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Species' thermal ranges predict changes in reef fish community structure during 8 years of extreme temperature variation

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Abstract

Aim: To assess whether observed thermal bounds in species' latitudinal ranges (i.e., realized thermal niches) can be used to predict patterns of occurrence and abundance changes observed during a marine heatwave, relative to other important life history and functional traits.

Location: Rottnest Island, Western Australia.

Methods: A time series of standardized quantitative surveys of reef fishes spanning 8 years of pronounced ocean temperature change is used to test whether accurate predictions on shifts in species occupancy and abundance are possible using species traits.

Results: Species-level responses in occurrence and abundance were closely related to the mid-point of their realized thermal niche, more so than body size, range size or trophic level. Most of the species that disappeared from survey counts during the heatwave were characterized by geographic ranges that did not extend to latitudes with temperatures equivalent to the ocean temperature peak during the heatwave. We thus find support for the hypothesis that current distribution limits are set directly or indirectly by temperature and are highly responsive to ocean temperature variability.

Main conclusions: Our study shows that reef fish community structure can change very quickly when exposed to extreme thermal anomalies, in directions predicted from the realized thermal niche of the species present. Such predictions can thus identify species that will be most responsive to changing ocean climate. Continued warming, coupled with periodic extreme heat events, may lead to the loss of ecosystem services and ecological functions, as mobile species relocate to more hospitable climes, while less mobile species may head towards extinction.

KEYWORDS
functional traits, ocean climate, resilience, Species Temperature Index, thermal niche, warming

1 | INTRODUCTION

Temperature critically influences the physiology, behaviour, abundance and distribution of terrestrial and marine species (Brierley & Kingsford, 2009; Parmesan, 2006; Sunday, Bates, & Dulvy, 2011). Differences in species-specific thermal tolerance, life history and dispersal traits are likely to underlie variability in species' responses to climate change (Parmesan & Yohe, 2003), leading to differing abilities among species to thrive, persist or move under changing temperatures (Crozier & Hutchings, 2014). Species-specific traits along with regional variation in speed and direction of realized temperature change, or climate velocity (Burrows et al., 2014), may result in highly heterogeneous responses across species from particular locations under warming and cooling (Burrows et al., 2011; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Sunday et al., 2015). Complex changes in the structure (i.e., species present and relative abundance) of ecological communities are thus expected, which can be difficult to differentiate from changes arising from natural variation or other human pressures.

The influence of temperature on whole communities starts with the physiological responses of individuals. Theory predicts that the ability of an organism to persist (be successful in growth and reproduction for example) is diminished as temperature increases further from the optimal temperature at which aerobic scope is greatest (Pörtner & Farrell, 2008). Under long-term exposure to elevated temperatures, individuals may sometimes survive over several seasons but are typically limited by energetic constraints such that they lack the ability to reproduce and compete, leading to population decline and extirpation (i.e., local extinction). The temperature range in which a species can survive, without, for example, predatory and competitive interactions or habitat patchiness, is referred to as the "fundamental thermal niche," while the subset of this temperature range in which populations actually persist in the wild is defined as the "realized thermal niche" (Magnuson, Crowder, & Medvick, 1979). In the absence of quantitative temperature–abundance relationships, the mid-point of the realized thermal niche has been used as a measure of a species' thermal affinity, also referred to as the Species Temperature Index (STI) (Devictor et al., 2012). Species' thermal affinity has been found to relate, on average, to the temperature of maximum local abundance, across the ranges of rocky and coral reef species globally (Stuart-Smith, Edgar, Barrett, Kininmonth, & Bates, 2015).

Here, we decompose local community structural change observed in reef fishes over time into three distinct processes: immigration (range extension), extirpation and abundance change. Although any combination of these three components of community change may and probably does occur as a direct result of climate warming, local immigration (range extension) has been the best documented, particularly for marine systems (Duarte et al., 2013; Last et al., 2011; Robinson et al., 2015; Southward, Hawkins, & Burrows, 1995; Tanaka, Taino, Haraguchi, Prendergast, & Hiraoka, 2012). The large-scale evidence of range extension may be because it is relatively easy to recognize novel species at a location compared to identifying the loss of resident species.

The realized thermal niche for many common species can be parameterized by linking occurrence data derived from the growing number of biodiversity databases with remotely sensed sea surface temperatures (SST). Measures such as the mid-point and limits (5th–95th percentiles) of the sea temperatures identified from occurrence data for species sampled comprehensively across their range may provide a tool for accurate predictions of species' response to temperature variability, in comparison with general species traits or biogeographic information, such as species' zones (i.e., tropical versus subtropical). In particular, the realized thermal maxima (95th percentile of realized thermal niche) are expected to predict the extirpations of species living at the warmest edge of their range (Bates et al., 2014a; Stuart-Smith et al., 2015). Although some notable exceptions exist (Bates et al., 2014a; Devictor, Julliard, Couvet, & Jiguet, 2008; Devictor et al., 2012; Lindström, Green, Paulson, Smith, & Devictor, 2013; Tayleur et al., 2016), metrics based on the realized thermal niche have not been widely applied as a predictor of community- and species-level changes to warming, particularly in relation to extreme heat events or to predict changes in species' abundance.

Warming-related changes to reef fish communities around the Australian continent since 2005 were recently assessed, with more pronounced variation at Rottnest Island (Western Australia) than at any other location (Stuart-Smith, Edgar, Barrett et al., 2017). This change appeared directly linked to anomalous ocean warming and was observed in both coral and rocky reef habitats. In the austral summer of 2010/2011, record high ocean temperatures were recorded along the coast of Western Australia (WA), an event that became known as the 2010/2011 marine heatwave (Pearce et al., 2011). At the peak of warming between the end of February and beginning of March 2011, anomalies recorded in the surface mixed layer of the ocean were ~5°C above the monthly mean for nearshore waters (Pearce & Feng, 2013). Ecological impacts of the marine heatwave were documented by Smale and Wernberg (2013), who recorded a range contraction in the habitat-forming seaweed *Scytothalia dorycarpa* at its warm distributional limit of approximately 100 km or around 5% of its global distribution, with potential flow-on effects for those species associated with this seaweed (Wernberg et al., 2016). Large-scale fish kills were also recorded, as well as temporary southward range shifts of pelagic megafauna, such as whale sharks and manta rays (Pearce & Feng, 2013).

Quantifying the magnitude and scale of change in reef community structure (abundance and occupancy) following exposure to the marine heatwave provides a valuable opportunity to identify the underlying mechanisms by which warming influences whole communities. We used quantitative data from annual subtidal reef fish surveys at Rottnest Island using standardized Reef Life Survey (www.reeflifesurvey.com) methods between 2008 and 2015. We first aimed to investigate changes in the structure of the entire fish community, using the Community Temperature Index (CTI) (the average STI across all species present).

Second, to test whether particular characteristics of species make them more likely to shift in geographic range or change in local abundance as a result of warming, we identified a number of functional and life history traits that are useful predictors of marine species geographic range extensions (Sunday et al., 2015). These traits may also relate to warming-related fluctuations in abundance, given abundance changes form an important part of range extension and population growth at newly settled range edges (Bates et al., 2014b; Mair et al., 2014). We thus ranked the importance of the realized thermal niche as a species-level trait against other functional and

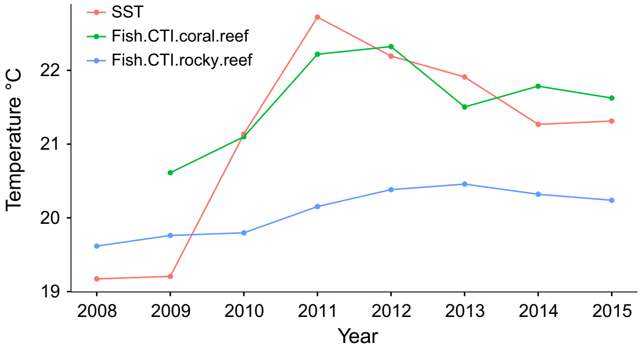

FIGURE 1 Sea surface temperature (SST) at Rottnest Island from 2008 to 2015, including the 2011 marine heatwave, and associated Community Thermal Index (CTI) trends for reef fishes on rocky and coral reef habitats. CTI represents the mean of the Species Temperature Index for all species recorded in a survey and is presented here as the mean across all surveys in each habitat each year. SST represents the mean of the 2 weeks prior to each survey date, recorded by the Integrated Marine Observing System buoy at Rottnest Island (https://portal.aodn.org.au) [Colour figure can be viewed at wileyonlinelibrary.com]

life history traits in predicting species responses to environmental warming and cooling trends.

Third, we investigated how the three proximate drivers of community structure change (immigration, extirpation and abundance changes) related to ocean temperature variability. Specifically, we tested the following predictions related to the shifts in occupancy and abundance of species before and following an extreme heat event:

1. Species moving into the community during the heatwave (climate immigrants) will have relatively warmer realized thermal niches than species already present (i.e., novel community members during the warming period represented range shifts of species with warmer affinity),
2. Extirpation (at least temporarily) will be more prevalent among species for which the temperature exceeds their current realized upper thermal limit (i.e., the 95th percentile of the warmest monthly SST values obtained from long-term climatology and observed across all occurrence locations; Stuart-Smith, Edgar, & Bates, 2017) and
3. Local increases or decreases in the abundance of species during warming and cooling periods can be predicted by their realized thermal niche.

2 | METHODS

2.1 | Field data on reef fish communities

Annual monitoring data were collected at Rottnest Island located 18 km west of Fremantle, Western Australia (−32.00 S, 115.52 E), by Reef Life Survey (RLS) divers in July 2008 and in May each year thereafter up to 2015. During underwater visual censuses (UVC), abundances and size classes of all fishes observed along transects were recorded to species level in duplicate 5-m-wide blocks either side of a 50-m transect line, laid along a depth contour over rocky or coral reef. Transect depths ranged between 2.5 and 10 m. There is no thermocline present within this depth range among these sites. Detailed methods can be found in an online methods manual (www.reeflifesurvey.com) and in Edgar and Stuart-Smith (2014). Multiple transects were surveyed at each reef site (mean: 2.9 ± 0.1 transects per site), with the number of sites surveyed also varying between years due to weather conditions preventing access to particular sites (mean 13.5 sites per year). Species' abundance in a given year was calculated as the mean density per 500 m^2 transect, with these data log-transformed (x + 1). A single site with coral reef habitat (Pocillopora Reef) was treated separately from kelp-dominated rocky reef habitat in order to identify possible differences in community structure between habitats and account for preferential recruitment of warmer water species to coral habitat.

Field survey data that form the basis of the Rottnest Island time-series analysis in this article are available for download from the Reef Life Survey Data Portal, accessed through https://reeflifesurvey.com.

2.2 | Sea surface temperature data

Sea surface temperature (SST) data collected by the Integrated Marine Observing System buoy at Rottnest Island were downloaded for the 2 weeks prior to the survey period from Australian Ocean Data Network data portal (https://portal.aodn.org.au). Average SST over these 2-week periods showed a clear multiyear footprint of the heatwave, but not as a single warm event. Progressively warmer temperatures occurred during the survey period each year from 2008 to 2011, SST remaining high in 2012 then cooling in subsequent years (Figure 1).

2.3 | Thermal niche and CTI parameterization

For each fish species recorded at Rottnest Island over the study period, we extracted the mid-point (STI) and 95th percentile of the realized thermal niche from a larger dataset reported in Stuart-Smith et al. (2015). The temperatures occupied by each species were estimated by matching local, long-term mean annual SST values to georeferenced species occurrence records for the global RLS dataset, supplemented with data from the Global Biodiversity Information Facility (www.gbif.org).

All of the Rottnest Island species have been comprehensively sampled by Reef Life Survey across their entire geographic ranges, with patterns in species limits presented in Stuart-Smith, Edgar, & Bates, 2017, and distribution patterns visible on the *Reef Species of the World* database of the RLS website (https://reeflifesurvey.com). We calculated the Community Temperature Index (CTI), as the average STI for all species recorded on transects on reefs located around Rottnest Island, weighted by their log (x + 1) abundance. CTI was

TABLE 1 Species' categories based on the presence–absence on reef surveys during the study period ($n = 148$ species)

Category	Criterion	Occurrence type	Prediction of species' thermal affinity
1	First occurred during the heatwave peak (2011 and/or 2012), but did not persist	Warming immigrant	Warmest
2	First appeared during the heatwave (2011 and/or 2012) and persisted (occurring in at least 1 year from 2013 to 2015)	Warming immigrant	Warm
3	Recorded in at least 1 year before heatwave, in 2011 or 2012, and at least 1 year after 2012	Present throughout	Moderate
4	Present before the heatwave (2008–2010) and after (2013–2015), but not in 2011/2012	Extirpated	Cool
5	Present before heatwave (2008–2010) but not subsequently	Extirpated	Coolest

used to describe SST-related structural change in the reef community for 2008–2015 (Figure 1).

2.4 | Categorization of species and time periods

Temporal trends in SST over the study period allowed division of survey years into warming (2008–2010), the heatwave (2011–2012) and post-heatwave cooling (2013–2015) periods. Species occurrences across these periods were used to distinguish warming immigrants and those extirpated, as distinct from other species that with temporal occurrence patterns unrelated to the heatwave. Five groups of species were identified (Table 1), and for each, we made a priori predictions of their relative thermal affinities based on rapid warming a driver (Table 1).

Abundance changes were also assessed, using mean log-transformed densities per 500-m^2 transect at sites where each species was recorded. The difference in abundance of each species between the warmest year (2011) and their mean abundance across the preceding 3 years (2008–2010) was used to indicate whether an increase or decrease in abundance occurred during the warming event. Additionally, to detect change in species' abundance related to a return to cooler temperatures, we calculated the difference between the maximum abundance in the warmest 3 years and their abundance at the end of the study (2015). There were 40 of 148 species for which abundance change could not be calculated using the above methods, and which were excluded from this particular analysis. The above occurrence analysis focussed on changes in species presence during warming and cooling periods, but this

TABLE 2 Several traits of reef fishes were identified with the potential to predict species' responses to warming

Trait	Explanation/hypothesis
Thermal affinity[b]	The mid-point of a species' realized thermal range. Ecological performance and occurrence may potentially change with changing temperatures
Range size[b]	Estimate of the geographic range extent of species determined from occurrences in the RLS database. Species with large ranges may be more likely to extend their ranges fastest due to fewer range limiting interactions and greater ecological versatility (Sunday et al., 2015)
Body size[a,c]	Maximum total length. Home range size can be positively correlated to body size (Kramer & Chapman, 1999), and body size is positively correlated to fecundity; therefore, species with larger maximum total length may extend their ranges more readily through adult movement and propagule pressure
Trophic level[a]	Mean TL. Lower trophic levels may be dependent on fewer trophic links to successfully establish in different ecosystems within newly expanded range (Sunday et al., 2015). Higher trophic levels are associated with larger body sizes and possibly potential to survive through periods of adverse environmental conditions (Trillmich & Limberger, 1985)
Trophic breadth[c]	The number of prey phyla recorded in dietary studies. Species with less specific prey requirements may be less constrained by prey availability and thus more likely to extend their range or increase in abundance when the composition of available prey varies
Frequency in range[b]	The proportion of sites a species has been recorded out of all those surveyed across its entire geographic range, calculated using the global RLS database. (1) More frequently occurring species may be more likely to spread to new locations on the edge of their range. (2) Less frequently occurring species may be inadequately sampled to detect trends related to warming
Global mean abundance[b]	Mean density per 500 m^2 across all surveys on which the species has been recorded in the RLS database. (1) Species typically found in high abundance may be more likely to spread to new locations at the edge of their range. (2) Species typically found in low abundances (rare species) are less likely to be sampled sufficiently for trends in abundance to be reliably quantified

Species-specific trait data were obtained from: [a]FishBase (http://www.fishbase.org/), [b]Reef Life Survey species profiles (http://www.reeflifesurvey.com/) and [c]published literature (Stuart-Smith et al., 2013, 2015).

abundance change analysis aimed to assess changes in local densities of species which were found more consistently throughout either warming or cooling periods. It relied on records in more than 1 year in each of these periods, and these 40 species did not satisfy this requirement.

2.5 | Species traits

Traits of particular importance for reef fishes include geographic range size, body size, trophic level and trophic specialization (Angert et al., 2011; Perry, Low, Ellis, & Reynolds, 2005; Sunday et al., 2015); Table 2). In addition, species' inherent commonness/rarity may also be important in influencing the likelihood of range shifts occurring or the magnitude of abundance changes, and also in influencing the probability of detecting species on underwater surveys (i.e., sampling adequacy). Therefore, we included two traits previously unassessed for marine species in this context: the frequency of occurrence and mean abundance, both calculated on the basis of RLS surveys across the entire global range of each species (as opposed to the study location). Range size was calculated as an index combining latitudinal and longitudinal extents, weighted by the density of presence records and corrected for global variation in the linear distances represented by one degree of longitude:

$$\sqrt{(d_\mathrm{v}\,\mathrm{stdev(Lat)})^2+(d_\mathrm{h}\,\mathrm{stdev(Long)})^2}$$

where d_v and d_h are the distances (in km) of one degree of latitude and longitude at the mid-point of a species' range, respectively, and stdev(Lat) and stdev(Long) are the standard deviations of the latitude and longitude in degrees of all occurrence locations for that species.

2.6 | Relationships between traits and warming immigrants and extirpated species

We used random forest (RF) modelling to assess the relative importance of traits in distinguishing between species classified within each of the five occurrence categories. We selected 10,000 trees with a correlation threshold of 0.5. RF provides high classification accuracy, an associated confidence measure %IncMSE (Breiman, 2001; Cutler et al., 2007), and, importantly, is suitable for handling correlated predictors. The RF analysis was run in R v3.2.3 (R Core Team, 2015) using the package RANDOMFOREST (Liaw & Wiener, 2002). Boxplots were used to examine the distribution of trait values among species in each category, separately for rocky and coral reef habitats, for those traits identified as of greatest importance in predicting group membership. Linear modelling (LM) with category (five levels) treated as a fixed factor was used to test for differences in mean STI values between categories, as run in R using the NLME package (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2016). Some categories in the coral habitat contained too few species to include habitat as an additional fixed factor to test for significance of habitat type. Sample size (the number of species) in each category between rocky and coral habitat was unequal; hence, data from both habitats were combined for the linear model and habitat excluded as a factor.

2.7 | Relationships between traits and trends in abundance

The most important traits identified by the RFs were then used as covariates in generalized additive modelling (GAM) of abundance trends of species using the NLME package in R (Hastie, 2015). Spline fits to the GAM model were added for smoothing, given the likelihood that relationships were not linear (Hastie & Tibshirani, 1995). Linear fits were applied in both warming and cooling abundance change models, and generalized least squares (GLS) linear models were used for final analyses of abundance changes with the function scale provided by the NLME package (Pinheiro et al., 2016). The scale and centre function for data transformation was used to allow direct comparison of coefficients among the traits. Separate analyses were run for warming and cooling time periods.

3 | RESULTS

3.1 | Community-level trends

Community Temperature Index of fishes in the coral reef habitat followed SST temperature changes closely, showing high community sensitivity to SST and negligible lag time. Fishes on rocky reef habitat, the predominant subtidal reef habitat around Rottnest Island, also followed the SST trend, albeit with less change and a 1- to 2-year lag (Figure 1).

3.2 | Immigration and extirpation

Among the variables tested, the random forest (RF) analysis ranked thermal affinity (Species Temperature Index, STI) as the most important trait in determining which of the five categories each species belonged to, based on species occupancy and abundance response to the heatwave (Figure 2a). Species in the groups representing warming immigrants (categories 1 and 2, Table 1) had warmer affinities in comparison with species that disappeared from surveys as a result of the heatwave ("extirpated"; categories 4 and 5, Table 1). The distributions of STI values among species within each category reveal similar affinities of species recorded on coral and rocky reef habitats, although a much warmer subset of coral-associated species recruited during the heatwave and persisted (category 2; Figure 2b). This group of species are all from much warmer locations, with distributions centred on locations where SST is more than 2.5°C warmer than the temperature at Rottnest during the warmest years of the study. There was no difference in the mean STI values of species in category 1 compared to category 2 (warming immigrants), but both categories contained mean STI values significantly higher than categories 3, 4 and 5 (species found throughout study period, those extirpated during but found post-heatwave and those extirpated and not recorded post-heatwave) ($p < .01$ Figure 2b).

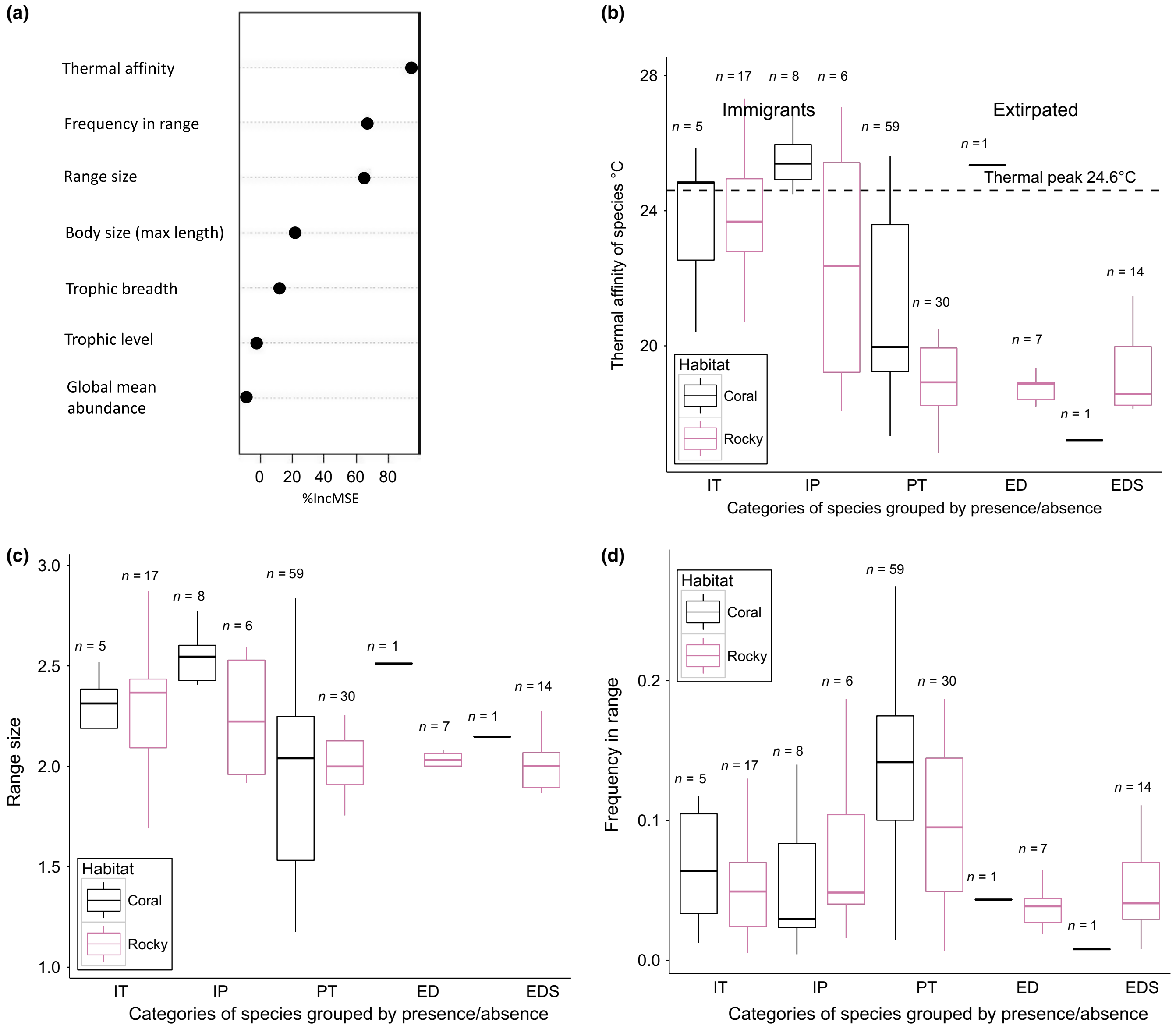

FIGURE 2 (a) Random forest importance plot for traits that best predict membership (among the variables tested) of species to five warming-related occurrence groups (as defined in Table 1). (b) Thermal affinity (Species Temperature Index, STI) of species in these groups. Species were assigned to a single thermal affinity group and were found in both rocky and coral habitats. Dashed line represents mean sea surface temperature (SST) during the 2011 warm peak, 24.6°C, calculated as the warmest mean monthly SST of the preceding 12 months to the 2011 surveys. (c) Distribution of log-transformed geographic range size and (d) frequency in geographic range values across all species assigned to each group (Table 2 provides the traits assignments for each group). Categories 1–5 represented here as IT, immigrant temporary; IP, immigrant persistent; PT, present throughout; ED, extirpated during heatwave; EDS, extirpated during and since the heatwave. Boxplot limits are 1.5× interquartile range [Colour figure can be viewed at wileyonlinelibrary.com]

Predictions of community change (Table 1) based on theory were largely supported by our observations. Species that were present throughout the study period (category 3) consisted of species with a large range of STI in the coral reef habitat, but only relatively cool-affinity species were in this category on the rocky reef habitat. Only two species surveyed in the coral reef habitat were classified as extirpated (categories 4 and 5; Figure 2b), and those species from the rocky habitat classed as those extirpated had cool affinities (Figure 2b). Thus, species which were locally extirpated, or were no longer common enough to be detected on surveys during the heatwave and following years, were clearly characterized by geographic distributions centred in cooler regions, with the mid-points of their realized thermal range generally less than 20°C.

The warming immigrants (categories 1 and 2) tended to consist of species with the largest range sizes and less frequent occurrence throughout their range, while species present before, during and after the heatwave (category 3) had the greatest frequency of occurrence. Rarer species, as defined by low frequency of occurrence across their range, tended to appear and disappear more than the widespread/frequent species, regardless of STI (Figure 2c,d). To

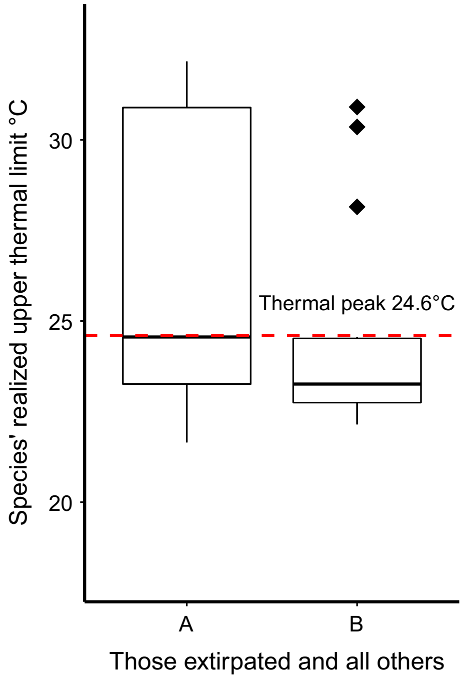

FIGURE 3 Species in categories 1, 2 and 3 (*n* = 125 species) were assigned to group A (warming immigrant or present throughout) and collectively display high variability in realized upper thermal limits, with the majority of group A species found at much warmer locations than the study location. Twenty of the 23 species assigned to categories 4 and 5, group B (extirpated during warming) had realized upper thermal limits that were exceeded by sea surface temperature (SST) in 2011 in both coral and rocky habitats at Rottnest Island. Dashed line represents SST during the warming peak in 2011. Boxplot limits are 1.5× interquartile range [Colour figure can be viewed at wileyonlinelibrary.com]

further explore differences in STI of extirpated species compared to other species (Table 1, prediction 2) and investigate the potential that these species were not absent from surveys during the warmest years simply by chance, the 95th percentile of maximum SST values from occurrence locations was examined. Of the 23 species extirpated (categories 4 and 5), 87% were found to have an upper realized thermal niche limit (95th percentiles) less than 24.6°C, the temperature exceeded during the warmest part of the study period (Figure 3). Thus, had these individuals remained at Rottnest Island during the heatwave, they would have exceeded the temperatures typical of the warmest locations in which they have previously been recorded. However, not all species for which SST exceeded their 95th percentile disappeared, some persisted through the warming.

3.3 | Abundance changes

A general trend for increasing abundance of reef fish species occurred during warming from the start of the study period to the warmest years of 2011–2012 (Figure 4). The magnitude of species' abundance increase was predicted by their STI (Figure 4), with a significant trend for species with warmer affinity to increase more in abundance (Table 3). A slight negative trend in abundance was observed across species during the cooling period, with a tendency for greater declines in abundance of species with the warmest STI (i.e., negative coefficient, Figure 4), although this was non-significant.

4 | DISCUSSION

We found that warming immigrants had the highest STI, measured as the mid-point on the realized thermal niche. Species range shifts thus appear to be facilitated by extreme heat events, with non-random immigration to the local community at Rottnest Island. Temporal patterns in species occurrence associated with warming and cooling periods were better predicted by the realized thermal niche than any of the other traits investigated, including traits known to be important among range-shifting species (Sunday et al., 2015). Of the other traits considered (Table 2), frequency of occurrence and range size were more important than body size. Frequently occurring species were, as expected, more often observed throughout the study period. By contrast, species' that were rarer may have been unobserved when present. Even so, species' presence was not influenced by whether they were typically rare (throughout their range) or small bodied, both additional characteristics that may influence detectability. The degree to which patterns of immigration related also to range size were less clear, however, due to a positive relationship between STI and range size.

We further found that any local extirpation observed during warming was most prevalent in those species with the coolest upper thermal limits. Species absent during the warm years, and also since then, possessed cooler affinities than other groups, and in 87% of these species, the heatwave exceeded their upper thermal limits. We thus find evidence supporting that temperatures became too warm for these species, and they either moved or suffered sufficient mortality and reduction in activity, such that they were no longer observed in surveys.

Even so, not all cool-affinity species were classified as extirpated. Those cool-affinity species that persisted through the warming event may possess physiological plasticity. Some organisms can acquire thermal tolerance within hours of extreme heat exposure (Hoffmann, Sørensen, & Loeschcke, 2003). Rottnest Island species that persisted through the heatwave may have upregulated heat-shock proteins, for instance, facilitating some level of tolerance to a sudden rise in temperature. Cool-affinity species that persisted through the heatwave may also have been relatively abundant initially, in which case a longer period of elevated SST could potentially lead to extended population decline and, ultimately, disappearance. Some of the species that persisted may also have been able to move to habitats in deeper water around Rottnest Island to avoid exposure to warmer surface currents, but were still observed in surveys.

We further found that abundance trends during warming and cooling periods were predictably related to the realized thermal niche. Given substantial natural variability in abundances of species, as well as sampling stochasticity, the significant relationship we observed between species' abundance change and STI during the warming period represents a novel and important finding. Some declines

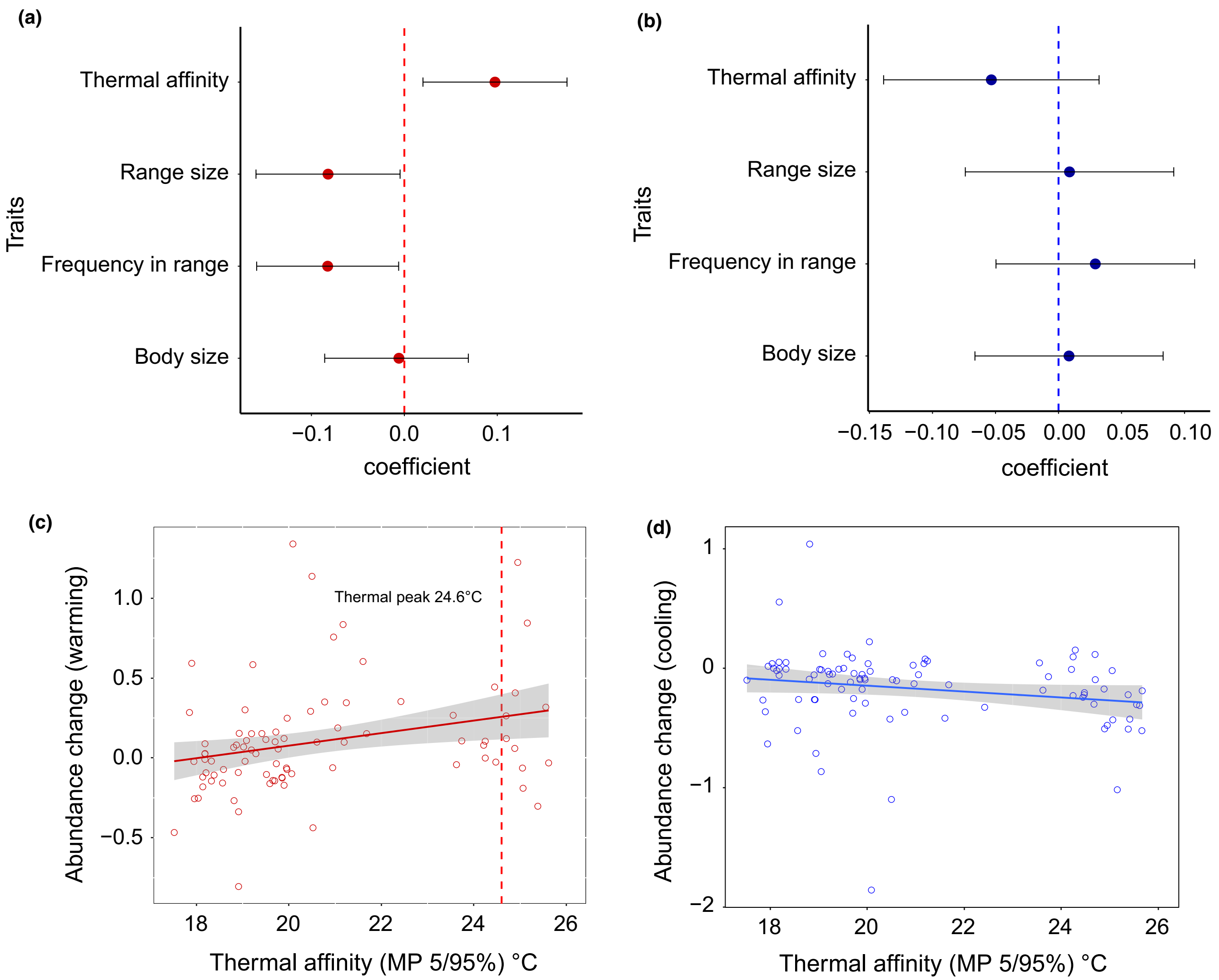

FIGURE 4 Effect sizes of the most important species traits for determining changes in abundance observed in reef fishes during warming (a,c) and cooling (b,d) periods. Regression coefficients are from scaled covariate data modelled with generalized least squares regression. Shading indicates the 95% confidence interval. Frequency in range and range size both had significant inverse relationships to abundance change during the warming period (Table 3, Figure 4a). Abundance changes were independent of species' body size in both warming and cooling scenarios. Vertical dashed line (c) indicates maximum mean sea surface temperature calculated from the 12 months preceding 2011 surveys. Abundance change in (c) is the log of the mean abundance of each species across sites in the heatwave year of 2011 minus the log of their typical pre-heatwave abundance (the mean between 2008-2010). Abundance change in (d) is the log of the mean abundance of each species at the end of the period (from surveys in 2015) minus the log of their maximum abundance in the preceding warmer years (2011-2014) [Colour figure can be viewed at wileyonlinelibrary.com]

in abundance were evident in cooler-affinity species, but local populations generally increased during the warming period, such that a net increase in community abundance was observed. Similar responses have been demonstrated in a number of fish communities (e.g., Simpson et al., 2011). Warming may increase overall productivity in particular circumstances, if species are (1) not resource-limited (by food and habitat availability) (Connell & Jones, 1991; Friedlander & Parrish, 1998), (2) not subjected to increased predation (Hixon & Beets, 1993; Hixon & Jones, 2005) or (3) not already at temperatures near or exceeding those optimal for growth, reproduction and other necessary processes (Pörtner & Farrell, 2008). Of the 148 species included here, 50 possessed thermal affinities warmer than local mean SST (and warmer than the heatwave temperature peak ~24.6°C). These species have substantial proportions of their geographic range in warmer waters, suggesting they may even perform better at warmer temperatures if local population performance follows a similar trend with temperature to the thermal performance curves observed in individuals (Pörtner & Farrell, 2008).

The combined patterns of immigration (range extensions), extirpation and abundance changes observed in our study underpin substantial community-level change on Rottnest Island reefs during the marine heatwave. The net change in the community was evident in the trends in the Community Temperature Index (CTI, Figure 1), which showed the fish community to be remarkably dynamic and

TABLE 3 Summary results table from generalized least squares examining the effect size of species traits on abundance change during extreme sea surface temperature warming and cooling

	Abundance change coefficients (dependent variable)	
Trait	**Warming (*SE*)**	**Cooling (*SE*)**
Thermal affinity (STI) (MP 5%–95%)	0.098* (0.039)	−0.053 (0.043)
Frequency in range	−0.083* (0.038)	0.029 (0.040)
Range size	−0.082* (0.039)	0.009 (0.042)
Body size (max length)	−0.006 (0.038)	0.008 (0.038)
Intercept	0.103** (0.035)	−0.187** (0.035)
Observations	89	98
Log likelihood	−37.6	−44.4
AIC	87.1	100.9
BIC	101.7	116.1

Bracketed values are standard error (*SE*), log likelihood indicates model fit, Akaike information criterion (AIC) and Bayesian information criterion (BIC) are information-based criteria that assess model fit, based on log likelihood. MP 5%–95% is the mid-point of the 5th–95th percentile of species thermal affinity (Species Temperature Index, STI).
*$p < .05$; **$p < .01$.

sensitive to temperature change. CTI tracked SST closely over the 8 years spanning the heatwave with little lag time, especially in the coral reef habitat, where CTI and SST remained within ~0.5°C of one another. This finding supports recent studies on birds (Devictor et al., 2008; Lindström et al., 2013; Tayleur et al., 2016) and butterflies (Zografou et al., 2014), indicating that CTI is a useful indicator of community-level change associated with environmental temperature trends. But our results contrast some terrestrial studies that found substantial time lags in CTI following warming (La Sorte & Jetz, 2012; Tayleur et al., 2016). Clearly, marine fish communities are highly dynamic, with rapid responses to temperature. Marine species may redistribute more rapidly than terrestrial species because there are less options for buffering temperature without relocating. Relocation is relatively easy in marine systems where adult fishes are highly mobile and larval stages disperse widely and experience fewer barriers in comparison with terrestrial habitats (Pinsky et al., 2013; Sunday, Bates, & Dulvy, 2012; Webb, 2012). Our study demonstrates the possibility of range shifts across great distance, over short time scales, in regions connected by boundary currents. On a background of gradual oceanic warming, extreme heatwave events will promote the arrival of immigrants, their survival once present, and eventually where suitable habitat and food resources exist, long-term persistence (Bates et al., 2014b; Figueira & Booth, 2010).

There are also further directions for future studies to increase our predictability of temperature-related community change. For instance, we did not investigate whether warming-related changes to species composition and community structure influence species interactions and ecosystem function. The prevalence of herbivores among warming immigrant fishes has recently been noted in the same region, and increases in herbivores can drive cascading impacts in temperate marine systems through grazing impacts (Wernberg et al., 2016). In other regions, such as southern Japan, an influx of tropical herbivores into a region of historically low diversity and biomass of herbivorous fishes has resulted in severe overgrazing of macrophytic algae, with regional losses of 40% of algal cover and colonization by hard corals (Vergés et al., 2014). Another direction for research is to tease apart the influence of ocean currents in mediating community change, and which presumably drive immigration of warm-affinity species towards cooler latitudes. Indeed, the timing of the arrival of tropical species at Rottnest Island coincided with a period of strong poleward current flow—an important vector for tropical larvae in this region (Hutchins et al., 1991; Hutchins & Pearce, 1994; Maxwell & Cresswell, 1981; Pearce & Hutchins, 2009; Pearce et al., 2011; Pearce, 2016).

5 | CONCLUSIONS

Our results demonstrate that metrics associated with species' realized thermal niches can predict species and community-level change in marine fishes subjected to extreme warming events. Furthermore, we observed a close relationship between STI and abundance changes, immigration and local extirpation, implying that reef fish species' contemporary geographic distributions closely match the temperature ranges required for their ecological success. Thus, STI could be used as an approximation for the net outcome of otherwise unmeasurable temperature-dependent processes that shape the distribution and abundance of fishes/species. Given that the structure of communities can change very quickly in predictable ways during extreme heat events, species most at risk from changing ocean climate should be identified and appropriate conservation management strategies identified.

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BIOSKETCH

The authors' research focuses on broad-scale trends in rocky and coral reef biodiversity related to pressures such as fishing, ocean warming, invasive species and pollution. The availability of data collected using standardized methods from the Reef Life Survey (RLS) programme, which covers not just coral reefs, but also rocky reefs from the Antarctic to the Arctic, allows uniquely broad questions to be tackled. The RLS groups' ultimate goals are to improve the way marine biodiversity is monitored, reported, managed and protected, through contributing to more ecologically informed policy at larger scales and by providing guidance to local management.

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