Resilience and signatures of tropicalization in protected reef fish communities

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Habitat reserves can promote ecological resilience to climate variability by supporting intact trophic webs and largebodied individuals¹⁻³. Protection may also alter community responses to long-term climate change by offering habitat for range-shifting species⁴. Here we analyse the species richness, diversity and functional traits of temperate reef fish communities over 20 years in a global warming hotspot and compare patterns in a marine reserve with nearby sites open to fishing. Species richness and diversity oscillated strongly on the decadal scale. Long-term warming signatures were also present as increasing functional trait richness and functional diversity, driven in part by a general increase in herbivores. Nevertheless, reserve sites were distinguished from fished sites by displaying: greater stability in some aspects of biodiversity; recovery of large-bodied temperate species; resistance to colonization by subtropical vagrants; and less pronounced increases in the community-averaged temperature affinity. We empirically demonstrate that protection from fishing has buffered fluctuations in biodiversity and provided resistance to the initial stages of tropicalization.

Communities protected from exploitation and other human activities are thought to possess greater resilience to climate impacts-the capacity to resist and recover from the effects of climate variability⁵. Mechanisms conferring resilience include a greater potential to buffer changes in community structure owing to higher species diversity, where a diverse community is more likely to functionally compensate if some species are lost⁵. Moreover, the set of functional traits present in reserves may differ from fished communities, including greater variety of functions, which may also enhance community resilience^{1,5,6}. Community dynamics are therefore expected to be more stable in protected versus fished communities. At the same time, longterm climate change trends are further impacting biological systems^{7,8}. Abundance and geographic shifts related to climate change are driving the tropicalization of temperate systems as species from more equatorial latitudes with relatively warmer thermal affinities replace those living closer to the poles^{9,10}. An unanswered question is whether protection from fishing will influence community resilience under the scenarios of both climate variability and ocean warming.

Empirical evidence to understand long-term climate change responses in marine reserves is limited. In particular, identity and abundance data for entire communities are scarce in rapidly warming regions. Moreover, disentangling short- and longterm biological responses requires adequate spatial and temporal replication at sites amenable for comparison of protected and fished areas. Here we take advantage of a 20-year data series initiated in 1992 of shallow reef fish abundance in temperate Australia, comprising underwater visual surveys in a marine reserve (protected) and nearby reference areas (fished)¹¹. This data set provides the unique opportunity to assess whether marine reserves facilitate resilience under environmental variability where ocean temperatures have risen over several decades (Fig. 1)¹².

We quantify changes in community structure using six metrics of richness and diversity. These include the traditional approaches of species richness and abundance-weighted diversity. Furthermore, we consider the richness and diversity of functional traits among individuals, which can illustrate new aspects of diversity^{13,14}, a unique application in the context of long-term community change. Moreover, because increasing individual body size is a welldocumented reserve effect^{15,16}, we also calculate biomass-weighted species (SDb) and functional diversity (FDb). Our functional metrics are based on ten traits representing thermal physiology, life history strategy, feeding ecology, behaviour, habitat use and geographic range breadth. For each metric, we test for differences between reserve and reference sites in mean values and patterns of variability that may reflect physical parameters associated with climate variability and long-term change (Fig. 1 and Supplementary Fig. 1 and Table 1).

Overall, mean species richness and functional richness were higher in the reserve, although not significantly so (Supplementary Table 2). Diversity values (all metrics: Fig. 2) were also comparable in reserve and reference communities. Hence, although fishing can lead to the removal of entire trophic groups and alter the complement of species present, and consequently the taxonomic and functional richness and diversity of the community⁶, we found no evidence for a difference in the variety of species or functions following the implementation of the Maria Island Marine Reserve.

However, we did detect relationships between biodiversity and climate variability. Significant fluctuations in species richness were apparent that corresponded with changes in nutrients and the Southern Oscillation index (SOI, Supplementary Table 2)—a commonly used metric for the timing of the dominant El Niño– Southern Oscillation climate mode. Abundance-weighted species diversity (SDa) and functional diversity (FDa) also fluctuated through time (Fig. 2c,d). Trends in abundance-weighted diversity therefore require careful interpretation when assessing reserve effects, as SDa and FDa were sensitive to order-of-magnitude

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Figure 1 | **Geographic and oceanographic setting of the Maria Island Marine Reserve.** The East Australian Current brings warm tropical waters polewards. Although most of the flow turns abruptly at ~32° S, a small portion continues south towards Maria Island, driving regional warming. **a**, Map showing distribution of survey sites along the eastern Tasmanian coast. Six sites were surveyed annually from 1992 to 2012 in the reserve (hatched area), whereas external reference sites fall outside reserve boundaries. **b**-**d**, Variability and trends in the SOI—an indicator of El Niño (low values) or La Niña (high values) events (**b**)—SST (**c**) and nitrate concentration (**d**), over the study period (Supplementary Methods provide details). Regression (dotted line) and 95% confidence limits (shaded) are from linear models (Supplementary Table 1).

changes in numbers of a numerically dominant species *Trachinops caudimaculatus* (for example, SDa: Supplementary Table 2 and Fig. 2). In comparison, weighting diversity measures by biomass (SDb and FDb) produced values that were less variable through time. Biomass-weighted diversity metrics more closely resembled richness patterns (Fig. 2e,f), and, even though overall biomass was higher in the reserve¹¹, indicated a similar distribution of biomass among species and functional groups in the reserve and reference communities. Our results demonstrate the value of long-term monitoring for understanding how climate cycles can influence communities following protection, but also suggest caution regarding the potential sensitivity of diversity metrics used to report community change to patterns of abundance in a single species.

Although richness and diversity values were similar in the reserve and reference sites, reserve communities displayed greater temporal stability on both annual and decadal scales. First, the magnitude of successive year-to-year changes in diversity at individual sites was lower in the reserve (significantly so for SDa, FDa and SDb; Fig. 3 and Supplementary Table S3). Second, the amplitude of the decadal oscillation in mean species richness and SDb was dampened in the reserve versus reference sites (Fig. 2 and Supplementary Table 2). Greater stability in the reserve cannot be explained by higher richness and diversity, which would be expected to increase community resilience to climate variability owing to functional redundancy (insurance hypothesis¹⁷). An alternate explanation lies in greater stability in the population abundances of species in the reserve¹⁸: the community shifted from smaller, more abundant fish to larger, less abundant fish following protection (Supplementary Fig. 3 and Table 4). In fact, the year-to-year differences in the abundance of two dominant small-bodied species

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Figure 2 | **Species and functional diversity at Maria Island over 20 years. a**-**f**, Species and functional richness (**a**,**b**), SDa and FDa (**c**,**d**) and SDb and FDb in reserve (n = 6) and reference sites (n = 6; **e**,**f**). Regression slopes (dashed lines) and 95% confidence intervals (shading) are predicted from linear mixed effects models (Supplementary Table 2). A single regression line indicates similar mean values for reserve and reference sites.

were significantly less in the reserve (Supplementary Table 3). Increased predation may limit natural cycles in abundance of prey species, essentially forming a feedback mechanism to promote stability^{18,19}. Greater short-term stability would also contribute to the long-term dampening of decadal cyclic patterns observed inside the reserve, but it is likely that long-term trends have also been facilitated by cascading changes in trophic interactions following protection^{19,20}. Our results consequently support the contention that direct and indirect effects are playing out on different timescales¹⁹, effectively increasing community resistance to both interannual climate variability and decadal-scale changes.

Resistance to climate variability was apparent in the reserve, however, increases in species and functional richness and FDb over the study period were common to both reserve and reference communities (Fig. 2 and Supplementary Table 2). Both functional metrics (functional richness and FDb) therefore tracked the warming trend (Fig. 1c and Supplementary Fig. 1), suggesting that the signature of the longer-term climate trend was more detectable in diversity metrics that incorporated functional traits, in comparison with traditional taxonomic diversity measures. However, direct comparisons of functional richness and FDb between communities are challenged because both are multimetric indices—identical values can represent different underlying trait combinations. Thus, we further analysed independent trends in species traits in the reserve and fished communities to ascertain whether increasing functional richness and diversity were underpinned by the same mechanisms.

The increases in functional richness and diversity can be partially attributed to an increase in herbivorous species over the study period. Both the proportion of herbivorous species



Figure 3 | Annual change in richness and diversity metrics. Mean $(\pm 1 \text{ s.e.m.})$ year-to-year differences in species richness (SR), functional richness (FR), SDa and FDa, and SDb and FDb in reserve (n = 6) and reference sites (n = 6) for the 20-year study period. Generalized linear mixed effects model results are in Supplementary Table 3. Values were scaled before differencing.

present in the community and biomass attributable to herbivores increased, exponentially in the case of biomass (Fig. 4 and Supplementary Fig. 4 and Table 5). This response is unlikely to be owing to a general decrease in predation intensity, as the abundance of larger fish in both the reserve and reference sites did not decline (Supplementary Fig. 3). Instead, warmingrelated poleward extension and increases in the abundance of herbivorous fish at high latitudes are expected because the digestion of algal and plant material is temperature-dependent, thereby limiting herbivorous fishes from occupying temperate latitudes where waters are relatively cold²¹. Increases in herbivores therefore seem to be an important signature of tropicalization in temperate reef communities and a potential mechanism of ecological and functional community change²².

The proportion of species with a large maximum body size also increased over the study duration, contributing to increases in functional richness and presumably FDb. However, this trend was limited to sites in the reserve where, in particular, several large-bodied carnivorous species increased following protection (Supplementary Fig. 5), leading to an increase in the mean maximum body size of species present by 2.5 cm per decade (Fig. 4b and Supplementary Fig. 4 and Table 5). Recovery of large-bodied species inside the reserve apparently represents an important response to protection, in addition to the better-documented biological responses of increasing biomass, individual body size and density in protected versus fished communities^{15,16}.

Community thermal affinity, measured as the upper realized temperature niche averaged across all species present, gradually rose, consistent with the tropicalization hypothesis (Fig. 4c). Even so, the increase in thermal affinity was not as strong in reserve sites ($0.08 \degree$ C per decade) in comparison with fished sites ($0.20 \degree$ C per decade, Supplementary Table 5) and was also lower than the rate of $0.19 \degree$ C per decade reported on the global scale for

the mean temperature preference of fisheries catch¹⁰. In fact, community thermal affinity in the reserve declined when weighted by biomass (Supplementary Fig. 4), due to the recovery of large-bodied temperate species following protection from fishing. Conversely, the steep increase in thermal affinity in the reference communities can be attributed to increasing colonization by warmwater species. An exponential increase in the abundance of some warm-water species occurred over the 20-year observation period at the reference sites (Supplementary Fig. 5). Furthermore, four range-shifting species (*Chromis hypsilepis, Heterodontus portusjacksoni, Hypoplectrodes maccullochi* and *Sphyraena novaehollandiae*: species from lower latitudes and atypical of Maria Island) were detected at reference locations, whereas none were recorded within the reserve boundary (Supplementary Fig. 5).

Hence both communities displayed an increase in herbivores, which presumably contributed to the overall increase in species and functional richness, and FDb. The reference sites, however, further displayed greater invasion by warm-water species, whereas large-bodied species increased in the reserve. These results imply an interaction between warming and recovery following from protection that has reshaped community structure and function inside the reserve.

We consider two mechanistic hypotheses for lower abundance and richness of warm-water species in the reserve. First, higher predation rates can result in biotic resistance to colonization²³. Averaged over the 20-year study period, large individuals (>25 cm) were more abundant in the reserve (by 41%) whereas small individuals (<10 cm) were less abundant (Supplementary Fig. 3 and Table 4). The potential for decreased survival of recruits, and thus colonization success, certainly exists owing to greater predation intensity inside the reserve^{24,25}. Indeed, many of the warm-water recruits that were relatively abundant in the reference locations were small in size and thus vulnerable to predation (for example, Parma microlepis, Supplementary Fig. 5). Second, biogenic habitat differences resulting from cascading effects of protection may provide different settlement cues for warm-affinity fish outside the reserve. For example, Centrostephanus rodgersii (also counted but excluded from the analyses of fish community diversity) is a range-extending urchin²⁶ that is limited from reserve communities, due to predation by lobsters, which has achieved large sizes under protection^{12,20}. However, the urchin has increased in abundance in the reference sites (Supplementary Fig. 6 and Table 6) and has overgrazed patches of the macroalgal bed. These barren patches may facilitate colonization by warm-affinity fish (invasional meltdown²⁷). Whether warm-affinity species are associated with urchin barrens presents an important line of research to advance understanding of colonization differences between the reserve and reference communities.

Intact marine communities protected from fishing buffer climate-related biological variability and resist colonization by



Figure 4 | Community-averaged functional trait values. a, Proportion of fish species that are herbivorous. **b-c**, Maximum body length (**b**) and thermal affinity (**c**) averaged across all species recorded on a survey. Regression slopes (dotted lines) and 95% confidence intervals (shading) are predicted from linear mixed effects models (Supplementary Table 5). A single regression line indicates similar mean values for reserve and reference sites.

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warm-affinity species. Although reserves may offer a suitable habitat for some species to establish and are therefore important conservation tools for habitat-limited species⁴, we add to this understanding by finding that reserves also have the potential to limit the spread of range-extending species. In the context of climate change, protected areas therefore have the potential to build community resilience through a number of mechanisms to promote species and functional stability, and resist the initial stages of tropicalization.

Methods

Field surveys. The Maria Island Marine Reserve (Tasmania, Fig. 1a) was established in 1991 along a 7 km length of coastline. Fish communities were surveyed annually from 1992 to 2012 (except 2003) using standardized visual census methods at six sites within the reserve and six external reference sites selected for their similarity¹¹. All surveys were undertaken in the austral summer to autumn (February-April) and involved recording the species, number and size class of all fish observed within 5 m of each side of a 200-m-long transect along the 5 m isobath. Size classes were in 2.5 cm increments to 15 cm, 5 cm increments from 15 cm to 40 cm and then 10 cm increments. Approximately 65% of the data were collected by N.S.B. and G.J.E., and other divers were distributed as evenly as possible between reserve and reference sites. Biomass was estimated by incorporating data on the abundance and size structure of each species on transects and species-specific coefficients for the associated length-weight relationship from FishBase²⁸. A correction factor was first applied to size data to account for bias in size estimates from divers²⁵. Furthermore, C. rodgersii were counted in 1-m-wide bands along transects at the same time as the fish surveys. These data were excluded during calculations of the diversity metrics but are reported in the Supplementary Information.

Richness and diversity calculations. Diversity is a function of species richness and how evenly species' abundances or biomass is distributed across a community. To calculate species and functional diversity we used the function divc (used to calculate Rao's quadratic entropy, Q; ref. 29), which incorporates the relative abundance (numbers of individuals) or biomass (kg) of each species per 2,000 m², using the functional diversity package in *R* (ref. 30). All values were converted to effective numbers¹⁴. For species diversity, the distances between all species were assumed to be one (where effective Q is mathematically equivalent to the inverse Simpson index), while the Gower dissimilarity matrix (converted to an ultrametric matrix using generalized least squares methods) was used for functional diversity, based on the trait matrix (described below). Furthermore, functional richness (convex hull volume, FRic; ref. 30) and the community-weighted mean trait values were calculated.

We selected ten traits: maximum body length, longitudinal range breadth, thermal affinity, trophic breadth, trophic group, water column position, diel activity pattern, gregariousness, macrophyte association and substratum preference (Supplementary Table 7). To calculate thermal affinity, we selected an upper percentile of the realized temperature distribution for each species. This statistic allows comparison of temperate species, many of which might otherwise live farther polewards but are constrained by the southern edge of the Australian continent, to subtropical species, which can fully achieve their fundamental thermal niche in Australia (Supplementary Methods). Water column position and macrophyte association contributed most of the variability in functional diversity (Supplementary Table 8).

Statistical models. We used fixed and mixed effects models fitted using maximum likelihood. Where appropriate, the random effect of site or year was included to control for variation in the response variable owing to repeated sampling. We tested for differences in community stability by modelling the oscillation in biological responses (using the sine and cosine function) and interactions between the reserve and reference sites. We also tested for a positive temporal trend (SOI and temperature increased over the study period: Fig. 1b,c). Furthermore, to explore shorter-term patterns with environmental parameters, we tested for significant relationships with oceanographic variables. Salinity was highly correlated with mean, minimum and maximum sea surface temperature (SST); silicate and nitrate were also correlated (Supplementary Fig. 1). We therefore included the following detrended physical and chemical data as predictors (year was included in all models to test for temporal trends, expected in response to warming): SOI, summer mean SST and nitrate concentration, in addition to the interaction between year and protection from fishing. The best model was selected based on Akaike information criterion, or in cases where models with different predictors had similar Akaike information criterion values we used multimodel inference to produce model-averaged parameter estimates and unconditional standard errors. The 70% confidence model set was calculated with the package MuMIn in each case, with the function model.avg, and component models reported in combination with the results summary table in the Supplementary Information where applicable. Before executing each model, we conducted collinearity diagnostics by calculating

generalized variance inflation factors for the fixed effects and excluded variables with generalized variance inflation factors values >2.5.

The model fit and residual structure were visually inspected to ensure that the test assumptions were met, and error structures (site-level variance and autocorrelation structure) were applied to normalize the residuals if required or when significant time lags were present. Alpha was adjusted to 0.025 to control for the increased probability of making a type I error.

See Supplementary Information for full methods.

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Author contributions

A.E.B., N.S.B., G.J.E. and R.D.S-S. conceived the idea for the manuscript. N.S.B., G.J.E. and others collected the fish data. A.E.B. analysed the data and drafted the manuscript with significant input from N.S.B., G.J.E. and R.D.S-S. N.J.H. and P.A.T. assisted with collating and interpreting the oceanographic data. All authors commented on manuscript drafts.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.E.B.

Competing financial interests

The authors declare no competing financial interests.