed with Hellinger transformation (Paliy & Shankar, 2016). Then, nMDS based on Bray–Curtis distance (stress value=0.11) was used for in situ observations because this method effectively handles ecological data that do not meet assumptions of linearity and normality. For the on-board experiment, PCA was applied (PCA axis 1 and PCA axis 2 together explained 69% of variation). PCA was chosen for this data set to reduce dimensionality and identify key gradients in environmental variables, which are typically more linear and normally distributed. Habitat use was finally compared among controls and CO_2 vents with a correspondence analysis (CA), as previously used for triplefin species and their microhabitat preferences (Wellenreuther et al., 2007), as recommended for non-linear responses to maximise the correspondence between species score and preferred habitat (Ramette, 2007).

The coordinates of each individual fish in the two-dimensional niche space were then used to compare niches among species and CO₂ levels. We assessed the total niche area of each species at control and vents sites, as well as the degree of overlap between treatments and among species within the same community, for each of the seven niche metrics in the four niche classes: isotopic, dietary (separate volumetric, count and biomass measures), habitat and behavioural (separate field and aquarium measures). The package 'Stable Isotope Bayesian Ellipses' was used in R (SIBER v2.1.3; Jackson et al., 2011). We used the standard Bayesian ellipses (95% confidence interval of the bivariate means) area corrected for small sample sizes (SEAc), as an indicator of niche breadth. This metric, which consider individual variability, will produce larger ellipses, for population with individuals that are widely dispersed in niche space, indicating flexibility and hence more generalist features. In contrast, populations with a narrow distribution of individuals have smaller ellipse areas, indicating a constrained niche and hence a higher degree of specialisation.

For statistical comparisons, we used the corresponding Bayesian standard ellipse areas (SEAb), which are iteration-produced, posterior probabilities (Jackson et al., 2011). Bayesian credible intervals were generated for each species and CO₂ treatment. For posterior comparisons, we assessed the probability of the SEAb of a species to be smaller at controls than at vents. To investigate potential shifts in niche use within species, we estimated the probability of control individuals to be contained within the ellipses of the same species at vents. Elliptical projections were created for each species using the posterior distribution with the function *maxLikOverlap*. We applied the correction for small sample size to the ellipses (SEAc) to minimise bias caused by data sets with small replicates. The SEAc was used to calculate the overlap between the same species at control and vents and among species within the same community. The overlap is expressed as the relative proportion shared between the two species in proportion to the total area occupied by each species (as per Equation 1).

$$\text{Overlap proportion} = \frac{\text{Overlap sp1 vs sp2}}{\text{SEA sp2} + \text{SEA sp1} - \text{Overlap sp1 vs sp2}} \quad (1)$$

Overlap values range from 0 (i.e. no overlap) to 1 (i.e. complete overlap). Niche areas which overlap by >60% are considered as sharing an ecologically significant amount of niche space (Guzzo et al., 2013; Schoener, 1968). All analyses were performed using the R Statistical Software (v4.1.2; R Core Team, 2021).

2.7.2 | Unified analysis of niche overlap among species at vents versus control

In order to incorporate the four different niche classes into a single measure of overlap, we adapted the methodology of Geange et al. (2011). This method allows to combine different types of data (e.g. categorical, continuous, elective score) into a single unified analysis of niche overlap by averaging over multiple axes. Null

model permutations tests are used to assess statistical differences. The novelty of this methodology lies in its ability to compare different niche classes even when measurements have been taken using different units of scales, through the combination of mixture models and kernel density estimations. After calculating niche overlap for each data type, it is possible to obtain unified measures of niche overlap by averaging niche overlap between species across each axis.

First, we quantified the local realised niche space for each fish species at control and vent along the four niche classes: (1) isotopes (continuous data); stomach content (continuous data); habitat association (elective score); and behaviour (continuous data) as per Geange et al. (2011). Habitat association was quantified as *Manly's Alpha* (Chesson, 1978; Manly et al., 1972), linking each individual habitat choice, to an association matrix with the percentage of habitat availability for each site (retrieved from Nagelkerken et al., 2018). The niche overlap (NO) measures how similar the niche of each pair of species (*i, j*) is, across each niche class. NO ranges from 0 to 1, for which a value of 0 indicates complete niche dissimilarity, while a value of 1 indicates complete niche similarity (perfect overlap). To obtain unified measures of niche overlap, including all niche classes, we averaged each NO between species *i* and *j* over each different axis *t* (the four niche classes). We then created unified measures of mean niche overlap and associated variance over the four niche axes, which are calculated with the following equation (Geange et al., 2011):

$$NO_{ij} = \frac{1}{T} \sum_{t=1}^T NO_{ij,t}$$

The measure of niche overlap can be interpreted as an indicator of the relationship between pairs of species. Consequently, the equation $di,j=1-NOi,j$ can be regarded as a gauge of the separation between species *i* and *j*. Higher values indicate greater dissimilarity between species. We then used nonmetric multidimensional scaling (nMDS), utilising these distance measures, to display niche relationship among the species for each treatment. Ecological significance in the unified niche overlap index was assessed applying null models with 10,000 permutations to statistically determine the overlap between species pairs at control and vent, and to define their distribution across niche space. This particular approach developed by Geange et al. (2011) accommodates individual variability and does not assume uniform behaviours among all members of a species, and it is particularly potent for assessing differences in the distribution along a niche axis among species.

2.7.3 | Intraspecific competition

Applying the conceptual model of Larocque et al. (2021), we assessed the competitive impact of community composition on species under ocean acidification. We quantified a potential interspecific competition proxy using the amount of overlap calculated in the unified analysis

of niche overlap between two species in relation to their density. Densities of fish species were retrieved from fig. 2a in Nagelkerken et al. (2017). If niche overlap among species is low, then the strength of interspecific interactions is weak, and the amount of interactions (infrequent or frequent) depends on the relative abundance of each species in relation to the species of interest. For instance, if the species of interest has a greater abundance, the other species will interact more frequently with it. Quantifying the interactive effects between species enables us to identify the most successful competitor, which could have the greatest impact on others, as well as the most vulnerable species (weak competitor) under future ocean acidification conditions.

3 | RESULTS

3.1 | Niche expansion/contraction

The isotopic niche was larger at vents than at controls for common triplefin and blue-eyed triplefin (Figure 1a, Table S2). Niche alterations based on stomach content analysis varied according to the methodology used to determine diet composition. Based on the relative volumetric contribution of prey items, the common and blue-eyed triplefins had smaller dietary niches at vents (Figure 1b, Table S2), whereas based on prey biomass and counts, the common triplefin had larger dietary niches at vents (Figure 1c,d, Table S2). Based on prey counts, the Yaldwyn's triplefin had a smaller dietary niche at the vents. The habitat niche was larger at vents for Yaldwyn's triplefin (Figure 1e, Table S2). Only the common triplefin displayed a larger behavioural niche at vents than controls, while that of the Yaldwyn's and blue-eyed triplefins remained unchanged, and that of the crested blenny decreased (Figure 1f), respectively. The common triplefin also showed an increased behavioural niche under elevated CO₂ in the absence of other species in an aquarium experiment, but a decreased niche in the presence of another triplefin species (Figure S2). Only the common triplefin demonstrated a high degree of niche plasticity expanding five out of the seven niches analysed.

3.2 | Niche shifts

The isotopic (Figure 2a), dietary (Figure 2b–d) and habitat (Figure 2e) niches shifted between controls and vents for all species for which respective data were available (overlap control versus vents for each species and each niche <60%, Table S3).

For the behavioural niche, only the crested blenny and Yaldwyn's triplefin exhibited a shift (overlap control vs. vents 23% and 53%, respectively, Table S3) between controls and vents, whereas the niche of the common triplefin and blue-eyed remained similar (overlap control vs. vents 72% and 76%, respectively; Figure 2f, Table S3). In the aquarium experiment, the common triplefin showed a shift of its behavioural niche under elevated CO₂, in the presence as well as absence of Yaldwyn's triplefins (Figure S3, Table S3). In contrast, the Yaldwyn's behavioural niche in the aquarium experiment remained

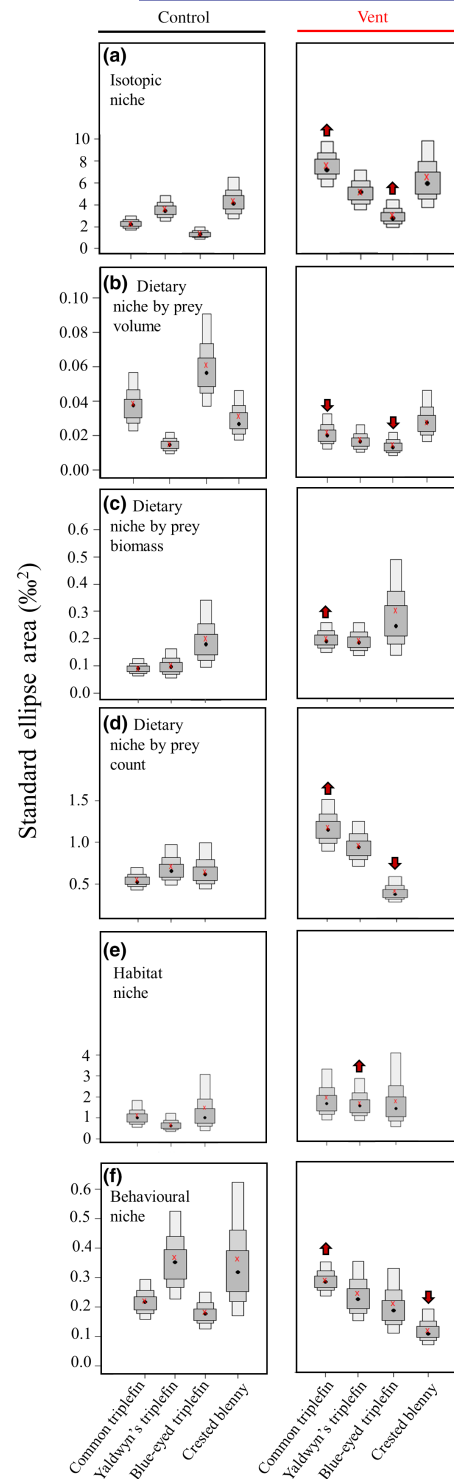


FIGURE 1 Niche breadth of various types of niche dimensions (trophic, habitat and behavioural) for four benthic fish species at controls and CO₂ vents. (a) isotopic niche based on carbon (C) and nitrogen (N) stable isotopes, dietary niche based on: (b) on prey volume, (c) prey biomass and (d) prey count, (e) habitat niche based on microhabitat use, and (f) behavioural niche based on behaviours recorded in situ (swimming, jumping, feeding, attacking and fleeing from an attack). Shown are Bayesian estimates (• = mode) with 50%, 75% and 95% credible intervals (shaded boxes) and maximum likelihood estimates (x) of SEA_c. Red arrows indicate a significant change in ellipse area from controls to CO₂ vents. See Table S2 for more statistical details.

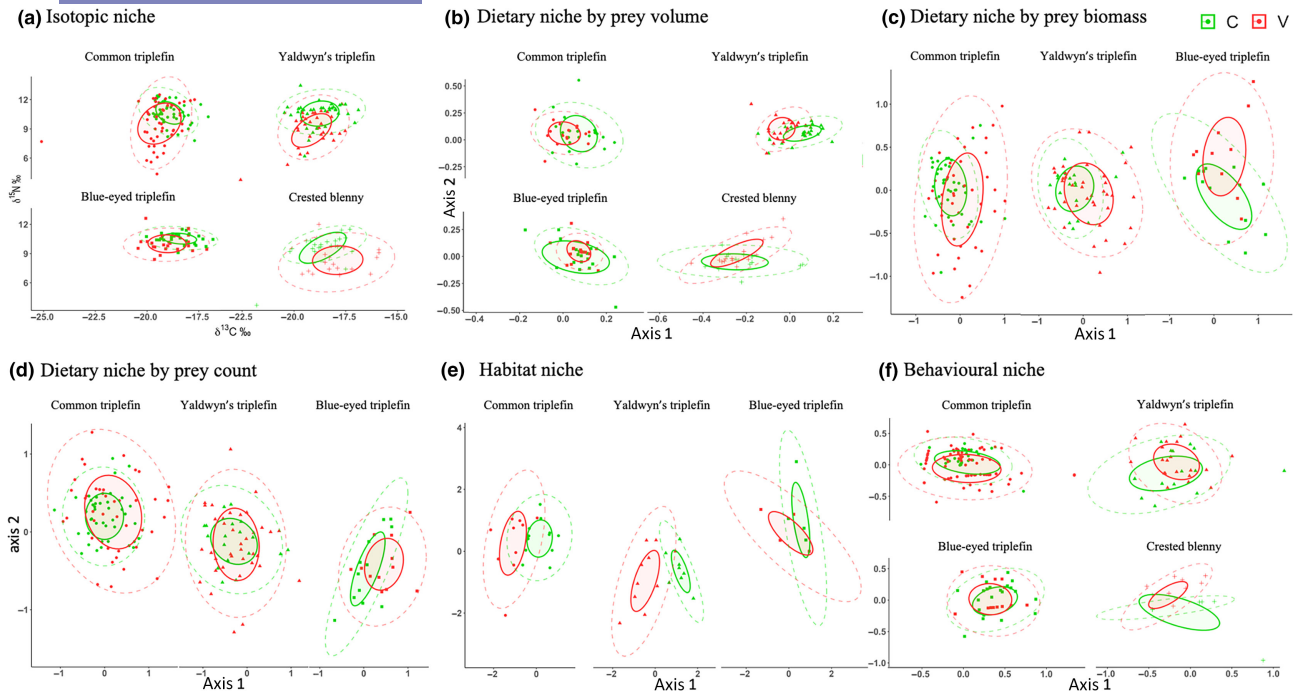


FIGURE 2 Niche space of four different niche dimensions for four fish species at controls and CO_2 vents. (a) isotopic niche based on carbon (C) and nitrogen (N) stable isotopes, dietary niche based on: (b) prey volume, (c) prey biomass and (d) prey count, (e) habitat niche based on microhabitat use, and (f) behavioural niche based on behaviours recorded in situ (swimming, jumping, feeding, attacking, fleeing from an attack). Standard ellipses areas (SEA_{40}) for each dimension were calculated from the two axes extracted from multivariate analyses, see Section 2 for each specific analysis. Ellipses including ~40% (solid line, standard ellipse) and 95% of the population (dashed line) are given for controls (green) and CO_2 vents (red). For statistical comparison, see Table S3.

unchanged across CO_2 treatment in the absence of the common triplefin, but shifted under elevated CO_2 in the presence of common triplefins (Figure S3, Table S3). Overall, all of the species shifted most of their niches, demonstrating some degree of phenotypic plasticity to changing conditions.

3.3 | Niche overlap among species

At the control site, the four species exhibited low overlap (<54%) for all niche dimensions considered, except for common triplefin and Yaldwyn's triplefin that shared 61% isotopic niche space (reflective of trophic position and carbon source) and 69% dietary niche space based on prey biomass, respectively (Table S4).

At the vents, only the crested blenny retained niche segregation with the other three species across all niche dimensions (overlap 0.05%–48%, Table S4). The other three species maintained a relatively low overlap (<30%) only in their habitat niche at the vents (Figure S4). For the trophic niches, the common triplefin and Yaldwyn's triplefin showed a relatively high overlap in their isotopic niche (65% overlap) and dietary niche based on prey volume (70% overlap). The blue-eyed triplefin showed relatively high overlap (>60%) with the common triplefin and Yaldwyn's triplefin in their dietary niche based on prey biomass and behavioural niche (Table S4). Broader niches of the common triplefin at vents increased the probability of overlap with the other species, potentially increasing the

level of competition. Only the crested blenny maintained niche segregation.

3.4 | Unified analysis of niche overlap

At the control sites, both the common triplefin and blue-eyed triplefin shared a similar unified niche space, which was significantly distinct from that of Yaldwyn's triplefin and crested blenny (Figure 3, Table 1). At the vents, however, only the crested blenny exhibited a dissimilar unified niche compared to the other three species.

3.5 | Intraspecific competition

When comparing the proportion of niche overlap with the relative abundance of species, there was an intensification in interactions at vents for three out of four species. The most abundant species (the common triplefin, Figure 4) was the least impacted by the other species, with their niche overlap increasing with only one species (Yaldwyn's triplefin), but interactions occurring at lower frequency (due to the lower abundance of Yaldwyn's triplefin) at the vents. In contrast, the two species (blue-eyed and Yaldwyn's triplefins) that were less abundant than the common triplefin experienced niche interactions with multiple species at the vents (Figures S5 and S6). Only one species (crested blenny)

maintained a low niche overlap with the other species at the vent sites (Figure S7).

4 | DISCUSSION

Ocean acidification can alter the ecological niches of fishes and modify the degree of niche overlap among them. Our unified analysis of niche overlap demonstrates how ocean acidification can reshape the multidimensional niche space of members of a fish assemblage, which may intensify competitive relationships among coexisting species. Indeed, at vents, the unified niche space of one species (Yaldwyn's triplefin) was modified to now overlap with that of two other species (common triplefin and blue-eyed triplefin). Such intensification in interactions is also demonstrated by our interspecific competition matrix, in which the two less abundant species (blue-eyed triplefin and Yaldwyn's triplefin) experienced increased niche overlap with other species at the vents. A similar scenario was, for example, found in flounders (Pleuronectidae) in the Baltic Sea, which are experiencing increased trophic overlap with estuarine species that are expanding their range due to climate change, benefitting from climate-driven higher water temperatures and declining salinity (Westerbom et al., 2018). Similarly, in the terrestrial environment, a climate-driven reduction in vegetation has increased the overlap in nesting sites of three species of co-occurring songbirds, affecting the fitness of two of the three ground nesting

species (Auer & Martin, 2013). In contrast, our most abundant species (the common triplefin), who is also the stronger competitor (Nagelkerken et al., 2017), only experienced increased niche overlap with one other species (Yaldwyn's triplefin), but because of lower abundance of the latter, the common triplefin would only experience infrequent negative interactions. Increased niche overlap under elevated CO₂ could strengthen competitive species interactions, which have previously been linked to reduced population sizes of Yaldwyn's and blue-eyed triplefins, in contrast to a population increase of the common triplefin at these vents (Nagelkerken et al., 2017). Hence, we conclude that ocean acidification can indirectly reshuffle and increase niche overlap among some species, intensifying interactions among members of a community with ensuing consequences for their population sizes.

Niche segregation or lack of resource limitation could allow for species coexistence even if niche overlap increases under climate change stressors. At vents, there was a greater degree of niche overlap among species across all niche dimensions (with the exception of habitat niche) compared to the control conditions. Stomach content composition, based on volume and biomass, revealed that all three triplefin fishes were converging their foraging towards similar prey groups at the vents, thus more strongly sharing similar food resources. It has been postulated that species that substantially overlap in any dimension of their niche space are more vulnerable to competition from other species (Hutchinson, 1957). In case of niche overlap and limited resources, such interaction could have detrimental impact if species fail to adapt and shift their niches (Human & Gordon, 1996). However, higher prey availability due to elevated CO₂, as is the case for our study sites (Nagelkerken et al., 2017), may allow coexistence between species despite significant niche overlap when resources are not limiting (Connell, 1980; Sale, 1974). The crested blenny employed a different strategy, to overcome the increasing competitive interaction, showing trophic niche differentiation with the other species at both the controls and vents. Although high prey availability may help lessen the competitive pressure between coexisting species, ocean acidification in general has the potential to intensify the interactions among species within a community. These findings suggest that ocean acidification can have complex and indirect effects on the community structure through changes in species interactions and their resource utilisation.

Indirect effects of ocean acidification, such as habitat simplification, can influence the ecological niche of species as well, thus modifying species interactions and re-structuring communities.

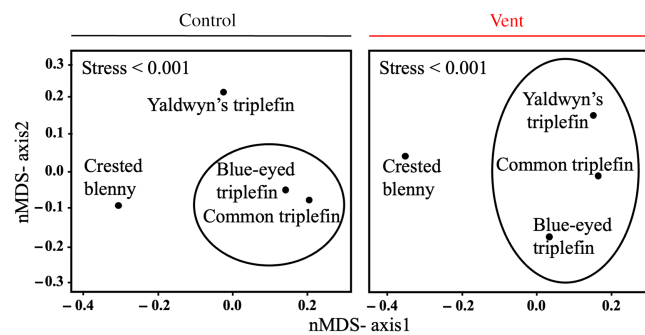


FIGURE 3 'Unified' niche overlap among four fish species incorporating habitat association (habitat electivity data, i.e. habitat use relative to habitat availability), stable isotopes, behavioural data and stomach contents. Ellipses encircle species occupying a similar niche and identified as not significantly different by a null model, as per Table 1.

TABLE 1 Mean niche overlap between the four fish species incorporating habitat association, isotopes, behavioural data and stomach content.

	Control			CO ₂ Vent		
	Blue-eyed	Common	Yaldwyn's	Blue-eyed	Common	Yaldwyn's
Blenny	0.57	0.55	0.56	0.55	0.60	0.50
Blue-eyed		0.70	0.65		0.69	0.66
Common			0.61			0.71

Note: Pairs that occupy statistically different niches, based on null model test, are in bold ($p < 0.01$).

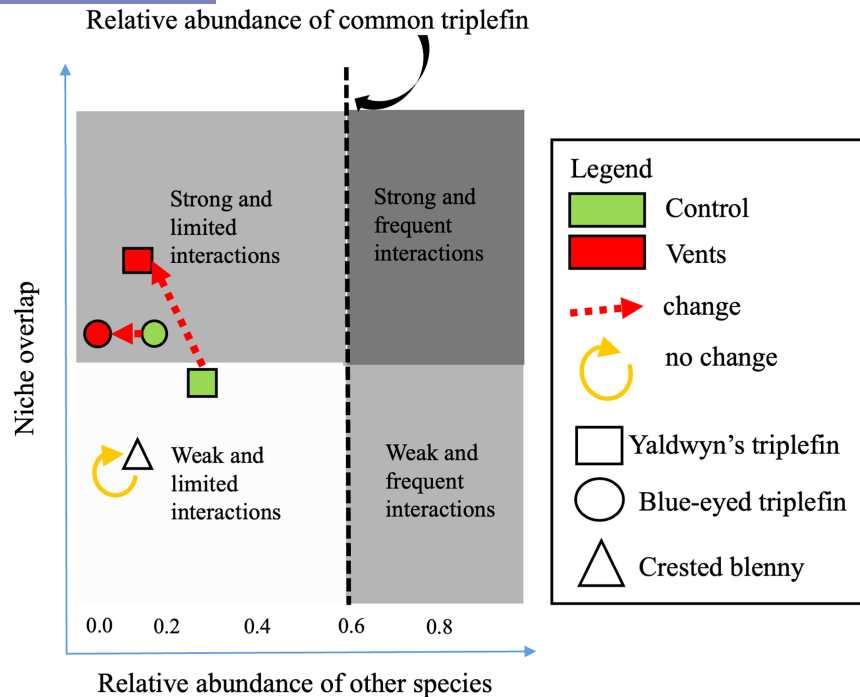


FIGURE 4 Conceptualised interspecific interaction matrix—that is, an abundance impact model based on unified niche overlap between species that capitalise on changes under high CO_2 (common triplefin) and those that do not. The grey scale indicates the potential level of impact on the common triplefin (light grey = negligible impact, medium grey = low to moderate impact and dark grey = high impact) based on the interaction strength of niche overlap (weak = overlap <60%—bottom quadrants, or strong = overlap >60%—top quadrants) and the frequency of potential interactions (infrequent or frequent) with the other species, based on the relative abundance if greater or lesser than the relative abundance of common triplefin. The relative density of the common triplefin changes from 0.6 (controls) to 0.8 (vents), but it is shown as a single vertical line as its relative abundance remains higher than the other species. The relative position of the crested blenny in relation to the common triplefin does not change between treatments.

The habitat simplification from kelp domination to turf algal domination, as observed at the vents (Nagelkerken et al., 2018), might be responsible for the observed adjustments to niche spaces, suggesting a degree of niche plasticity associated with changes in the habitat structure. At vents, the three triplefin species shifted their habitat niche, demonstrating plasticity to a changing environment and maintaining low niche overlap with the other species. Thus, the three triplefin species can maintain habitat segregation, showing different microhabitat use between controls and vents, despite a simplification of the environment. Such habitat separation might be a key mechanism to allow for long-term coexistence under elevated CO_2 . Studies on coral reef fishes have demonstrated how important is the ability to adapt resource utilisation according to changing habitat (Plass-Johnson et al., 2018). The capacity of a species to adjust their resource utilisation in response to a changing habitat is critical, especially in the context of climate change.

Due to the multiple stressors associated with climate change, it may be challenging for many species to increase the width of their niches to incorporate changing conditions. For the various niches considered, the common triplefin was the only species that experienced an increase for five out of seven niche dimensions under ocean acidification. Generalist species typically have higher flexibility of increasing their niche compared to more specialist species and are often favoured under intensifying anthropogenic pressure

(Stuart-Smith et al., 2021). This has also been observed for generalist fish species at CO_2 vents in the Mediterranean (*Gobius incognitus*, Spatafora et al., 2022) as well as in New Zealand (common triplefin, Nagelkerken et al., 2017) where these generalists were able to capitalise on the increased food resources at vents, boosting their population sizes and fitness (Nagelkerken et al., 2021). Similarly, it has been reported that thermal generalist lizard species can benefit from climate warming and efficiently exploit high-elevation cold habitats, enhancing their fitness (Chamaillé-Jammes et al., 2006; Zamora-Camacho et al., 2016). There is thus evidence from both marine and terrestrial systems that generalist species have the potential to thrive under environmental change and increase their population sizes. In contrast, other fish species at our vents experienced population decreases and/or species losses (Nagelkerken et al., 2018). Hence, under resource alteration due to climate change, having a wider niche across multiple dimensions could play a fundamental role as an adaptive mechanism for benefiting and persisting in a high- CO_2 world.

Species that show niche plasticity and adjust to changes in food resources or habitats under climate change might be more capable of avoiding strong competitive interactions. We revealed that all four fish species showed a significant degree of niche plasticity under elevated CO_2 (summary Table S5). All species showed shifts in all niche dimensions considered, except for the behavioural niche for blue-eyed

triplefin and the habitat niche for the common triplefin. These results demonstrate the potential of phenotypic plasticity for all of our species. Being able to adjust to altered dynamics and changing resources is fundamental for survival and ensuring access to resources (Fox et al., 2019). Thus, a plastic niche can maintain or increase population persistence in response to changing conditions ensuing from climate change impacts. Where conditions drive niches overlap, niche shift can be a mechanism to maintain niche segregation to enable coexistence. This is a similar mechanism used by range-extending species, which through trophic segregation can coexist with local species in novel mixed communities (Kingsbury et al., 2020). While all our fishes demonstrated adjustability of their niche under future climate, only the generalist species was able to take advantage of a changing environment, increasing its population size through an increase of niche space and niche shifts. Species with a plastic niche appear to more easily adapt to changes in resources or habitats under climate change.

In conclusion, our results show the capacity for species to alter at least some of their niches through niche modification. Yet, it is the increase in niche width (i.e. a wider use of resources) that appears to drive significant population increase of just one species, consequently creating altered interactions with other sympatric species. Moreover, species that are able to broaden their niche across multiple dimension may benefit or persist in a high-CO₂ world. Through this comprehensive analysis of niche space, across multiple dimensions and traits, we reveal potential strategies of sympatric fish species to persist in future oceans.

AUTHOR CONTRIBUTIONS

Vittoria Cipriani and Ivan Nagelkerken conceived the ideas and designed the methodology; Ivan Nagelkerken, Sean D. Connell, Silvan U. Goldenberg and Timothy Ravasi collected the data; Vittoria Cipriani analysed the data; Vittoria Cipriani and Ivan Nagelkerken 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 conflict of interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x0k6djhtq> (Cipriani et al., 2024).

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SUPPORTING INFORMATION

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

Table S1. Sample size (# individuals) for all data collected over a period of five years.

Table S2. Comparison of niche breadth between control and vent, based on standard ellipse areas for small sample sizes ($SEAc^* \cdot \%^2$) and Bayesian inference ($SEAb \cdot \%^2$) with probabilities of the posterior distribution.

Table S3. Niche conservation or shift of the same species among different treatments, based on the overlap (%) of the standard ellipses area ($SEAc$).

Table S4. Niche similarity between species within the same community (control or vents) based on the overlap of the standard ellipses area ($SEAc$).

Table S5. Summary table for niche breadth increase (red arrow) and/or shift in orientation (yellow arrow) for each species in relation from control to vent site.

Figure S1. Conceptual graph illustrating the multifaceted nature of successful adaptation, showcasing the interplay between diverse niche traits (shift, breadth and overlap) and niche dimensions (habitat, trophic and behaviour).

Figure S2. Mean standard ellipse area ($SEAc$) for common triplefin and Yaldwyn's triplefin collected at control and vents representing behavioural niche in aquarium experiment, alone and in the presence of the other species (+).

Figure S3. Behavioural niche space shift based on aquarium experiment.

Figure S4. Habitat niche space for three triplefin species based on

the combination of 7 microhabitats and three orientations in situ, at the community level.

Figure S5. Conceptualised interspecific interaction matrix–abundance impact model, based on unified niche overlap between a species that maintain niche segregation (crested blenny) and the other species of the community.

Figure S6. Conceptualised interspecific interaction matrix–abundance impact model, based on unified niche overlap between a species that is unable to capitalise on changes under high CO_2 (blue-eyed triplefin) and the other species of the community.

Figure S7. Conceptualised interspecific interaction matrix–abundance impact model, based on unified niche overlap between a species that is unable to capitalise on changes under high CO_2 (Yaldwyn's triplefin) and the other species of the community.

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