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# Contrasting Population Trajectories of Temperate Reef Fishes and Invertebrates Following Seasonal and Multi-Decadal Temperature Change

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## ABSTRACT

Temperature perturbations from climate change affect ecosystems through short-term pulse events, such as heatwaves, and chronic long-term shifts. Temperate rocky reef ecosystems have been observed to show substantial ecological change as a result of short-term temperature fluctuations, but the longer-term impacts of temperature change remain poorly understood. Here, we investigate temperate reef fishes and mobile invertebrates along Tasmania's east coast, contrasting trends in species richness, abundance, and community structure across seasons within a year to those observed over three decades of warming. Fishes exhibited dynamic seasonal shifts, but interannual changes in richness and abundance balanced out over decades with limited overall net change. In contrast, invertebrate communities changed little seasonally but suffered significant long-term losses. Our study revealed short-term ecological changes driven by temperature to be incongruent with long-term shifts. Species responded in varying ways, depending on life history and ecology. Fishes apparently tracked short temperature pulses, while less mobile invertebrates, such as echinoderms and molluscs, tolerated short-term fluctuations but exhibited long-term decline. Multi-scale studies across a broad range of taxa are needed to clarify thermal responses. The most vulnerable taxa—those facing long-term thermal stress—may be overlooked through decisions based on short-term studies, risking major biodiversity loss.

## 1 | Introduction

Accelerated warming and increased heatwave frequency are causing significant and widespread shifts in ecosystems across various spatial and temporal scales (Grimm et al. 2013; Hoegh-Guldberg and Bruno 2010; Ling and Keane 2024; Pandolfi et al. 2020; Walther 2010). To better understand how temperature will shape biodiversity in the future, a multi-scale approach is essential (Waldock et al. 2018). However, obtaining long-term, fine-resolution data across large geographic areas (i.e., decadal monitoring with extensive taxonomic resolution at regional to continental scales), despite being highly valued in science and policy (Hughes et al. 2017), is both logistically and financially challenging, often forcing a trade-off between the spatial and temporal extent of research (Lovell et al. 2023; Nathan et al. 2022; Waldock et al. 2018). As a result, our understanding of how fine-scale temperature variations contribute to long-term ecological change remains limited.

Fewer thermal refugia exist in the oceans compared to land, requiring species to either respond rapidly to temperature change by shifting their distribution, locally vanishing, or developing thermal tolerance (Antão et al. 2020; Dawson et al. 2011; Gunderson and Stillman 2015; Pinsky et al. 2019;

Sunday et al. 2011). Several investigations focusing on large-scale distributional range shifts demonstrate highly dynamic patterns to temperature fluctuations in the field, particularly for migratory species of fishes, birds and mammals (Burrows et al. 2019; Dahms and Killen 2023; Lenoir et al. 2020; Lenoir and Svenning 2015; Poloczanska et al. 2013). Acclimatization to environmental change is more challenging to observe due to the multiple interacting factors influencing adaptive processes that occur over several generations of a species. Nonetheless, evidence of thermal tolerance exists for certain macroalgae (Fernández et al. 2020; Savva et al. 2018), corals (Pandolfi et al. 2011; Rowan 2004), and reef fishes (Munday et al. 2017; Rodriguez-Dominguez et al. 2019). These studies, however, largely come from controlled experiments in aquaria that fail to account for other environmental variables and community-level impacts that occur beyond a single generation of a species. Therefore, the nature of the effects of temperature on ecological communities remains poorly understood. For large mobile invertebrates, such as echinoderms, molluscs, and crustaceans, data are scarcer (although see Fenberg et al. 2023), and recent research has indicated disproportionate population declines in rapidly warming temperate regions (Edgar et al. 2023).

Temperate rocky reefs provide essential benefits to both ocean health and human communities (Russell 2020). Nevertheless, associated species are exposed to significant risks with warming because the arrival of poleward migrating species from lower latitudes subjects local ecosystems to novel ecological stress (Blowes et al. 2019; Chaudhary et al. 2021; Cheung et al. 2009; García Molinos et al. 2015; McLean et al. 2021; Meyer et al. 2024). The addition of tropical and subtropical fauna into temperate communities intensifies competition for local resources, such as food and shelter, and can alter the balance of ecological roles within a community, with negative consequences that can compromise the integrity and functioning of these ecosystems (Verges et al. 2016; Wernberg et al. 2011). For example, recent reports have documented an alarming transformation of macroalgal forests, characteristic of temperate reefs, into barren habitats caused by widespread and accelerated urchin herbivory, extending under ocean warming and tropicalization (or 'thermophilization') (Carnell and Keough 2020; Ling and Keane 2024; Veenhof et al. 2023). This is particularly concerning given that temperate seas are warming at some of the fastest rates globally (Cheng et al. 2023; Cheng et al. 2022).

We examined changes in temperate reef biodiversity in Tasmania, Australia, along a 200 km coastline that is warming at four times the global average (Oliver et al. 2017; Oliver et al. 2018). We compared changes in community structure, abundance, and species richness of fishes and mobile invertebrates, contrasting reef community responses to seasonal temperature variation within a year with trends observed over the last 30 years of reef monitoring. Our aims were: (1) to examine how biodiversity shifts with warming and cooling within a single year by identifying reef community responses to seasonal temperature variation; (2) to identify any difference in trends between two major taxonomic groups—fishes and invertebrates; and (3) to assess whether seasonal trends are helpful in predicting long-term ecological change. We used data collected using the Reef Life Survey methods (Edgar et al. 2020; Stuart-Smith et al. 2017) and through the Australian Temperate Reef Collaboration (Edgar and Barrett 2012) (a monitoring program for understanding changes in temperate marine parks since 1992). We predicted that the broad seasonal range of temperatures experienced on temperate reefs can serve as a proxy for understanding long-term ecological change under various temperature scenarios, particularly with respect to different responses of the more mobile fishes and less mobile invertebrates.

## 2 | Materials and Methods

### 2.1 | Biodiversity Data

Fishes and mobile invertebrates were recorded through the ongoing monitoring programs of the Reef Life Survey (RLS) (Edgar et al. 2020; Reef Life Survey (RLS) 2024; Stuart-Smith et al. 2017) and Australian Temperate Reef Collaboration (ATRC) (Edgar and Barrett 2012). The seasonal data was collected using RLS methods to contribute to their broader citizen-science program, which archives data in a publicly available repository (www.reeflifesurvey.com), whereas the long-term data were from the ATRC. Both programs apply comparable underwater visual surveys along 50 m-long transect lines, where species are counted by scuba divers searching out from the transect line within a 5 m-wide block for large and conspicuous fishes and a 1 m-wide block for small and cryptic fishes. Similar to cryptic fishes, large (> 2.5 cm) mobile invertebrates are counted in 50 × 1 m blocks on both sides of the transect. Most transects (> 95%) were laid between 3 and 10 m depth. This method allows for the estimation of the abundance of most shallow-water reef fauna detectable by divers using underwater visual surveys. Common sessile organisms (e.g., mussels, oysters), smaller snails or shells (i.e., < 2.5 cm), or species that dwell in the substrate or underneath rocks (e.g., ophiuroids), which may be abundant in the reef, are not considered in the surveys given the difficulty in standardizing density estimates.

We performed surveys using this method along 200 km of Tasmanian coastline on a latitudinal gradient at eight different sites consisting of a mix of temperate habitat—including low-canopy rocky reefs to macroalgal forests, exposure to physical and oceanographic factors such as wave-exposed coasts versus sheltered embayments. Sheltered and exposed sites were considered separately in the analysis because the different habitats and food resources lead to different community structures for fishes and invertebrates. These sites were (a) Binalong Bay, (b) Bicheno, (c) Spring Beach, (d) Fortescue Bay, (e) Primrose, (f) Taroona, (g) Tinderbox, and (h) Ninepin Point (Figure 1). The first four sites, Binalong Bay, Bicheno, Spring Beach, and Fortescue Bay, are located on the east coast of Tasmania and are more directly affected by offshore swells and changes in the poleward-moving Eastern Australian Current. The reef can extend deeper than for other sites investigated, although all surveys were performed at approximately 5 m depth. The golden kelp *Ecklonia radiata* tends to form low canopies at these sites.

The other four sites—Primrose, Taroona, Tinderbox, and Ninepin Point—have a more southerly distribution, and

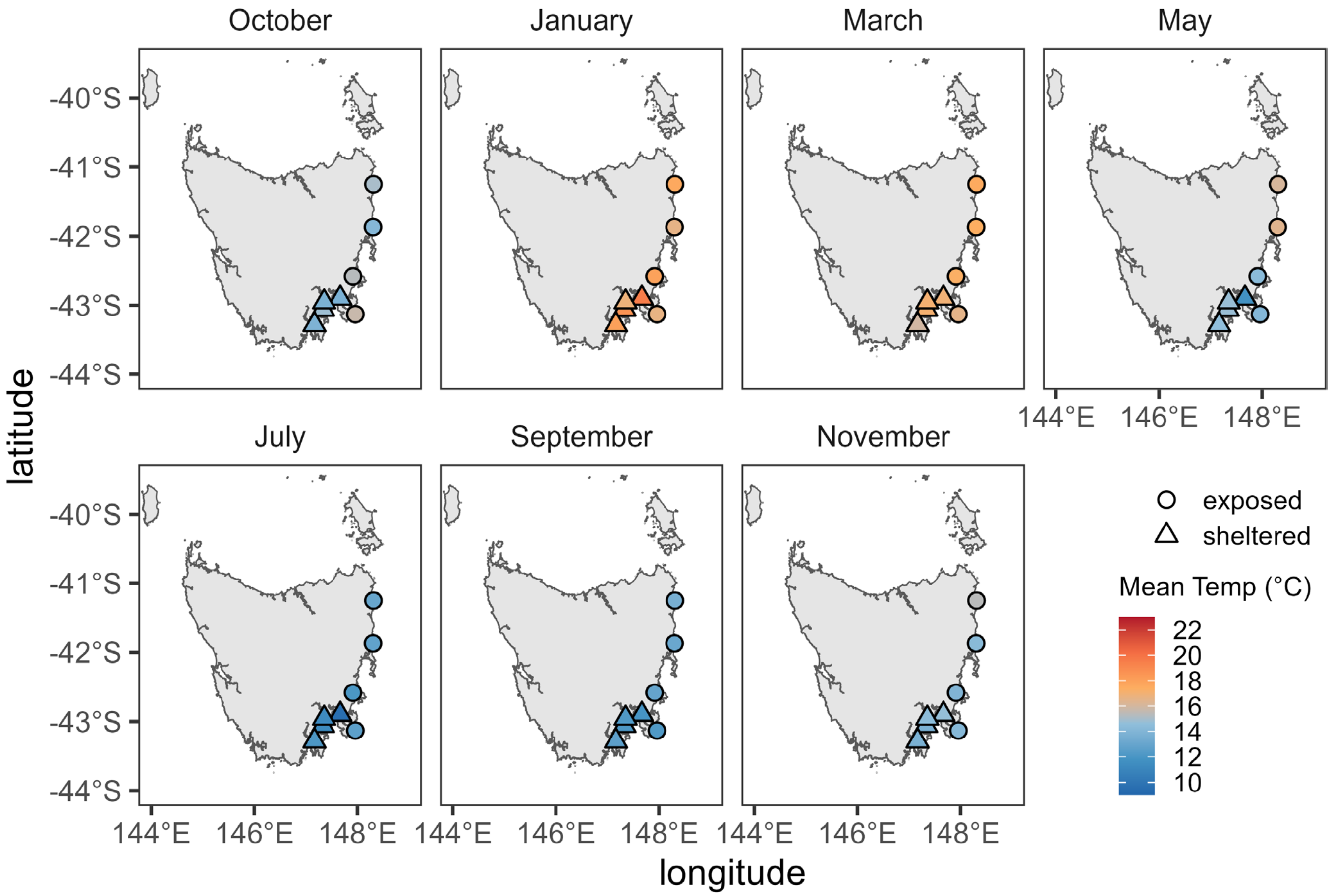

**FIGURE 1** | Seasonal temperature fluctuations across wave-exposed and sheltered sites in Tasmania (October 2022—November 2023). Study sites at wave-exposed (open circles) and sheltered (open triangles) locations ranged from 10°C to 22°C. Surveys were conducted every 2 months at each site, recording the identity and abundance of all mobile reef fauna detectable by divers using underwater visual censuses ($n = 129$) and local ocean temperatures from in situ loggers. From north to south, fished sites included in this study were: (a) Binalong Bay, (b) Bicheno, (c) Spring Beach, (d) Fortescue, (e) Primrose, (f) Taroona. Two marine reserves established in 1991 were also investigated: (g) Tinderbox and (h) Ninepin Point. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

embayment headlands tend to protect the reefs from swell (although conditions can change dramatically when the winds and swells come from the south), with less influence from the Eastern Australian Current. These sites are shallower and tend to have lower visibility as they receive more direct runoff from urbanized areas. Sponges and seaweeds in the genera *Caulerpa, Hormosira*, and *Sargassum* typically cover the substrate of the reefs. The last two sites, Tinderbox and Ninepin Point, were established as no-fishing marine reserves in 1991. For each survey, two transects were laid end-to-end or in parallel at least 10 m apart where reefs did not extend beyond 100 m lengthwise. Surveys were conducted at approximately 6-week intervals from October 2022 to November 2023, covering all seasons within a year. Abundance counts were summarized per block alongside the 50 m transect to obtain density estimates per 250 $m^2$ for conspicuous fishes and 50 $m^2$ for cryptic fishes and invertebrates, and densities were averaged per site and survey date.

Our study included a total of 170 surveyed species, representing 89 bony fishes, 33 gastropods, 13 asteroids, 8 echinoids, 8 crustaceans, 7 elasmobranchs, 3 cephalopods, 3 bivalves, 3 crinoids, 2 holothurioids, and 1 pycnogonid.

### 2.2 | Temperature Data

Sea-surface temperature (SST) for the 30 years of ATRC data preceding the seasonal surveys was obtained from the United States National Oceanographic and Atmospheric Administration's (NOAA) Coral Reef Watch program (Harris et al. 2017; NOAA 2019), which produces global daily SST values modeled at 0.05° (~5 km) raster resolution. SST was extracted from daily rasters using geographic coordinates and dates matching individual biodiversity surveys. For each survey, SST was calculated as the overall mean from the 2 years leading up to the survey date, to account for stochastic variability over long-term trends. We acknowledge that using satellite-derived SST may have its limitations for fine-scale temperature variability, particularly considering it as a proxy for benthic ecology (Smale and Wernberg 2009). Nevertheless, we consider this approach adequate for assessing decadal trends, where longer-term smoothed changes were the primary focus (and noting that all species in the surveys are closely associated with the reef substrate and likely experience the same thermal conditions at any given time).

Finer-scale temperature data were collected within a year (from October 2022—November 2023) during seasonal sampling using Electric Blue 27 mm EnvLoggers, which were placed at substrate level and left at each site recording ambient temperature every hour at 0.1° resolution. Temperature data from Fortescue Bay were obtained through Odyssey XTreem Temperature and PAR loggers, recording temperature at 0.06° resolution every hour for the period of November 2022–November 2023. Logger removal and redeployment generated temperature outliers during the period of March 2023–April 2023; consequently, in situ logger data were complemented using satellite data from NOAA to fill in missing dates through the same approach as specified above.

### 2.3 | Community Trends and Analysis

We used statistical software R (version 4.3.1) with the data.table (Dowle and Srinivasan 2023) and tidyverse (Wickham et al. 2019) packages to process the data. Multivariate analysis of community structure and trends was investigated using the vegan (Oksanen et al. 2013) package.

We performed separate analyses between seasonal (bimonthly sampling from 2022 to 2023) and decadal (yearly sampling 1992–2022) data. We used all eight sites for the seasonal analysis and included five of these sites (i.e., Bicheno, Spring Beach, Primrose, Tinderbox, and Ninepin Point), where long-term monitoring data was available for the decadal analyses.

To examine changes in community structure, we used a canonical analysis of principal components (CAP) with Bray-Curtis dissimilarities. First, we constructed community matrices separately for fishes and invertebrates, based on the assumption that these groups could respond differently to temperature due to their differences in mobility. For both groups, matrices were produced using the mean abundance from the transects conducted at the site on each sampling event. Therefore, each row in the matrix corresponds to a survey ID (i.e., the site and date the sampling was performed) and each column has the mean density from that sampling event per species. Density data was standardized using the squared root transformation to down-weight dominant or extremely rare species when calculating Bray-Curtis dissimilarities.

We used the capscale function from the vegan package to produce the CAP ordinations using the mean temperature observed at each sampling event as the constraining variable. This was used to find the axes of greatest variation in dissimilarity of community responses to temperature. This approach assists in identifying relativities between seasons in temperature-influenced variation. We then aggregated the sample scores (along the constrained axis) by averaging across sheltered and wave-exposed sites for each seasonal sampling interval and computed standard errors around the mean. We plotted these values versus the sampling date and mean temperature from each sampling event to visualize changes in community composition throughout the seasons.

Further, we tested whether changes in community composition within a year were consistent between seasons for sites of different exposure to wave actions. We used a distance-based redundancy analysis (dbRDA) including temperature as a conditioning variable and fitted the month-by-exposure interaction to determine the centroid scores across the entire ordination. We then performed a permutation test by constraining permutations by year. For both fish and invertebrate communities, the month-by-exposure term was not significant ($p = 0.265$ and $p = 0.845$, respectively), exposure was significant ($p = 0.05$ in both cases). Therefore, both groups showed different communities in exposed and sheltered sites, but differences in communities throughout the seasons were consistent for both exposure categories. This assessment supported the ordination results produced by the CAP analysis.

To calculate seasonal biodiversity changes across sites, we used abundance and richness metrics, transforming abundance counts across species by down-weighting values to the Poisson error using the 'dispweight' function from the vegan package (i.e., transformed data according to dispersion weight). These metrics are provided per 500 $\text{m}^2$ for fishes and 100 $\text{m}^2$ for invertebrates, given that each site contained two 50 m transects surveyed following the methodology described above in the Biodiversity Data section (except for Fortescue Bay, which only had one survey transect). We then used generalized additive and linear mixed-effects models (GAMM, GLMM) from the mcgv (Wood and Wood 2015) and glmmTMB (Bolker 2019) packages to evaluate trends through time (i.e., non-linear) and temperature (i.e., linear), respectively. GAMMs are semi-parametric models that incorporate smooth functions to capture non-linear relationships between predictors and the response variable. They are particularly useful for evaluating trends over time, as they allow for flexible modeling around seasonal fluctuations and are robust to issues like collinearity among predictors. In contrast, GLMMs are parametric models that assume a specific functional form for predictor-response relationships (e.g., linear), making them more appropriate when the effects of predictors such as temperature are expected to follow a predefined pattern. We performed a preliminary analysis employing GAMMs for both time and temperature and found that the effective degrees of freedom (EDF) for the latter was 1.34, indicating a lack of evidence for non-linearity. We considered exposure and site as fixed and random effects, respectively, with abundance defined under a smoothing function with $k = 5$ to prevent overfitting, $n = 56$, and a cyclic cubic regression spline with Restricted Maximum Likelihood (REML) for the GAMMs, and a Gaussian family with identity link for the GLMMs. We modeled richness (i.e., the number of different species within a site at a given date) trends the same way.

We assessed the raw data and residuals to test for spatial and temporal autocorrelation using the acf function from the stats package in R. However, given that the sites used in our analysis were approximately 100 km apart, spatial autocorrelation was unlikely to be an issue for model fits. Similarly, temporal autocorrelation was unlikely to affect the analyses given that we did not consider dates within a site as independent of each other. Our models considered sites as random factors, and dates were included within a smoother term with a cyclical regression spline to help account for non-independence across spatial and temporal factors.

For the long-term data, we followed the same steps for the CAP analysis, but instead we used generalized additive models (GAM) for all five long-term sites (Bicheno, Spring Beach, Primrose,

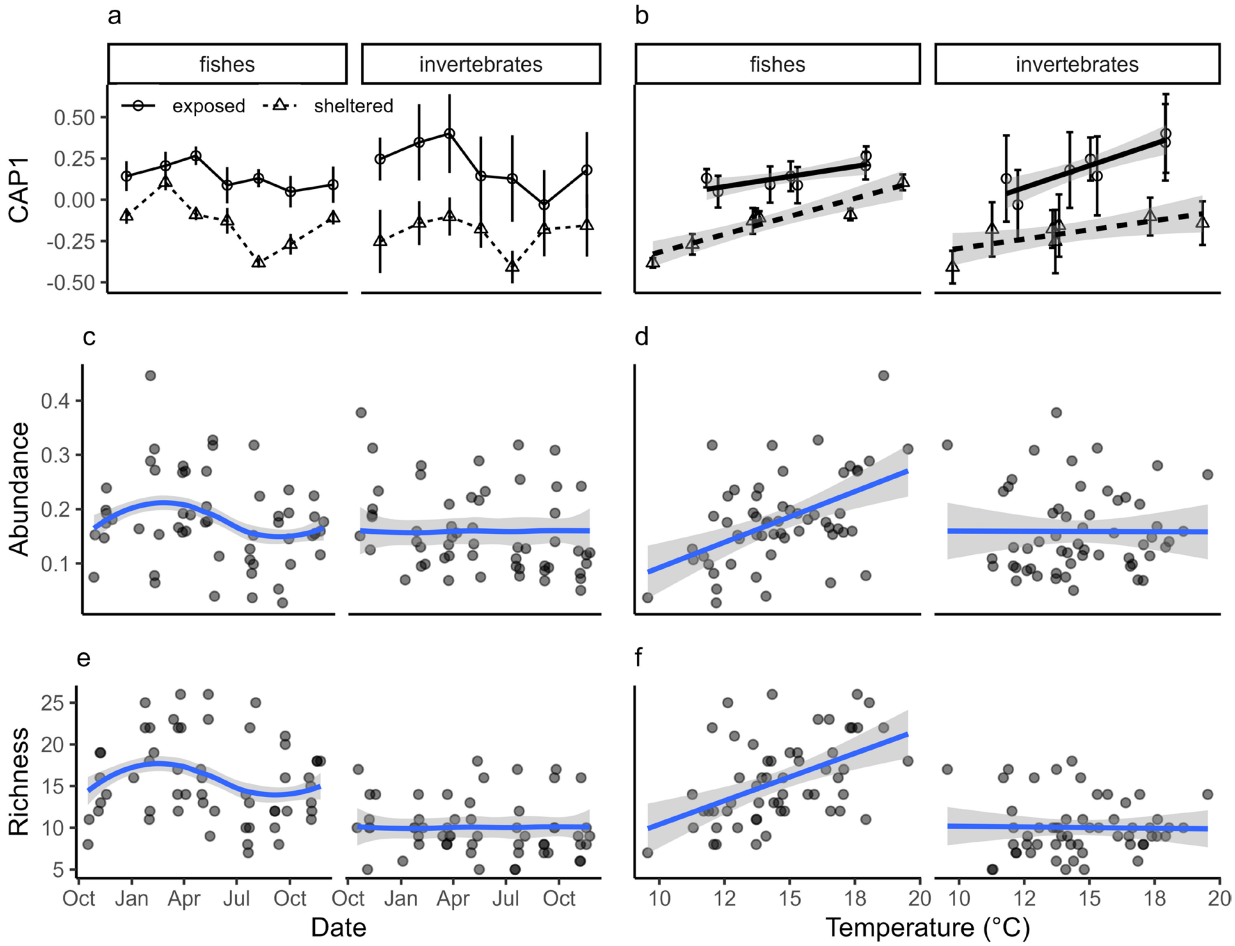

**FIGURE 2** | Seasonal biodiversity trends differed between temperate reef fish and invertebrate communities. Changes in community structure (a, b) associated with seasonal temperature change were evident using CAP with Bray-Curtis dissimilarities and temperature as a constraining variable. Sample scores were averaged for wave-exposed ($n=4$) and sheltered sites ($n=4$) with SEM (error bars). Abundances (dispersion-weighted—see methods; (c, d) and richness (number of species at each site; (e, f) were measured for each site at bimonthly intervals ($n=7$ surveys per site), showing significant seasonal cycles (a, c and e) for fishes but negligible change for invertebrates. Temperature change throughout the year (b, d and e) was positively related to biodiversity metrics for fishes but not for invertebrates. 95% confidence intervals are shaded with grey bands. Plots are partitioned into fishes ($n=76$ species) and invertebrates ($n=51$ species). Abundance and richness metrics are provided per 500 $m^2$ for fishes and 100 $m^2$ for invertebrates.

Tinderbox, and Ninepin Point) to visualize the trends in community changes with temperature and over time. While these models served to visualize changes in community structure, we relied on biodiversity metrics (i.e., abundance and richness) to quantify these changes. As above, abundances were scaled with dispersion-weighting, and richness was defined as the total number of species within a site at a given date. We used GLMMs with season (i.e., summer/winter) as a fixed effect, site as a random factor, and a Gaussian family with an identity link to examine trends in abundance and richness with temperature and over time. We did not use GAMMs for analyzing these patterns as seasonal cyclical data within a given year were unavailable; therefore, the GLMM approach seemed appropriate to adequately describe expected linear relationships without unnecessary complexity.

Lastly, we estimated the loss of species over the entire timeseries by converting density data (i.e., abundance counts) to binomial data (i.e., presence-absence). We modeled species' presence from 1992 to 2023 using a GLMM with a binomial error distribution and site as a random factor. We did this separately for fishes and invertebrates and for temperature and time, respectively.

Data and R code scripts can be found in GitHub at https://github.com/yannherfux/rls_seasonal (Herrera Fuchs 2025) (DOI: https://doi.org/10.5281/zenodo.15265389).

## 3 | Results

### 3.1 | Seasonal Biodiversity Trends

Dissimilarity amongst communities was greatest between peaks of cold and warm months (Figures 1 and 2a,b). Communities situated on wave-exposed shores (i.e., sites a–d in Figure 1) were distinct from those in sheltered embayments (i.e., sites e–h in Figure 1). Communities of fishes between sheltered and exposed sites were most similar in January, whereas invertebrate communities tended to be more similar in September, although with high variability in the data (Figure 2a). Higher temperatures, measured by in situ temperature loggers, were associated with greater overall abundances and species richness in fishes ($p<0.01$, $F=2.85$, $\mathrm{edf}=1.79$, Abundance ~ Date, GAMM; $p<0.01$,

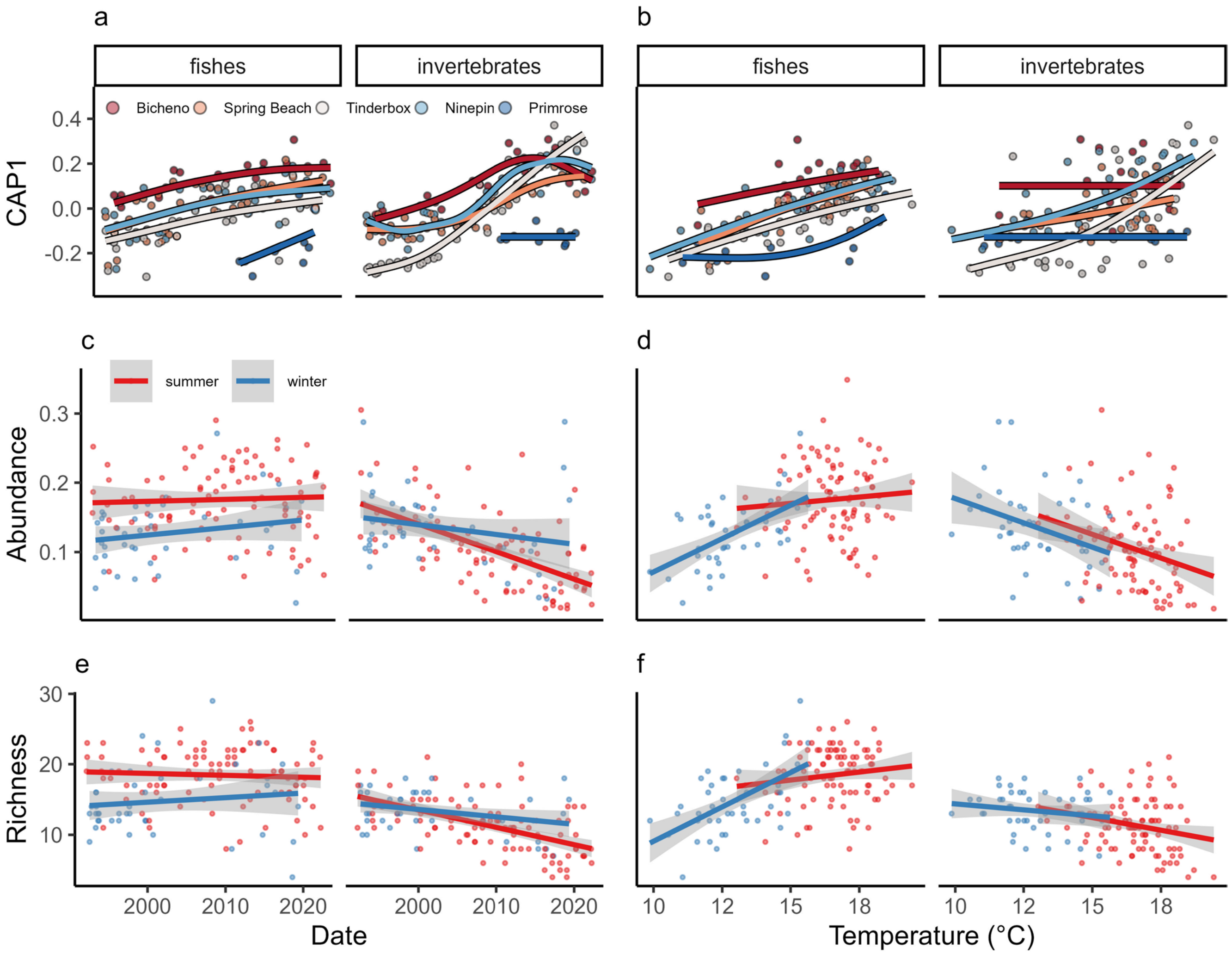

**FIGURE 3** | Decadal biodiversity trends indicate little net change in temperate reef fishes but declines in invertebrates. Changes in community structure (a, b) associated with long-term temperature change are shown with GAMs for five sites with long-term monitoring data (CAP analysis with Bray-Curtis dissimilarities and ordination constrained by temperature; sites colored red to blue from warmest to coldest mean annual temperatures). Abundance (dispersion-weighted—see methods; (c, d) and richness (number of species at each site; (e, f) are partitioned into summer (red) and winter (blue) trends, showing limited net change through time (a, c, and e) for fishes but declines for invertebrates. Biodiversity metrics were positively related to temperature (b, d, and f) for fishes but negatively related to temperature for invertebrates. 95% confidence intervals are shaded with grey bands. Plots are partitioned into fishes ($n = 96$ species) and invertebrates ($n = 74$ species). Abundance and richness metrics are provided per 500 $m^2$ for fishes and 100 $m^2$ for invertebrates.

$F = 2.74$, edf $= 1.76$, Richness ~ Date, GAMM; $p < 0.01$, $z = 4.46$, SE $= 0.04$, Abundance ~ Temperature, GLMM; $p < 0.01$, $z = 4.08$, SE $= 0.25$, Richness ~ Temperature, GLMM, Figure 2c–f), whereas invertebrates changed little in relation to temperature ($p = 0.72$, $F = 0$, edf $< 0.01$, Abundance ~ Date, GAMM; $p = 0.83$, $F = 0$, edf $< 0.01$, Richness ~ Date, GAMM; $p = 0.93$, $z = 0.09$, SE $= 0$, Abundance ~ Temperature, GLMM; $p = 0.82$, $z = 0.23$, SE $= 14$, Richness ~ Temperature, GLMM) (Figure 2c–f).

## 3.2 | Decadal Biodiversity Trends

Decadal biodiversity trends contrasted with those observed between seasons, with respect to which taxonomic group appeared to respond most strongly through time with temperature change. Invertebrates showed steady declines in abundance and richness through time, and as temperatures increased ($p < 0.01$, $z = -7.76$, SE $< 0.01$, Abundance ~ Date, GLMM; $p < 0.01$, $-8.02$, SE $< 0.01$, Richness ~ Date, GLMM; $p < 0.01$, $z = -4.28$, SE $< 0.01$, Abundance ~ Temperature, GLMM; $p = 0.01$, $z = -3.47$, SE $= 0.21$, Richness ~ Temperature, GLMM, Figure 3c–f), reflecting significant changes in invertebrate communities across all sites monitored since 2000 (Figure 3a,b). Fishes, on the other hand, displayed increased abundance and richness with warming ($p < 0.01$, $z = 2.93$, SE $< 0.01$, Abundance ~ Temperature, GLMM; $p = 0.01$, $z = 3.73$, SE $= 0.23$, Richness ~ Temperature, GLMM, Figure 3c–f), where steeper slopes were observed over three decades when considering surveys conducted in winter compared to those undertaken in summer (winter effect size $= 1.77$, summer effect size $= 0.47$); however, the net effect of the

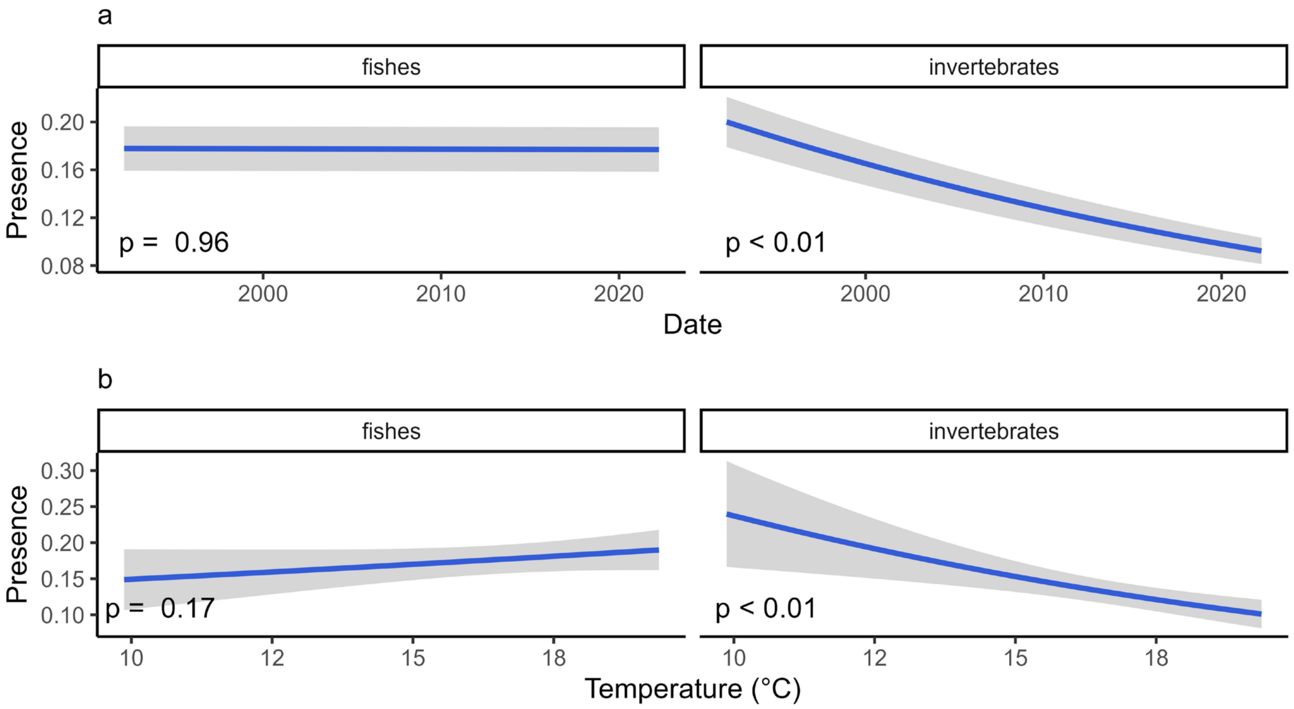

**FIGURE 4** | Long-term biodiversity loss associated with temperature change was observed for temperate reef invertebrates but not fishes. Significant declines in the likelihood of observing invertebrate species through time were associated with warmer temperatures, with 50% less probability through the last 30 years. The probability remained unchanged for fishes (a) although increases were observed with warmer temperatures, but these were non-significant (b). Presence was quantified using a GLMM with a binomial error distribution by reducing abundances to presence-absence data for each species. 95% confidence intervals are shaded in with grey bands. Plots are partitioned into fishes ($n = 96$ species) and invertebrates ($n = 74$ species). Presence is provided per 500 $m^2$ for fishes and 100 $m^2$ for invertebrates.

temperature fluctuations on the fishes through time was limited ($p = 0.22$, $z = 1.25$, SE $< 0.05$, Abundance ~ Date, GLMM; $p = 0.12$, $z = 1.57$, SE $< 0.01$, Richness ~ Date, GLMM, Figure 3c–f). In other words, although fish communities did fluctuate with temperature, little cumulative effect was apparent—losses of individuals and species tended to be balanced out by subsequent gains over the course of decades (Figure 3).

### 3.3 | Long-Term Ecological Change

We used a generalized linear mixed-shallow-watereffects model (GLMM) with a binomial error distribution to assess the likelihood of observing fishes and invertebrates with increasing temperature and time by reducing abundances to presence-absence data for each species. Significant declines were detected for invertebrates through time ($p < 0.01$, $z = -7.1$, SE $< 0.01$, Figure 4a), with ~50% less probability of observing a species towards the end of the monitoring period. This strong reduction was clearly associated with overall warmer annual mean temperatures ($p < 0.01$, $z = -3.74$, SE $= 0.03$, Figure 4b). No equivalent changes were observed for fishes over the last 30 years ($p = 0.96$, $z = -0.06$, SE $< 0.01$, Figure 4a), indicating that species were equally likely to be detected at the beginning and end of the monitoring period. The likelihood of observing fishes increased slightly with warmer temperatures, although these trends were non-significant ($p = 0.17$, $z = 1.36$, SE $= 0.02$, Figure 4b).

## 4 | Discussion

Our findings highlight diverging patterns in the temporal dynamics of temperate reef fauna following seasonal and long-term temperature change. As expected, community change was strongly associated with temperature, but our study indicates that community changes driven by short-term thermal variability do not necessarily relate to long-term ecological impacts. This suggests that conclusions drawn from short-term studies need broader ecological and taxonomic perspectives as well as better data resolution to understand potential future biodiversity trajectories along spatial and temporal gradients. For example, a reduction in species richness and abundance during warmer periods may not lead to an overall loss of biodiversity in the long term, while apparent short-term community stability could mask potential long-term biodiversity declines. Therefore, our results underscore the need for integrated multi-scale studies to gain a more comprehensive understanding of how temperature shapes reef ecosystems.

Community responses to temperature fluctuations appeared strongly associated with species' mobility and behavioral responses to thermal extremes. Fishes are generally highly dynamic, and seasonal patterns can arise from the flux of 'climate migrants' from warmer regions appearing as recruits in the warmest seasons only (Bates et al. 2014; Fredston-Hermann et al. 2020; Fredston et al. 2021; Gervais et al. 2021). Consequently, shifts in community composition can occur with new species arriving during warmer summers but potentially disappearing over winter (Figueira and Booth 2010), unless juveniles successfully survive this period during vulnerable life stages (Brodersen et al. 2011). In contrast, local species that persist in a wide range of temperatures (Moore et al. 2023; Sunday et al. 2011; Vinagre et al. 2019) may alter their activity patterns, feeding rates or show hibernation behaviours to allow persistence during periods of less favourable temperatures (Reeve et al. 2022; Speers-Roesch et al. 2018; Sunday et al. 2014). Our bimonthly sampling (i.e., every 2 months) from the same sites within the same year revealed a reduction in observed fish richness and abundance as temperatures dropped during colder months. Given very few of the studied species have migratory behaviour or switch habitats, these trends must largely relate to a reduction in activity and movement in situ and therefore occurrence on our visual surveys. The extent to which some fishes emigrated to thermal refugia remains unclear but is unlikely for the majority of species in the study area, which have very small home ranges. A reduction in fish activity during cooler winter months likely decreases predation pressure on smaller fish species, invertebrates, and macroalgae, potentially leading to different ecological dynamics (i.e., shifts in species interactions) and community composition between seasons (Speers-Roesch et al. 2018). Invertebrates, on the other hand, were more consistently recorded on surveys throughout the year, having a more limited ability to leave the study sites or alter behavior (Figure 2).

The exposure of sites to physical oceanic features versus local reef conditions was an important factor influencing the seasonal patterns observed in reef communities. During summers, the extension of the Eastern Australian Current (EAC) into Tasmania introduces warmer water and associated species to wave-exposed sites along the eastern coast (Garcia Molinos et al. 2022) (i.e., sites a– d in Figure 1). However, as temperatures drop in colder months, some species may fail to overwinter, particularly in colder southern sites where temperature differentials to the exposed sites increase. This likely explains part of the variation in community composition throughout the year. For fishes, community composition varied significantly between summer and winter, with the greatest dissimilarity observed between sheltered and exposed sites during the coldest months (Figure 2). For invertebrates, community composition at wave-exposed sites changed with summer warming, potentially influenced by the dispersal and establishment of juveniles or planktonic larvae facilitated by the EAC (Hidas et al. 2007; Suthers et al. 2011), and shifted towards the winter as the EAC retracted and the survival rate and settlement of warmer species decreased. Notably, in July, community dissimilarity was greatest in sheltered sites, where colder spells driven by local effects (shallow bays cooling overnight rather than oceanographic current changes) likely negatively impacted the survival of warm-affinity invertebrates.

Seasonal variability in fishes due to behavioral and life-history characteristics can, at least in part, also explain why they showed the opposite trend over multiple decades—that is, minimal net change. Our bimonthly surveys indicated a close association between biodiversity metrics and temperature change (Figure 2), suggesting that fishes responded more rapidly than invertebrates to short-term warming and cooling cycles, potentially conditioning them for decades of temperature fluctuations. While fish populations varied year-to-year in response to temperature, the slopes running through the last three decades of abundance and richness imply little overall net change (Figure 3). Previous studies in Tasmania showed similar oscillatory patterns amongst fish communities, species, and temperature over time, but biodiversity trends changed little in the long-term (Barrett et al. 2023; Barrett et al. 2007; Soler et al. 2022; Stuart-Smith et al. 2010). Therefore, fish communities not only demonstrate rapid adjustment to short-term seasonal variability but also dampened decadal cycles, with populations 'rebounding' as temperatures fluctuate.

Given the dynamic nature of fish populations, with abundances and richness fluctuating according to temperature, community composition likely shifted frequently, as population increases in some species compensated for declines in others. This pattern supports diversity in species' responses to thermal environments, where seasonal cycles drive frequent community restructuring, possibly enhancing functional diversity and resilience to environmental change (Walker et al. 2023). This supports the hypothesis that biologically diverse ecosystems tend towards stability (McCann 2000), as community composition will naturally be driven by competing species in a way that minimizes overlap through spatial or temporal segregation. For example, a study on estuarine fish found that species that grouped seasonally displayed asynchronous abundance fluctuations at monthly intervals, yet a constant stable trend when aggregated over time (Shimadzu et al. 2013). Well-connected protected areas can amplify this effect by supporting larger populations, preserving functional richness, and maintaining stronger asynchronous fluctuations in populations compared to areas open to extraction experiencing ocean warming (Bates et al. 2013; Benedetti-Cecchi et al. 2024; Roberts et al. 2017). However, in Tasmania, stability is perceived as minimal net change, as fish communities consistently rebounded with temperature across multiple scales, with population fluctuations balancing out over the study period, in contrast to the steady one-way trajectory observed in invertebrates.

Long-term temperature trends indicated that warming had a greater effect on fish abundance and richness during winter, suggesting that communities were generally more sensitive to thermal change in colder environments (Figure 3). Similar trends were observed for arthropods (Fitzgerald et al. 2021) and grassland ecosystems (Kreyling et al. 2019). A study in the Mediterranean predicted that the impact of winter warming on community assemblages could be four times greater than in the summer, due to thermal conditions giving rise to earlier associations amongst species and predator–prey interactions (Clark et al. 2020). Overwintering success of juvenile fishes has also been observed as a key trait underlying the tropicalization of temperate reefs, with warmer temperatures driving an increase in the density of range-expanding juveniles along the southeastern Australian coast (McCosker et al. 2022). Thus, the potential for rising winter temperatures to be of greater ecological concern than summer peaks should not be overlooked, especially since cooler temperatures during temperate winters tend to persist longer than the brief spikes of summer heat at our study sites. As fish activity increases during warmer winters, we may witness a shift in ecosystem function, with intensified competition, herbivory, and predation of smaller fishes and invertebrates, potentially reducing the recovery periods that colder seasons typically afford prey species. Further research on this topic would greatly benefit our understanding of potential long-term climate shifts.

Invertebrates, despite their short-term resistance to seasonal temperature fluctuations, declined long-term (Figures 3 and 4). Studies have shown that marine invertebrates possess adaptive strategies for coping with changing temperatures, often by modifying their metabolic functions to manage thermal stresses (Paganini et al. 2014; Pörtner and Farrell 2008; van der Walt et al. 2021). While temperate invertebrates generally exhibit wide thermal tolerances and can adapt to temporal temperature shifts, the energetic costs of these adaptations—such as reduced respiration rates at the expense of feeding—are high and may be unsustainable in the long term (Morley et al. 2014; Newell and Branch 1980). Warming in Tasmania has exceeded 1.5°C mean water temperature over the last half-century, likely contributing to a range of direct and indirect impacts on reef biodiversity. These include a widespread loss of the habitat-forming canopy kelp *Macrocystis pyrifera* and increased grazing pressure from warmer water herbivores (Edgar et al. 2023; Johnson et al. 2011). In an era of rapid global warming, conditions are potentially changing too rapidly for ecological or evolutionary adaptation. With limited mobility and no contiguous reef habitats extending further south, these invertebrate species face especially significant challenges to persist.

By examining the decadal trends in invertebrate communities, our results suggest that temperature was clearly an important driver of biodiversity change in temperate reefs over the study period, although habitat alterations due to grazing, pollution, and fishing pressure also likely increased (Worm and Lotze 2021). Primrose, the site that displayed the coldest temperatures in this study (which reaches temperatures >4°C cooler than the exposed east coast sites due to its location in a shallow sheltered embayment), remained overall unchanged in terms of invertebrate community structure, retaining an invertebrate community resembling the other sites 30 years ago (Figure 3). Primrose's local features likely offer a cool thermal habitat that still supports a relatively unchanged invertebrate community, despite pressure from additional stressors. While warmer water species occupy the site during summer months, the significant drop in temperature over winters likely favors the persistence of invertebrate species that were potentially more abundant decades ago along the rest of the Tasmanian coast. If this trend is consistent across similar sites, these areas could serve as local refugia for the recovery and restoration of invertebrate populations.

The contrast in responses between fish and invertebrate communities suggests that the effects of warming on reef biodiversity should not be generalized across taxonomic groups. In our study, the invertebrates comprised 90 species from 10 classes and 5 phyla, yet these extremely diverse groups collectively responded in a distinct way from the two classes of fishes within a single phylum. These responses were not just distinct but effectively opposite—invertebrate community metrics were negatively related to temperature over three decades of monitoring, while fish metrics were positively related (Figures 2 and 3)—at the same set of sites (i.e., which underwent the same temperature changes). The stark differences between this diverse group of invertebrates—related morphologically only by the absence of a backbone—and the fishes reveal a layer of complexity that should be addressed at finer taxonomic resolution to better understand these dynamics. Long-term marine biodiversity data tend to be highly unevenly distributed among taxa, generally best representing birds, mammals, fishes (especially those which are commercially important), and planktonic communities. Given their more mobile life histories, we hypothesize that many of these taxa would follow trajectories similar to the fishes in our study. In contrast, taxa such as macroalgae, corals, and other sessile invertebrates (e.g., sponges, bryozoans) may exhibit responses more akin to the mobile invertebrates observed here.

While common metrics like richness and abundance may appear stable over time, species turnover (i.e., changes in taxonomic composition within a community) can occur without being detected when taxonomic resolution is lacking. A study on long-term biodiversity trends across various taxonomic groups in Europe found this was true for plants, although less so for marine fishes and invertebrates (Pilotto et al. 2020). Thus, incorporating broader taxa coupled with finer taxonomic resolution in biodiversity monitoring will greatly improve our understanding of temperature-driven changes across species and communities. While our work sets up some broader possible expectations for other taxa, further research is needed to investigate and refine our understanding of taxonomic variation in long-term biodiversity changes with temperature. Our study clearly shows that the short-term trends most often reported may lead to inaccurate expectations over time.

The marine invertebrate communities we studied appear especially sensitive to warming and face a higher risk of local extinction than fishes (Johnson et al. 2025) (Figure 4), underscoring the need for targeted conservation efforts. While marine protected areas are a useful tool, their effectiveness depends on restoration strategies to ensure population recovery. Since their declaration as marine reserves, two of our study sites (Tinderbox and Ninepin Point) recovered declining populations and increased biomass in several fish species (Barrett et al. 2007; Soler et al. 2022). However, rises in rock lobster abundance, a major benthic predator, negatively impacted several other invertebrate species (Barrett et al. 2023; Barrett et al. 2009; Soler et al. 2022). Therefore, protection status alone may not lead to all desired conservation outcomes, as trade-offs from predator–prey interactions can impede certain populations from recovering. Further intervention, such as captive breeding and reintroduction programs, active removal of invasive species, capture quotas for commercial species, and habitat restoration and management, may be needed to salvage dwindling populations of the most vulnerable species. Very few conservation programs are designed specifically for threatened marine invertebrates, in part because the conservation status of most species remains largely unknown (Chen 2021). Around the world, nearly 50% of the marine invertebrate species in the IUCN Red List are categorized under ‘least concern’ and over 30% as ‘data deficient’, while much of the focus remains on tropical coral reefs (Chen 2021; Ponder et al. 2002).

Temperate reef faunas, despite their high commercial and cultural values, have historically received little conservation attention. Southern Australia and Tasmania, due to their long isolation from other major landmasses and relatively stable ocean climate over tens of millions of years, harbor a high level of endemic species with deep evolutionary histories, yet they lack proximity to potential refuges where these species could reestablish (Edgar et al. 2023). The loss of this unique biodiversity would result in a decline in essential ecosystem functions, such as water filtration, nutrient cycling, and habitat engineering, which are predominantly driven by invertebrates (Chen 2021). These functions are critical for maintaining the health and resilience of temperate reefs, especially in a warming ocean. Therefore, a decline in invertebrate populations would not only weaken these reefs' ability to support diverse marine life but also likely diminish the billions of dollars in ecosystem services generated annually, including food, recreation, and coastal protection (Russell 2020). A greater priority should be given toward the conservation of these species and their reef ecosystems, as their decline represents a significant loss to the diversity of life on Earth.

This study reveals a sharp contrast between taxa in relation to the multi-scale effects of temperature on reef ecosystems, where fishes responded dynamically but invertebrates experienced long-term declines. The findings suggest that the most responsive taxa (i.e., fishes) on short time scales may not be the most at risk, as they can adjust more rapidly to thermal fluctuations. In contrast, taxa that do not show short-term changes (i.e., invertebrates) are accumulating stress, with potential collapse that may only become apparent through long-term monitoring. We here emphasize the long-term decline of invertebrate communities in Tasmania, using a multi-scale approach across a broad range of taxonomical data, which is rare amongst the literature. Continuous monitoring is critical, but safeguarding biodiversity may also depend on proactive recovery and restoration of the most vulnerable species and habitats to sustain a more resilient environment for future generations.

## Author Contributions

**Yann Herrera Fuchs:** data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing – original draft. **Graham J. Edgar:** conceptualization, data curation, formal analysis, funding acquisition, methodology, supervision, validation, writing – review and editing. **Neville S. Barrett:** resources. **Lara Denis-Roy:** data curation, formal analysis, resources, writing – review and editing. **Shenae Y. Willis:** data curation, resources, writing – review and editing. **Hunter Forbes:** data curation, formal analysis, resources, writing – review and editing. **Rick D. Stuart-Smith:** conceptualization, formal analysis, funding acquisition, methodology, resources, supervision, validation, writing – review and editing.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15265389 and GitHub at https://github.com/yannherfux/rls_seasonal. Fish and invertebrate abundance and biomass data were obtained from the Integrated Marine Observing System (IMOS) at https://reeflifesurvey.org. Sea-surface temperatures were obtained from NOAA Coral Reef Watch Version 3.1 at https://coralreefwatch.noaa.gov/product/vs/data.php.

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