RESEARCH ARTICLE

Sea temperature and habitat effects on juvenile reef fishes along a tropicalizing coastline

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Abstract

Aim: Temperate marine systems globally are warming at accelerating rates, facilitating the poleward movement of warm-water species, which are tropicalizing higher-latitude reefs. While temperature plays a key role in structuring species distributions, less is known about how species' early life stages are responding to warming-induced changes in preferred nursery habitat availability. We aim to identify key ecological and environmental drivers of juvenile reef fishes' distributions in the context of ocean warming.

Location: South-eastern Australian coastline from 30 to 37°S.

Methods: We used a decade of underwater visual census data to uncover latitudinal distribution patterns of juvenile reef fishes and habitats across 1000 km of coastline, from subtropical to temperate latitudes. We modelled how benthic habitat cover, depth, wave exposure and sea surface temperature influence distributions of warm-water and cool-water juvenile reef fishes on temperate rocky reefs.

Results: We found sea surface temperature was typically the most important factor influencing densities of juvenile fishes, regardless of species' thermal affinity or latitudinal range extent. Juveniles of tropical and subtropical range-expanding fishes responded more strongly to warmer temperatures and lower wave exposure, while juveniles of temperate species responded more strongly to benthic habitats. Species' responses to greater availability of temperate reef habitat-formers such as kelp and other macroalgae contrasted, being positive for temperate and negative for tropical and subtropical juvenile fishes.

Main conclusions: The availability of both suitable habitat and sea temperatures for species' early life stages is important considerations when predicting changes in reef fishes' distributions in the context of ocean warming. Warming-induced isotherm shifts and feedback loops constraining the persistence of key temperate reef habitat-formers will favour range-expanding tropical reef fishes colonizing higher-latitude reefs, while disadvantaging some macroalgal-associated resident temperate species. Such varying responses to warming-induced environmental changes may strongly influence the structure of emerging tropicalized reef assemblages.

1 | INTRODUCTION

The abundance and distribution of marine species globally are changing rapidly in response to rising ocean temperatures induced by anthropogenic climate change (Lenoir et al., 2020; Pinsky et al., 2020; Poloczanska et al., 2013). As marine species' distributions shift towards cooler latitudes, assemblages reorganize with cascading implications for ecosystem structure and functioning (Pecl et al., 2017). In warming temperate marine systems, range-expanding tropical species may be more opportunistic and can sometimes perform better in warming-impacted habitats than their temperate counterparts (Kumagai et al., 2018). Indeed, models predict the continued widespread contraction of cool-water habitat-formers such as kelps along temperate coastlines in response to increasing temperatures in future decades (Davis et al., 2021; Kumagai et al., 2018; Martínez et al., 2018). Climate-driven shifts in the distribution of habitat-forming species that support diverse ecological assemblages and critical ecological processes will have significant cascading consequences for entire coastal ecosystems (Vergés et al., 2019). However, these impacts are still emerging and yet to be fully understood.

Temperature plays a key role in structuring global marine biodiversity (Tittensor et al., 2010), particularly species distributions (Payne et al., 2021; Stuart-Smith et al., 2017), which will continue to change as isotherms continue to accelerate in the 21st century (Sen Gupta et al., 2015). Evidence indicates that within the marine realm, temperate and boreal reefs will be more acutely affected by anthropogenic climate change because the magnitude of ocean warming is greater at higher latitudes (Burrows et al., 2011). Warming can directly or indirectly facilitate the reorganization of biodiversity on higher-latitude reefs through assisting species dispersal and establishment. Increasing ocean temperatures facilitate marine species' movements from lower to higher latitudes either by creating thermal conditions viable for warm-affinity species to survive or enabling habitat-forming species that range-extending tropical species depend upon to establish (Bates, Pecl, et al., 2014; Yamano et al., 2011). While much evidence suggests warmer ocean temperatures drive the advancement of tropical marine species poleward to temperate reefs (Feary et al., 2014; Pecl et al., 2017), not all species responses have been uniform, and the relevance of other factors governing species' distributions is an important consideration, including habitat availability and behavioural adaptations by range-expanding species at recipient reefs (Bates, Pecl, et al., 2014).

Substantial evidence has already shown warming-induced compositional shifts in marine assemblages at temperate latitudes, ranging from gains and losses of local populations, to changes in relative abundances (Day et al., 2018; Smith et al., 2021; Vergés et al., 2016). The process of tropicalization, whereby warm-affinity species become increasingly dominant (Vergés, Steinberg, et al., 2014), is increasingly evident as temperate reefscapes reconfigure into novel assemblages composing habitat-forming species with functionally different structures and traits to the natural state. Novel, tropicalized temperate reefscapes are emerging where shifts occur in the dominant benthic habitat-formers, in particular from cool-water habitat-forming species such as kelps and other canopy-forming macroalgae to warm-water habitat-formers such as coral (Nakamura et al., 2013; Yamano et al., 2011), tropical seaweeds (Tanaka et al., 2013) and/or turf-forming algae (Filbee-Dexter & Wernberg, 2018).

While tropicalization is broadly induced by ocean warming, the specific mechanisms triggering the transition of temperate reefs to tropicalized states vary in their nature and spatial and temporal scales; for example, from short-term extreme marine warming events to intensified herbivory by urchins and range-extending tropical herbivorous fish facilitated by gradual ocean warming (Ling et al., 2018; Vergés et al., 2016; Wernberg et al., 2016). The rapid rate of environmental change is outpacing the ability of habitat-forming species to adapt, leading to dramatic shifts in their abundance and distribution that may be representative of tipping points and likely irreversible in many cases (Wernberg et al., 2016).

The abundance and distribution of habitat-forming species such as kelps, other canopy-forming macroalgae, seagrasses and corals strongly influences fish assemblages (Gillanders & Kingsford, 1998; Quaas et al., 2019) by creating complex three-dimensional biogenic structures and providing food and refuge from predators (Steneck et al., 2002). The nursery function these habitats provide for juvenile fishes supports reef fish population replenishment and maintains biodiversity (Fulton et al., 2016; Wernberg et al., 2019). Other than the biogenic characteristics of habitats, physical attributes of habitats such as depth and wave disturbance can also determine their suitability as nurseries for juvenile fishes (Beck et al., 2016; Fulton & Bellwood, 2004). Juveniles tend to be more specialized in their habitat use than adults (Morton & Gladstone, 2011), so distributions of juvenile fishes may be more sensitive to changes in the availability of preferred biogenic and physical habitats and resources within reefscapes relative to adult conspecifics (Kingsford & Carlson, 2010), although plasticity in habitat use by juvenile coral reef fish arrivals to temperate reefs has been noted (Beck et al., 2017). Nonetheless, in the context of tropicalization and associated threats for the persistence of cool-water habitat-formers such as kelps, understanding the strength of functional links between habitats and species abundances and relationships with ocean temperatures is crucial for predicting outcomes for the recruitment of juvenile fishes on warming temperate reefs.

Given the likely decline of kelp forests and potential expansion of coral and turf algal habitats associated with the tropicalization of temperate reefs, what then are the likely consequences for tropical and subtropical fishes which are migrating into these temperate

habitats? Moreover, how will juveniles of temperate rocky reef species that are typically strongly habitat-related (Choat & Ayling, 1987; Curley et al., 2002) respond to the climate-mediated retraction of kelp habitats from temperate coastlines? The shallow rocky reefs of south-eastern Australia provide an ideal opportunity to explore these questions. Habitat-forming kelp forests dominate much of the shallow coastal environment of south-eastern Australia. Forming part of the Great Southern Reef (Bennett et al., 2015), the shallow rocky reefs of south-eastern Australia harbour high levels of biodiversity, including many endemic species (Wernberg et al., 2019). However, tropicalized reefs are already emerging in this ocean-warming hotspot (Hobday & Pecl, 2014), with reefscapes previously dominated by kelp forests transitioning to low-biomass turf algal-dominated reefs in some regions (Vergés et al., 2016), and range-expanding subtropical corals colonizing higher-latitude rocky reefs (Booth & Sear, 2018; Ling et al., 2018). If, as anticipated, these habitat shifts are an early indication of future reef states along this warming coastline, long-term ecosystem monitoring at both broad and local resolutions will be key to detecting and understanding how assemblages are responding to the direct and indirect effects of rising ocean temperatures.

A key driving force underlying the species shifts occurring along this coastline is the rapidly warming, poleward-flowing East Australian Current (EAC; Wu et al., 2012), which strongly influences the distribution of marine biota in this region. The poleward flow of the EAC facilitates the advection of warm tropical water and reef fish larvae hundreds of kilometres south along the coast of south-eastern Australia from tropical to temperate latitudes (Booth et al., 2007). Each summer-autumn, the EAC delivers pulses of expatriated juvenile tropical and subtropical reef fishes to temperate reefs, temporarily increasing the diversity of fishes in recipient assemblages (Booth et al., 2007; Feary et al., 2014). Spatial and temporal variation in recruitment pulses of warm-water juvenile fishes are suggested to be related to EAC-driven impacts on larval supply, alongshore and cross-shelf transport and retention (Booth et al., 2007). While thermal tolerances currently constrain the survival of range-expanding reef fishes through the breeding cycle (Figueira & Booth, 2010), the ecological success of these fishes at higher-latitude reefs in the future may be facilitated by sustained increases in water temperatures.

Apart from EAC dynamics and sea surface temperature, other factors identified as important influences of juvenile fish distributions in south-eastern Australia include availability of suitable benthic habitat (Beck et al., 2017; Curley et al., 2002), wave exposure (Beck et al., 2016) and predator–prey interactions (Bates, Barrett, et al., 2014; Edgar & Stuart-Smith, 2009). Previous research that has examined links between these factors and juvenile fish distributions has primarily focused on range-expanding species (e.g., Booth et al., 2011; Figueira & Booth, 2010; Fowler et al., 2018), with less attention given to temperate species, despite the rising threat of warming-induced losses of cool-water habitats from rocky reefs in this region (but see Fulton et al., 2016). Broad-scale investigations relating a range of ecological and environmental factors and juvenile fish distributions are also relatively rare and are in part due to the

logistical and financial challenges of monitoring such a geographically vast coastline. Even at local resolutions, long-term studies of entire juvenile fish assemblages are relatively scarce, and few have focused on future patterns of recruitment through the lens of tropicalization. Determining the factors that will contribute to the persistence of reef fishes is critical information for managers devising plans to future-proof ecosystems on warming temperate coastlines.

Citizen science programmes play a valuable role in rigorously collecting ecological data over expansive spatial and temporal scales, thereby overcoming some of the challenges and limitations faced by marine management and researchers in situations (Edgar et al., 2020). Here, we take advantage of a long-term citizen science dataset of reef fish abundance and benthic habitat data collected via underwater surveys carried out in subtropical to temperate rocky reefs along the south-eastern coast of Australia to: (1) describe latitudinal patterns in the composition of juvenile fish assemblages, (2) identify the main ecological and environmental drivers of variation in the distribution of species abundances of juvenile fishes at shallow rocky reefs and (3) use these relationships to infer the responses of range-expanding vs resident temperate juvenile fishes to shifts in the distribution of habitats on tropicalized temperate reefs in the future. We hypothesized that the predicted climate change-induced loss of dominant habitat-formers from temperate rocky reefs will have negative repercussions for recruitment of reef fishes that strongly associate with these habitat types. We also expected that the resulting habitat shifts towards greater availability of non-macroalgal habitats that are more typical for warm-water reef fishes could facilitate the recruitment of range-expanding reef fishes to tropicalized temperate reefs.

2 | METHODS

2.1 | Fish and benthic habitat data

The data for fish counts, length-class and benthic habitat composition were obtained from underwater visual censuses conducted as part of the citizen science Reef Life Survey (RLS) programme. The RLS dataset used for this study comprised 812 surveys at 163 sites along almost 1000 km and six degrees of latitude from 30 to 37°S along the south-eastern Australian coast (Figure 1a, Table S1). Study sites were distributed across marine protected areas (MPAs) and open areas outside MPAs. MPAs are established at five of the six study locations but are absent from the southern-most location at 37°S. Study sites encompassed both no-take areas (NTAs) (48 sites) and areas partially or completely open to fishing (FZs) (115 sites) (Table S1.1). The dataset of surveyed sites encompassed subtropical to temperate coastal environments, with a difference in mean summer sea surface temperatures (SST) across the latitudinal extent of about 5°C (Figure 1b; SST analyses are described in Section 2.2). Data were collected over 10 years (2008–2018) during the period of peak fish recruitment in the study region, December to May (Booth et al., 2007).
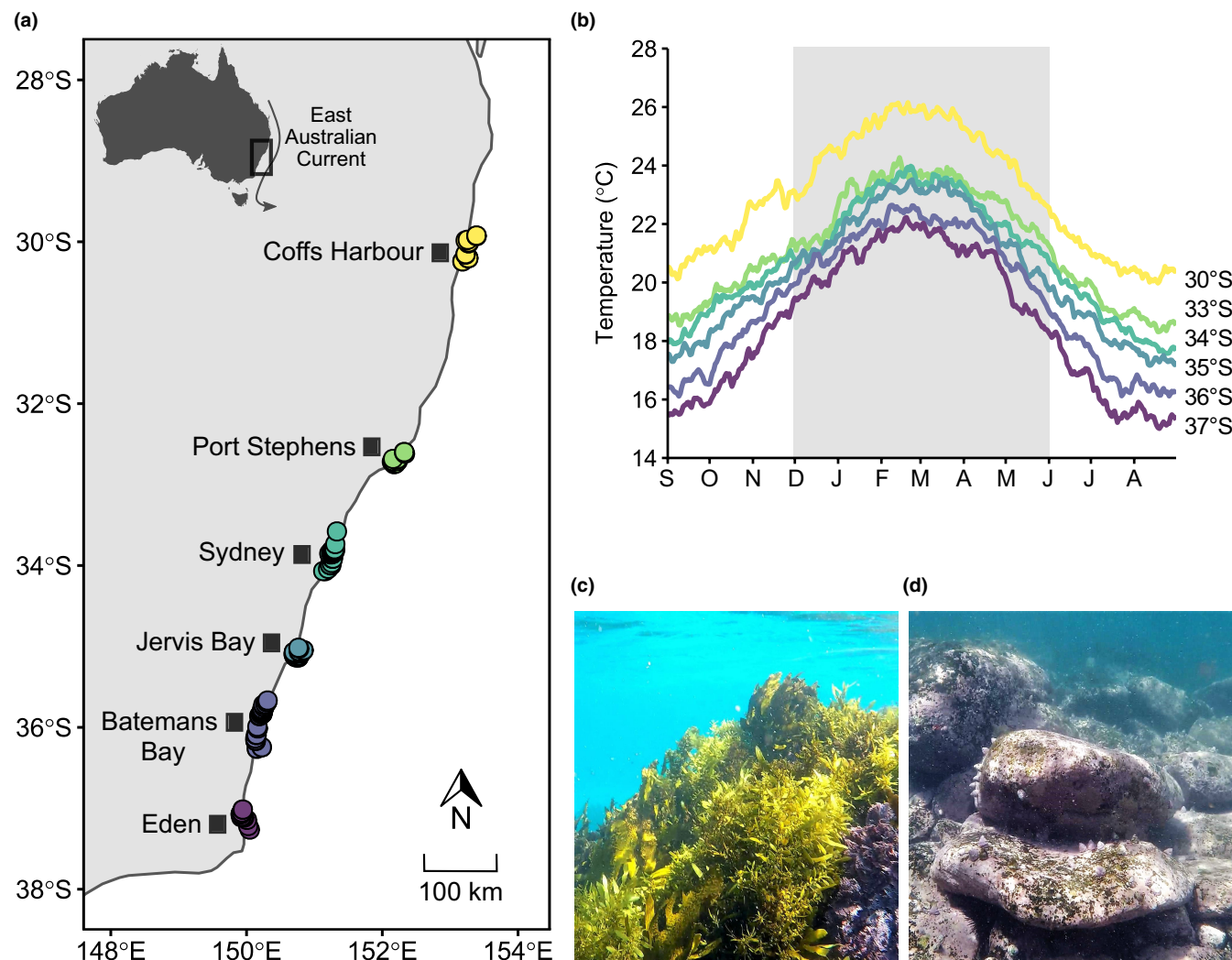
FIGURE 1 (a) Study region and location of Reef Life Survey programme sites used in analyses. (b) Mean daily sea surface temperatures (SST) at the six latitudes in the study region for the period 2008–2018. Daily SST values were extracted for each site within a latitude from gridded NOAA OISST data and averaged across the 10-year study period. Shading indicates the period of the year that was the focus of the analyses. Photographs depict habitats typical of shallow rocky reefs along the south-eastern Australian coast: (c) mixed macroalgal assemblage and (d) crustose coralline algae-dominated rock. Photo credits: The authors

A description of the standardized quantitative fish and benthic habitat census and data collection methods is provided in an online methods manual (http://www.reeflifesurvey.com) and published literature (Edgar et al., 2020; Edgar & Stuart-Smith, 2014). Briefly, surveys involved underwater visual census conducted by trained scientific and recreational SCUBA divers along a 50 m transect line, which was laid along a depth contour, with all fishes observed within 5 m of the transect line recorded and their size estimated, giving a total transect area of 500 m². Fishes were identified to the lowest possible taxonomic level; analyses in this study included fishes identified to species level only. Data quality assessments of RLS have demonstrated that trained RLS citizen scientists generate fish and invertebrate data of equivalent quality to those of professional scientists (Edgar & Stuart-Smith, 2009).

Assessment of benthic habitat composition for each survey was carried out through analysis of 20 habitat photoquadrats, which were taken by RLS divers with a digital camera pointed vertically downward at the substrate every 2.5 m along the same 50 m transect lines set for fish surveys. Photoquadrat images were taken at a height sufficient above the seabed (generally about 0.5 m) to encompass an area of the benthos of about 0.25 m². Photoquadrat images were available for all surveys used in analyses in this study. Per cent cover of the dominant habitat types was quantified from the habitat photoquadrat images via scoring using a grid overlay of five points per image, giving 100 points per transect, and aggregated into nine broad habitat groups designed to be suitable for the analyses. The habitat groups defined for the study comprised the biotic categories of kelp (principally the Golden kelp *Ecklonia radiata*), macroalgae, turf algae, seagrass, crustose coralline algae, coral (generally hard coral growth forms such as encrusting or plate but also comprising soft corals) and sessile invertebrates, and abiotic categories of rock and unconsolidated sediment (encompassing sand, pebbles and rubble) (e.g. Figure 1c,d).

Because length at maturity data was not available for most fish species in the dataset, juvenile fishes were generally considered as those binned in size classes that were ≤25% of the fish species' maximum adult length, as these data were available for all species. For large-bodied species with maximum adult length >80 cm (e.g. *Chrysophrys auratus*; Australasian Snapper), individuals with lengths ≤20 cm were considered juveniles. Maximum adult length data were obtained from FishBase (www.fishbase.org, Froese & Pauly, 2020). Species were classified into ecoregion groups of tropical, subtropical and temperate based on distributional data obtained from a combination of sources including distribution maps available through RLS (https://reeflifesurvey.com/species/search.php), Fishes of Australia (https://fishesofaustralia.net.au/) and Atlas of Living Australia (https://fish.ala.org.au/) (a complete species list is provided in Table S1.5). Individual transects with fewer than five juvenile fishes in total were excluded from analyses to minimize spurious relationships with habitats.

2.2 | Environmental variables

The environmental variables considered for each survey in the dataset were depth, wave exposure and sea surface temperature (SST). Depth was recorded by RLS divers at the time of each survey and represents the mean depth of the transect; surveys included in analyses were conducted at shallow reefs with depths of 1–20 m (mean 7.1 ± 0.1 m). Locations of sites varied from sheltered bays to open coastlines subjected to different degrees of exposure to the region's prevailing south-south-easterly (SSE) swell and wind (Shand et al., 2011). Wave exposure was determined for each site by measuring the direction faced by the coastline nearest to the site, and rescaling the values from 0 to 1 according to alignment with the prevailing SSE swell, where 1 represents maximum exposure, as per Turnbull et al. (2018).

SST data were extracted from the NOAA 1/4° daily Optimum Interpolation Sea Surface Temperature (OISST) product (https://www.ncdc.noaa.gov, accessed March 2020). For each survey, daily SST data from the cell grid matching the survey location were extracted. Three SST variables were calculated for each survey to use in modelling: mean, maximum and minimum SST. A mean SST was calculated for each survey as the average of SST values for the three months prior to the survey occurrence. The maximum and minimum SST value per quarter (December–February or March–May) that matched each survey date were also extracted and used in models. Time series of mean daily SST over the 10-year study period (2008–2018) were constructed for each of the six latitudes in the study region to examine latitudinal patterns in SST. Daily SST values for the entire 10-year study period were extracted for each site from the gridded NOAA 1/4° daily OISST dataset. Time series were constructed for each latitude by averaging SST values across all sites within a latitude over the 10-year study period.

2.3 | Statistical analyses

Latitudinal trends in juvenile fish communities and habitats were explored with univariate and multivariate statistical analyses carried out using PRIMER v6 (Clarke & Warwick, 2001) with the PERMANOVA+ADD-on (Anderson et al., 2008). For each latitudinal degree, the mean (per survey, 500 m^2) juvenile fish density and species richness were calculated. Mean density was firstly calculated at the site level, and then, the mean of site means calculated for comparisons among latitudes. Species richness was firstly calculated at the survey level to minimize bias due to variation in the number of transects surveyed at each site (Edgar & Stuart-Smith, 2014). A measure of habitat diversity for surveys was determined using Shannon's diversity index, where a higher index value indicates that a greater number of habitat types are present and the proportion of different habitat types is more equal (Wedding et al., 2011).

Permutational analyses of variance (PERMANOVA) were used to test for univariate differences in juvenile fish density and species richness, and habitat diversity among latitudes. Similarity matrices based on Euclidean distance were constructed from untransformed density, species richness and habitat diversity data (Anderson et al., 2008). PERMANOVA was also used to examine variation in the multivariate structure of juvenile fish assemblages. Prior to this analysis, fish density data for surveys were $\log(x + 1)$ transformed to down-weight the contribution of highly abundant species, and a Bray–Curtis similarity matrix was constructed. All PERMANOVAs included the factors latitude (fixed) and site (random, nested within latitude), and were run with a minimum of 9999 permutations, type III sum of squares and permutation of residuals under a reduced model (Anderson et al., 2008). Where a significant result for a factor was obtained, pairwise PERMANOVA was used to explore the results further. Because the study sites were subject to different levels of protection from fishing, additional PERMANOVA tests were performed to assess the effect of protection level for the same juvenile fish metrics, as well as predator density (see Appendix S2).

A principal coordinates analysis (PCO; Anderson et al., 2008) was performed to visualize differences in juvenile fish assemblages among latitudes. To assist in visualization, the PCO was conducted for fish densities at the site level. The PCO was performed on a Bray–Curtis similarity matrix of square-root transformed mean fish densities. Vectors showing the site level means of habitat cover and environmental variables that were correlated (Pearson's $r > .4$) with the ordination structure were included as overlays on the PCO.

The species generalization index (SGI) for the fish species recorded was sourced from work previously carried out by Stuart-Smith et al. (2021), with the exception of 28 species (out of a total of 207 species) for which this value was not available because of insufficient sample size (see Table S1.5). The SGI is an estimate of the habitat niche breadth of a species, with SGI values <15 indicating that the species occurs in a relatively narrow range of reef habitat types (specialists), while species with SGI values >25 are considered habitat generalists within their range. The community generalization

index (CGI) was calculated for each survey as the mean of SGI values among all species recorded on the survey, weighted by the log(x + 1) of their density. While juvenile fishes may be more specialized in their habitat use than adults of the species, SGI values are only available for adults and provided a general indication of potential habitat specialization for the purposes of this study.

2.4 | Statistical modelling

Generalized additive modelling (GAM) with a full subsets approach (Fisher et al., 2018) was used to investigate which habitat and environmental variables best explained the variance in juvenile fish densities. GAM analysis was selected due to its ability to model non-linear relationships between dependent and continuous predictor variables that frequently occur in ecological data. We present in this study the model results for seven selected species of interest: *Parupeneus spilurus* (Black-spotted goatfish; family Mullidae), *Chaetodon guentheri* (Gunthers butterflyfish; family Chaetodontidae), *Thalassoma lunare* (Moon wrasse; family Labridae), *Prionurus microlepidotus* (Australian sawtail; family Acanthuridae), *Ophthalmolepis lineolatus* (Southern maori wrasse; family Labridae), *Pictilabrus laticlavius* (Senator wrasse, family Labridae) and *Enoplosus armatus* (Old wife; family Enoplosidae). These species were selected based on several criteria which included firstly being among the most commonly recorded species in the surveys (typically with a frequency of occurrence in surveys of ≥20% at one or more of the latitudes surveyed) and therefore suitable for full subsets GAM analysis (Table S1.2). Secondly, these seven species were selected because they have been identified as changing significantly in abundance over the last 17 years in warming tropicalized reefs in south-eastern Australia where kelp has declined (Smith et al., 2021). This includes two temperate fish species identified as decreasing in occurrence (*O. lineolatus* and *P. laticlavius*), and five species with varying ecoregional affinities identified as increasing in abundance (*P. spilurus*, *C. guentheri*, *T. lunare* (all tropical), *P. microlepidotus* (subtropical) and *E. armatus* (temperate)) (Smith et al., 2021). These species include tropical and subtropical coral reef species known to be expanding their range in south-eastern Australia and Australian endemic temperate species. The selected species also represent different trophic groups and have varying degrees of habitat specialization. As a group, we consider that these species are broadly indicative of the juvenile fish assemblage that occurs on shallow rocky reefs in south-eastern Australia during the peak fish recruitment period.

Due to variation in presence/absence of benthic habitat types among latitudes, separate GAMs were fit for each species at each latitude. The global predictor variables considered for the models were depth, wave exposure, maximum SST, minimum SST and mean SST. Benthic habitat variables (per cent cover of kelp, macroalgae, turf algae, seagrass, crustose coralline algae, coral, sessile invertebrates, bare rock and unconsolidated sediment) with sufficient coverage (≥5% relative cover) at a latitude were also included in the models. Depth, wave exposure, SST variables and benthic habitat

variables were treated as fixed effects. Site and recruitment season year were included as random effects to account for any spatial or temporal autocorrelation. Prior to analysis, predictor variables were transformed by either square-root or log(x + 1) where required to improve distribution.

The full subsets GAM analyses fitted all possible combinations of predictor variables, up to a maximum of three variables, while excluding models with variable correlations >0.28, which could otherwise cause issues with collinearity among predictor variables and result in model overfitting (Fisher et al., 2018). Predictor variables were smoothed using cubic regression splines with a maximum of five knots. Models were fitted using a Tweedie error distribution which is more robust to overdispersed and zero-rich data than other members of the exponential distribution family (e.g. poisson, gamma; Shono, 2008). Residual plots were examined to check model assumptions. Models were compared using the Akaike's Information Criterion (AIC) optimized for small samples sizes (AICc), with the most parsimonious model selected based on the lowest AICc (Δ AICc ≤2) and least number of predictor variables (Burnham & Anderson, 2002). R^2 values provided an indication of the predictive power of the model. Response plots of the most parsimonious models were used to visualize the strength and direction of relationships between the density of juvenile fishes and habitat and environmental variables (included in Figure S1).

The relative importance of each predictor variable was determined by summing the AICc weights for all models containing each variable (Burnham & Anderson, 2002). The calculated variable importance scores were then plotted in a heatmap to identify the relative importance of predictor variables across all possible models in influencing juvenile fish densities. Modelling and plotting were carried out with the R language for statistical computing (version 4.0.5; R Core Team, 2021) using functions from the "FSSgam" (Fisher et al., 2018), "gamm4" (Wood & Scheipl, 2019), "mgcv" (Wood, 2017), "mgcViz" (Fasiolo et al., 2020) and "ggplot2" (Wickham, 2016) packages.

2.5 | Structural equation models

Structural equation models (SEM) were used to explore the indirect and direct effects of habitat and environmental variables and estimate their relative effects in explaining variation in densities of juvenile fishes. The piecewise SEM approach was selected due to its advantages over traditional SEMs that are particularly relevant to ecological data, including the capability of piecewise SEMs to include random effects and non-normal distributions, and the ability to handle smaller sample sizes (Lefcheck, 2016; Shipley, 2009). Piecewise SEMs were constructed separately for each species by latitude combination included in the full subsets GAM analyses. Individual piecewise SEMs were developed using the variables resulting from the full subsets GAM model selection process and incorporating paths that represented plausible ecological processes. Individual piecewise SEMs considered all benthic habitat variables and wave exposure where these appeared in GAMs that had AICc scores within

two units of the lowest AICc GAM resulting from the full subsets GAM analyses, because models within this threshold can have similar explanatory power (Burnham & Anderson, 2002). Mean SST and depth were included as global variables in all piecewise SEMs due to their known influence on benthic habitat distribution. Covariation was fixed between benthic habitat variables to avoid spurious correlation in the piecewise SEMs. Consistent with the full subsets GAM analyses, the random factors of site and recruitment season year were included in the paths in the piecewise SEMs. Coefficients and their significance for each path in the piecewise SEMs, and conditional R^2 values for response variables (i.e. an evaluation of model fit taking into account fixed plus random effects) were extracted and path models built to illustrate relationships. The piecewise SEM and full subset GAM analyses result closely conferred, and for presentation purposes, we include four species-level path models that best represent the varying suite of interdependent relationships among variables that influence juvenile fish densities in the study region.

All paths in the piecewise SEMs were based on generalized linear mixed-effect models with negative binomial distribution and were fitted using the "lme4" package (Bates et al., 2015). Prior to modelling, all variables were scaled (by two standard deviations) to allow comparison of the relative effect of predictor variables. The piecewise SEMs were generated using the package "piecewiseSEM" (Lefcheck, 2016).

3 | RESULTS

3.1 | Latitudinal patterns in juvenile fishes and benthic habitats

Juvenile fishes from 207 species comprising 55 families were recorded from 812 surveys conducted during the 10-year period across the 30–37°S latitudinal range. Overall juvenile fish density and species richness varied across the latitudinal range (Figure 2a,b), with juvenile fish density (PERMANOVA, pseudo-F = 6.36, p = .0026) and species richness (pseudo-F = 22.99, p = .0001) generally decreasing from lower- to higher-latitude reefs (Table S1.3). Pairwise tests showed that densities were significantly lower at latitude 36°S reefs compared all other latitudes (Figure 2a, Table S1.4). Species richness of juvenile fishes differed significantly among latitudes and sites (pseudo-F = 1.72, p = .0001; Table S1.3), with differences among latitudes significant for all but two pairwise tests (Figure 2b, Table S1.4). Juvenile fish density and species richness were generally comparable between no-take and fished areas at locations with MPAs (Tables S2.1 and S2.2).

Habitat composition at the latitudinal level was a mosaic, with no one habitat type clearly dominating the seafloor (Figure 2c). Reefs at 30°S comprised a particularly diverse mix of habitat types that included algae-dominated rocky reefs typical of the
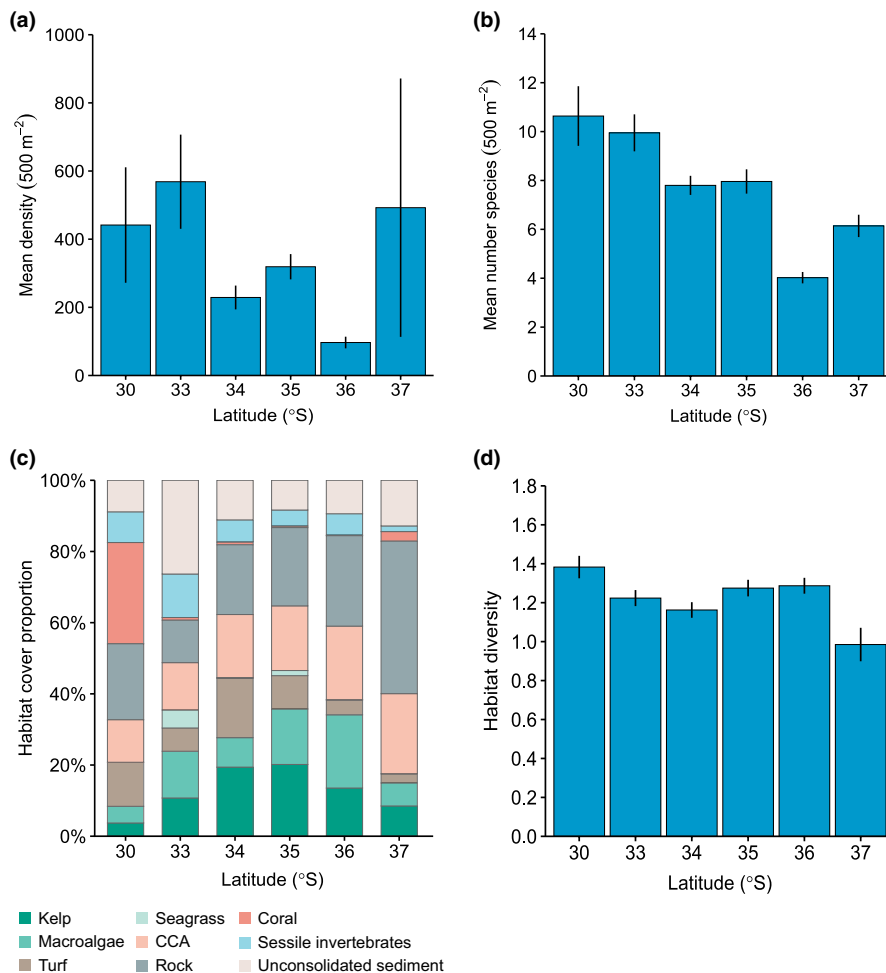

FIGURE 2 Latitudinal trends in juvenile fish (a) density, (b) species richness, (c) benthic habitat type cover and (d) habitat diversity. Mean values ± SE per survey (500 m^{-2}) shown for a, b and d. CCA, crustose coralline algae

temperate zone, and sites with coral cover that were more typical of tropical coral reefs, reflecting this location's position in a tropical-temperate transition zone. The mid-latitude reefs (33–36°S) were characterized by approximately equal proportions of coverage of submerged macrophyte habitat types and crustose coralline algae and bare rock. Reefs in cooler-temperate waters at 37°S contained significantly lower habitat diversity than all other latitudes (PERMANOVA pseudo-$F = 4.42$, $p = .005$–.04 in pairwise tests; Figure 2d, Table S1.4) and had relatively high coverage of crustose coralline algae and bare rock, and low coverage of submerged macrophyte habitat types, indicative of sea urchin barrens common on rocky reefs at this location (Andrew & O'Neill, 2000). There was no relationship between habitat diversity and juvenile fish densities (Kendall correlation test, $p > .05$). However, there was a significant weak to moderately strong positive relationship between habitat diversity and species richness at higher-latitude reefs (36°S: Kendall's $\tau = 0.18$, $p = .002$; 37°S: Kendall's $\tau = 0.29$, $p = .03$).

Juvenile fish assemblage structures varied strongly among latitudes (pseudo-$F = 10.41$, $p = .0001$–.003 in pairwise tests; Table S1.4). Fish assemblages varied between no-take and fished areas at two of five locations with MPAs, 30°S and 34°S, although these differences were only weakly significant (Table S2.2). Fish assemblages in the PCO were separated into three relatively distinct groupings (Figure 3). Assemblage groupings appeared correlated with gradients of coverage of particular habitat types, indicating that assemblages at lower-latitude reefs were associated with coverage of coral, mid-latitude reefs with turf algae and higher-latitude reefs with macroalgae as well as greater wave exposure. The influence of SST on assemblage structure was also apparent from the spatial arrangement of fish assemblages in the PCO.

The CGI values for juvenile fish assemblages tended to increase with latitude, indicating a trend towards greater dominance by habitat generalist species at higher-latitude temperate reefs (Figure 4). Driving this pattern were tropical species considered more habitat specialist contributing relatively high densities to the fish assemblages at reefs at 30°S. This included *Dascyllus trimaculatus* (three-spot damsel, family Pomacentridae, SGI = 20.5) and *Thalassoma amblycephalum* (two-tone wrasse, family Labridae; SGI = 22.9), which as juveniles are generally associated with anemones and coral habitats, respectively (Stuart-Smith et al., 2015), and were rarely recorded south of this latitude. Elsewhere, fish assemblages tended to be dominated by juveniles of schooling planktivorous species that occupy the water column and utilize a variety of habitats across their range, corresponding to higher CGI values for assemblages at these latitudes. Habitat generalist species that strongly contributed to the juvenile fish assemblages in terms of densities and frequency of occurrence included the planktivorous species *Trachurus novaezelandiae* (Yellowtail scad, family Carangidae; SGI = 26), *Trachinops taeniatus* (Eastern hulafish, family Plesiopidae; SGI = 37.3) and the kyphosids *Atypichthys strigatus* (Australian mado; SGI = 32.4) and *Scorpis lineolata* (Silver sweep; SGI = 45). Apart from reefs located at 37°S, there was no relationship apparent between the diversity of habitats available and CGIs for juvenile fish assemblages. For reefs at 37°S, higher habitat diversity tended to correspond to greater generalization in juvenile fish assemblages (Kendall's $\tau = 0.22$), although this relationship was marginally non-significant ($p = .09$).

3.2 | Drivers of juvenile fish distribution

The full subset model analyses indicated that among the biological and physical habitat and SST variables examined, SST most strongly influenced the distributions of juveniles of two tropical and one subtropical range-extending species that were frequently recorded in surveys conducted outside of the species' usual range: *P. spilurus*, *C. guentheri* and *P. microlepidotus*. SST mean, SST maximum or SST minimum was included in the most parsimonious models and had the highest variable importance scores for each of these three species at the latitudes examined, with juvenile fish densities positively correlated with warmer SST (Table 1, Figure 5).

The density responses of these juvenile tropical and subtropical fishes to benthic habitat variables differed among species, but the strength of effect was consistently weaker than the effect of SST. This was most pronounced for *C. guentheri* which exhibited no clear association with a particular habitat at reefs at 33°S where this species was most frequently observed (Figure 5). Among the other range-expanding species, benthic habitat variables that significantly predicted juvenile fish densities in models included a positive relationship with unconsolidated sediment for *P. microlepidotus* (both latitudinal models, 33°S and 34°S) and with turf algae for *P. spilurus* (two of four latitudinal models, 30°S and 35°S) (Table 1, Figure S1). Juveniles of *P. microlepidotus* and *P. spirulus* tended to avoid reefs with kelp cover (Table 1, Figure 5). Juveniles of these three species showed consistent responses to wave exposure, with sheltered sites supporting greater densities of these fishes. This correlation was particularly strong for *C. guentheri* juveniles.

Unlike the other range-expanding tropical and subtropical reef fishes, the influence of SST relative to habitat cover was weak for *T. lunare* (Moon wrasse; family Labridae). The species model indicated that bare rock cover and depth were the best predictors of densities of juvenile *T. lunare* at reefs at 33°S (Table 1). Juveniles of *T. lunare* were associated with shallow reefs dominated by bare rock (Figure 5).

For the temperate species, greater juvenile fish densities were frequently positively related to cover of submerged macrophyte habitat types, with the influence of SST typically being less important in comparison to habitat availability. The full subset GAM analysis revealed that higher numbers of juveniles of *E. armatus* at reefs at 35°S, and *O. lineolatus* at reefs at three of the six latitudes examined, were positively related to increasing cover of kelp (Table 1, Figure S1). The strongest driver of densities of juveniles of *P. laticlavius* at reefs at 35°S was cover of macroalgae (Table 1, Figure 5). Though the effect was weaker, macroalgae cover was also important in driving the distribution of juveniles of *E. armatus* and *O. lineolatus*
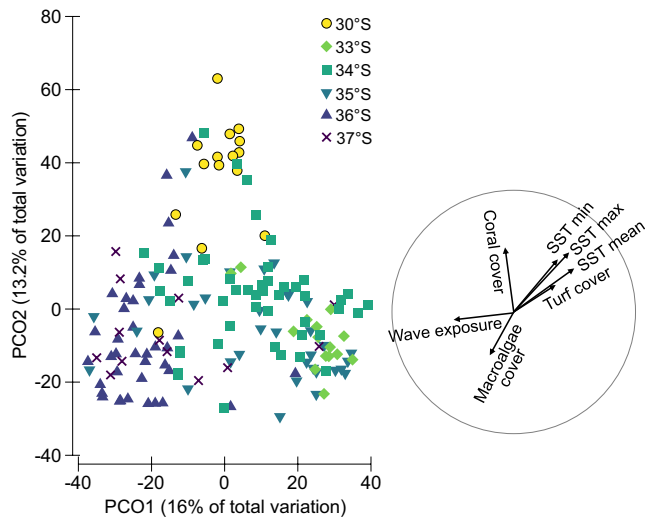
FIGURE 3 Principal coordinates (PCO) ordination of juvenile fish assemblages on south-eastern Australian reefs. The PCO was conducted at the site level for ease of presentation. Shown are the benthic habitat and environmental variables that are correlated (Pearson's $r > 0.4$) with the ordination structure. SST, sea surface temperature
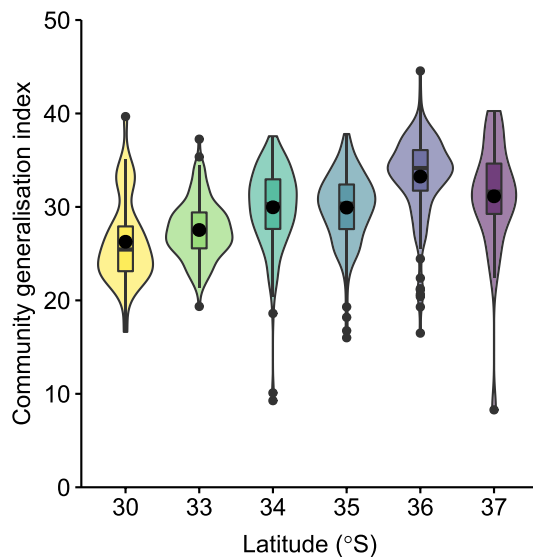

FIGURE 4 The community generalization index (CGI) values for juvenile fish assemblages on south-eastern Australian reefs. CGI values were calculated for each survey in the dataset. Boxplots show the median and interquartile range, with means indicated by black circles

(Figure 5). Together with these benthic habitat variables, mean SST was the second most important predictor of densities of juvenile *E. armatus* and *P. laticlavius*, with warmer temperatures corresponding to greater densities of these fishes (Figure 5). It should be noted however that the inferential power of the models for these species was low (Table 1). For *O. lineolatus*, the influence of SST on the distribution of juvenile fishes was less clear, with the strongest influence of SST being negative for this species (Table 1, Figure 5).

3.3 | Structural equation models

The piecewise structural equation models (SEMs) further confirmed the importance of SST relative to biological (benthic cover) and physical (depth, wave exposure) habitat variables in driving juvenile densities of the focal species. Strong direct positive links between SST and juvenile densities were observed for three of the range-expanding species, *P. spilurus* (at 35°S), *C. guentheri* and *P. microlepidotus* (at 34°S), with this effect being significant for the two tropical species *P. spilurus* ($p = .03$) and *C. guentheri* ($p = .003$) (Figure 6a–c). Densities of the latter species had a strong negative relationship with wave exposure ($p = .03$). There was also a significant positive indirect effect of SST on densities of juveniles of subtropical *P. microlepidotus* (mediated by kelp cover, $p = .03$) as well as *P. spilurus* (mediated by turf algae cover, $p = .0008$). Kelp cover was significantly ($p = .008$) and negatively related to densities of juvenile *P. microlepidotus*. For the temperate wrasse species *O. lineolatus*, SST displayed a stronger influence than habitat cover or depth on densities of juvenile fishes (at 36°S); however, this effect was negative and highly significant ($p = .0004$) (Figure 6d). Juvenile densities of this species had positive relationships with cover of kelp and macroalgae, although the effect of macroalgae cover was stronger and also significant ($p = .003$). Depth had an indirect negative effect on densities of juvenile *O. lineolatus*, with this effect mediated via cover of macroalgae.

4 | DISCUSSION

Warming of temperate reefs is prompting a range of direct and indirect effects on species' distributions. How species respond to shifts in isotherms and habitat composition, and interactions between these factors, will greatly influence the composition of emergent assemblages on warming temperate reefs. The importance of these factors is amplified during species' early life stages due to both direct effects of temperature and limitations in suitable habitat for settlement, feeding or refuge.

The present study builds on previous findings by using a long-term citizen science dataset to elucidate the key ecological and environmental drivers of juvenile fish distributions at regional and local, species-specific scales, along one of the most rapidly warming coastlines globally (Hobday & Pecl, 2014). We identify that habitat shifts on tropicalized reefs are likely to facilitate range expansion by warm-water fishes, as also shown in some previous studies (Beck et al., 2017; Nakamura et al., 2013), but also highlight potential vulnerabilities of cool-water reef fishes to these changes.

We show that despite clear evidence of functional links between habitat types and juvenile densities for some species, among the ecological and environmental variables examined, the strongest and most consistent predictor of juvenile fish densities on shallow rocky reefs in south-eastern Australian coastal waters was sea surface temperature (SST). Overall, SST featured as a variable predicting juvenile fish densities in the most parsimonious

TABLE 1 Best generalized additive models for predicting juvenile fish density for selected species of interest

Latitude	Model	Δ AICc	ω AICc	R^2	edf
Parupeneus spilurus					
30°S	Coral cover + Turf cover	0.00	0.15	.35	5.00
33°S	Kelp cover + SSTmean	0.91	0.18	.26	17.2
34°S	Wave exposure + SSTmax	0.00	0.15	.38	34.1
35°S	Turf cover + SSTmax + SSTmin	0.00	0.84	.25	30.9
Chaetodon guentheri					
33°S	Wave exposure + SSTmean	0.94	0.26	.22	15.0
Thalassoma lunare					
33°S	Rock cover + Depth	0.00	0.19	.18	12.2
Prionurus microlepidotus					
33°S	Unconsolidated sediment cover + SSTmean	0.00	0.33	.09	9.28
34°S	Kelp cover + Unconsolidated sediment cover + SSTmean	0.00	0.98	.12	9.26
Ophthalmolepis lineolatus					
30°S	Depth + SSTmean	0.00	0.31	.21	6.54
33°S	Kelp cover + Sessile invertebrates cover	0.00	0.40	.26	15.5
34°S	Unconsolidated sediment cover + SSTmean	1.87	0.08	.21	30.3
35°S	Turf cover + Depth	0.00	0.24	.21	22.7
36°S	Kelp cover + SSTmean	0.00	0.31	.15	11.7
37°S	Kelp cover	0.00	0.74	.60	7.77
Enoplosus armatus					
35°S	Kelp cover + SSTmean	0.00	0.26	.03	6.86
Pictilabrus laticlavius					
35°S	Macroalgae cover + SSTmean + SSTmin	0.00	0.52	.06	25.2

Note: The models listed are those with the lowest AICc (ΔAICc ≤2) value and fewest variables.

Abbreviations: edf, estimated degrees of freedom; SST, sea surface temperature.

model for six of the seven species examined, reaffirming the significant influence of temperature on marine species' distributions (Edgar, Alexander, et al., 2017; Stuart-Smith et al., 2017; Tittensor et al., 2010). Densities of juvenile fishes typically responded positively to warmer SST, with this response being stronger for range-expanding species observed outside of their historical range. Considering that one of the key regulating factors currently constraining the successful recruitment of warm-water reef fishes to higher-latitude reefs in south-eastern Australia is winter SST (Figueira & Booth, 2010), and that long-term monitoring indicates that winter SSTs are increasing, barriers inhibiting the persistence of tropical and subtropical reef fishes on temperate reefs may be relaxed in coming decades. Other mechanisms that influence dispersal and transport of fish early life stages not captured in this study, such as current strength and proximity to the coast, also likely contribute to the patterns observed (Booth et al., 2007; Suthers et al., 2011). Investigating these processes is inherently difficult via observational studies (Cowen et al., 2007), and although disentangling the individual effects of multiple environmental drivers in species models is challenging, it warrants further research. Nonetheless, the strong correlations between SST and density responses of cool and warm-water juvenile fishes

observed across a broad latitudinal range provides support for the important role of SST in determining juvenile reef fish distributions in south-eastern Australian waters.

Juveniles of tropical and subtropical range-expanding fishes tended to avoid kelp and macroalgae, two of the key habitat-formers that dominate temperate shallow rocky reefs. Instead, densities of range-expanding juvenile fishes were positively influenced by the availability of abiotic or turf algal habitats. The presence of kelp and macroalgae on temperate reefs in south-eastern Australia is suggested to inhibit the recruitment of tropical fishes (Beck et al., 2017). Our findings are also consistent with recent research that identifies warm-water range-expanding fishes including *P. spilurus* (Black-spotted goatfish), *C. guentheri* (Gunther's butterflyfish), *T. lunare* (Moon wrasse) and *P. microlepidotus* (Australian sawtail) as potential "winners" of tropicalization. Long-term monitoring indicates increasing abundances of tropical and subtropical species such as these on reefs where kelp forests have disappeared in a south-eastern Australian tropicalized system at 30°S (Smith et al., 2021). Should the habitat shifts that have already occurred at the northern extent of our study region be indicative of future conditions, recruitment hotspots for range-expanding juvenile fishes could emerge along the entire south-eastern Australian coastline.
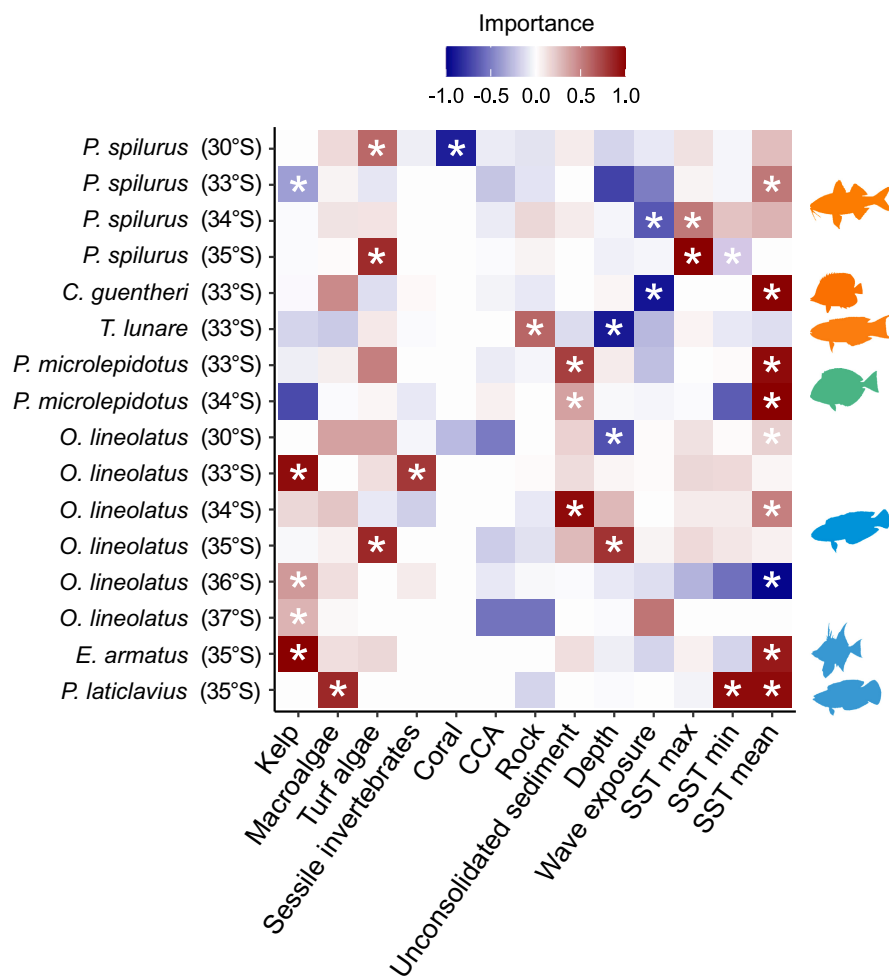
FIGURE 5 Heatmap showing the relative importance of predictor habitat and environmental variables in explaining the densities of juveniles of selected species, based on the full subset of fitted models. Positive relationships are indicated by red shading and negative relationships by blue shading, with the strength of the shading relative to the importance of the predictor. Variables in the most parsimonious models are indicated by an asterisk (*). Tropical, subtropical and temperate reef fish species are indicated by orange, green and blue icons respectively. CCA, crustose coralline algae; SST, sea surface temperature

The observed pattern of association of juvenile fishes with relatively unstructured habitats may seem non-intuitive, as fishes' early life stages are particularly vulnerable to mortality due to processes such as predation from larger fishes (Dahlgren & Eggleston, 2001), and the structural complexity provided by kelp and other canopy-forming macroalgae should offer greater refuge spaces relative to simplified habitats (Holbrook et al., 2002; Steneck et al., 2002). However, kelp and macroalgae also provide refuge for ambush predators, and juvenile fishes may be less susceptible overall to mortality from predation in more open areas that are out of reach by these predators (Hoey & Bellwood, 2011). Alternatively, these tropical and subtropical fishes may be displaying a natal behavioural response, whereby their avoidance of structurally flexible, moving habitat-formers occurs due to associations with structurally stable habitat-formers such as coral within their native range (Wilson et al., 2010). As in previous studies (e.g. Beck et al., 2016), the tendency of the range-expanding species examined here to avoid more exposed reefs where wave action on temperate habitat-formers would be higher suggests species' behavioural as well as physical attributes (e.g. swimming ability; Fulton & Bellwood, 2004) should not be overlooked when predicting fish recruitment outcomes. Given that storms are expected to increase in frequency and severity due to climate change (Babcock et al., 2019), direct and indirect (e.g. via

dislodging of kelp; Wernberg et al., 2019) influences of wave action on juvenile fish distributions could potentially become stronger. Resource use can also drive juvenile fish-habitat associations, for example herbivorous fishes with turf algae, which they consume.

The establishment of range-expanding tropical and subtropical fish populations in temperate environments is therefore likely to be partially dependent on their ability to successfully take advantage of a preferred habitat among those available in the reefscape, where the choices available may be foreign to their species (Cure et al., 2018). The persistence of tropical range-expanding species such as *P. spilurus*, *C. guentheri* and *T. lunare* on higher-latitude reefs is less likely to be constrained by habitat, since there is ample availability of the habitat types (e.g. bare rock, unconsolidated sediment, turf algae) typically preferred by these species on temperate reefs. Moreover, tropical species with traits that favour range expansion, such as broad habitat niches, low dietary specialization and few larval settlement requirements in their contemporary range, should be more able exploiters of local resources and thus better colonizers of temperate habitats (Monaco et al., 2020; Stuart-Smith et al., 2021), once they are unconstrained by thermal conditions. Our findings suggest that for tropical vagrant species with attributes such as these, the successful colonization of warming temperate reefs is likely to be determined more by physiological (thermal) than ecological (habitat) limitations.

FIGURE 6 Path diagrams of structural equation models for the relationships between juvenile fish densities and habitat and environmental variables for (a) *Chaetodon guentheri* at 33°S, (b) *Prionurus microlepidotus* at 34°S, (c) *Parupeneus spilurus* at 35°S and (d) *Ophthalmolepis lineolatus* at 36°S. Arrow widths are proportional to effect sizes (coefficients) for each path. Paths are labelled with coefficient values. Significant paths are indicated by dark lines and non-significant paths with semi-transparent lines. The significance level of effect is denoted by asterisk (*$p < .05$, **$p < .01$, ***$p < .001$). Black and red arrows indicate positive and negative relationship between variables, respectively. R^2 values shown for response variables are the conditional R^2, which take into account fixed and random effects. SST, sea surface temperature; Sessile inverts., Sessile invertebrates; Unconsolidated sed., Unconsolidated sediment
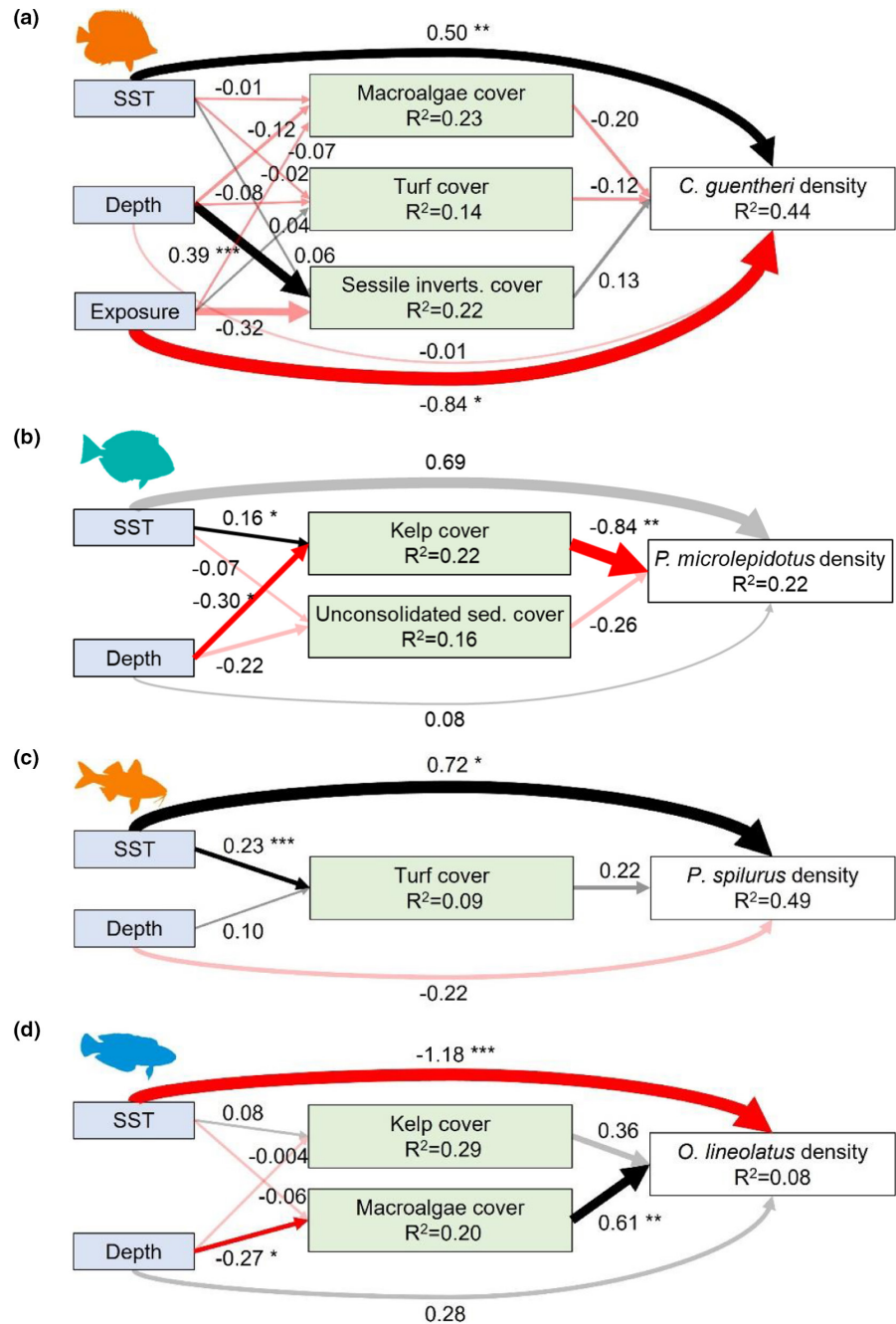
Increasing abundances of tropical and subtropical herbivorous fishes have been implicated in declines in the distribution of kelp forests and other canopy-forming macroalgae from temperate coastlines globally, including both the east and west coasts of Australia, Japan and the Mediterranean (Vergés et al., 2016; Vergés, Tomas, et al., 2014; Wernberg et al., 2016). Tropical herbivorous fishes' permanent presence on tropicalized reefs indicates that thermal and habitat conditions are suitable for recruitment and reproduction of these fishes well outside of their nominal distributional range (Nakamura et al., 2013; Zarco-Perello et al., 2021). Our investigations highlight the importance of warmer SST as the key mechanism facilitating range-expanding tropical and subtropical herbivores such as *P. microlepidotus* recruiting to temperate reefs. These herbivorous

fishes likely benefit from the mosaic-like arrangement of habitats typical of shallow rocky reefs, settling in preferred habitat patches within the reef that are free of submerged macrophytes and consuming the abundantly available algal resources. Future increases in SST that enable overwintering by range-expanding warm-water herbivorous fishes are expected to lead to increased levels of herbivory (Basford et al., 2015). Although many of these fishes are not able to directly overgraze large macroalgae, they are very effective at maintaining reefs free of canopy-forming macroalgae by consuming early life history stages of species like kelp (Zarco-Perello et al., 2021).

It appears that a complex interplay of environmental (warming sea temperatures) and physiological (habitat plasticity) factors is contributing to the recruitment and persistence of range-expanding

herbivorous fishes on tropicalized reefs. As warmer conditions are realized, what may ultimately result is a positive feedback loop whereby intensified herbivory of temperate habitat-forming species by expanding populations of tropical and subtropical herbivorous fishes further facilitates tropicalization. The presence and cover of turf algae and hard corals in temperate Australian reefs respond positively to reductions in the extent of kelp habitats (Ling et al., 2018), suggesting that in the absence of kelp forests, through a release of competitive interactions, the tropicalization feedback loop will favour a compositional shift towards simplified low-biomass turf algae and/ or coral-dominated reefscapes (e.g. Vergés et al., 2019; Wernberg et al., 2016; Yamano et al., 2011). The cascading impacts for associated fish assemblage structures will lead to shifts in trophic composition and associated energy flows on temperate reefs (Holland et al., 2020; Smith et al., 2021; Vergés et al., 2019) that are yet to be fully resolved, but also involve interactions with management practices.

Managing tropicalized systems will require a combination of traditional and out-of-the-box conservation approaches. It will also involve decision-makers selecting among strategies that focus on preserving current ecosystem states or adapting to almost inevitable ecosystem change. Among the more traditional approaches, effective no-fishing marine protected areas (MPAs) where populations of predatory fishes and lobsters have strongly recovered may be able to resist establishment of range-expanding species, as has been observed on higher-latitude Australian reefs (Bates, Barrett, et al., 2014). No-take MPAs could therefore potentially facilitate natural biological top-down control of early life stage and small range-expanding fishes by enhancing predation rates, conferring some resistance to climate-driven change. However, the no-take areas in the MPAs investigated in this study appear only weakly effective at improving large predatory fish densities (see Appendix S2), limiting the scope of top-down control compared to other MPAs in this region (Edgar & Stuart-Smith, 2009; Edgar et al., 2017). An appropriately designed and well-enforced system of no-take MPAs could be a useful tool to slow the pace of tropicalization while enabling scientists and managers to collaboratively develop novel strategies to future-proof marine ecosystems (Bruno et al., 2018). More novel management approaches include building resilience by restoring habitat-formers (Layton et al., 2020), assisting colonization by range-expanding habitat-formers with similar functional traits to existing species or developing new fisheries that target range-expanding species (Vergés et al., 2019). These measures have flow-on implications that require careful consideration before being implemented.

Kelp forests are used as nursery habitats by juveniles of some reef fishes in Australian temperate waters (Fulton et al., 2016; Wernberg et al., 2019), and other temperate marine regions globally (Bertocci et al., 2015). Kelp habitats emerge as an important nursery habitat for a few temperate reef fish species in this study. This includes the endemic southern maori wrasse, *O. lineolatus*. Concerningly, the declining occurrence of *O. lineolatus* on tropicalized reefs in south-eastern Australia points to this species as an important potential "victim" of tropicalization (Smith et al., 2021). This decline may be an early indication of the detrimental effect of the tropicalization-induced overgrazing of kelp forests (Vergés et al., 2016) leading to the loss of suitable nursery habitat for the recruitment of this species. Similar impacts are likely to apply to other temperate wrasses on tropicalizing reefs, as these fishes often associate with kelp and canopy-forming macroalgal habitats on rocky reefs as juveniles (Fulton et al., 2016). Ongoing declines in the distribution of kelp forests on shallow rocky reefs could have substantial implications for the recruitment of temperate fishes that depend on these habitats as nurseries. Moreover, should the negative effect of peak seasonal SST on juveniles of temperate wrasses we observed be indicative of a broader species pool, constraints on thermal niches must also be considered alongside nursery habitat availability for these fishes, particularly at higher-latitude reefs.

The endemic temperate wrasse *P. laticlavius* appears to closely associate with macroalgal habitats in its juvenile stage, consistent with its macroalgal-specialism as an adult (Curley et al., 2002). We expect that changes in habitat composition as reefs are tropicalized will more deeply impact the recruitment of juvenile reef fishes with stronger functional links to habitats, such as *P. laticlavius*, if there is a decline in the availability of preferred habitats. Habitat specialist fishes may be constrained in their capacity to adapt to new or rapidly changing environments by narrow thermal tolerances, distributional ranges, or resource obligation. Indeed, *P. laticlavius* is particularly vulnerable to changes associated with tropicalization in subtropical south-eastern Australian reefs (Smith et al., 2021). Reef fish species endemic to temperate regions could be more sensitive to tropicalization due to limited geographical ranges and ecological specializations (McKinney, 1997). This poses major challenges for managers responsible for safeguarding endemic temperate species. Ensuring the persistence of species with functional traits that confer vulnerability to ocean warming and limited scope for latitudinal expansion could entail devising management solutions to identify, protect and restore habitat refuges within species' ranges to assist their capacity to adapt to climate change stressors. The conservation challenge will be particularly great for marine systems such as Australia's Great Southern Reef that have high levels of endemism (Bennett et al., 2015), as endemic species hotspots are likely to be especially vulnerable to climate change (Dirnböck et al., 2011).

The community generalization index, an indication of the composition of habitat niche breadths of species within assemblages, generally increased from lower to higher-latitude reefs within the study region. Conversely, species richness was reduced at higher-latitude reefs relative to lower-latitude reefs. Together, this suggests that greater availability of urchin barrens habitats typical of many cool-temperate reefs along this coastline favours generalist species, but at the expense of species richness. This is consistent with a recent assessment of the response of fish communities to macroalgal vs. barrens habitats in temperate south-eastern Australia reefs (Stuart-Smith et al., 2021). Transitions from kelp forests and canopy-forming macroalgal habitats to unvegetated rocky habitats could therefore contribute to a broader biotic homogenization of warming temperate reefs (Olden, 2006; Stuart-Smith et al., 2021). Habitat substitutions inhibiting the recruitment of ecological specialists could lead

to losses of functional characteristics from warming temperate marine systems. Nonetheless, urchin barrens are a key habitat provider for range-expanding tropical fishes on temperate reefs (Beck et al., 2017; Coni et al., 2021). This could create another feedback loop and emphasizes the role of shifts towards less structurally complex habitats in facilitating the emergence of novel, rather than biotically similar, tropicalized assemblages.

In the face of rapid changes in species distributions, sustained long-term monitoring of marine assemblages is critical to providing a baseline for constructing predictions about future outcomes for biodiversity and ecosystem functions. Our investigation was possible only through analysis of data made available through the RLS programme. Nevertheless, a potential source of bias relevant to this study is the likelihood that densities of smaller sized fishes are underestimated by visual surveys by divers, and this may be exacerbated as the cover of kelp and other canopy-forming macroalgae on surveyed reefs increases. While we were able to detect important drivers of juvenile fish distributions for some species, only a small proportion of the total species pool in these waters could be quantitatively examined. Further research is required to determine how juveniles of a broader range of fishes vary in their responses to habitat shifts on tropicalized temperate reefs, how interactions between habitat and SST vary with fish trophic group, and how fish grazing and habitat feedbacks contribute to the emergence of novel assemblages in warming coastal environments.

5 | CONCLUSION

In warming temperate reefs, the availability of suitable habitat and sea temperatures are key factors that will influence the abundance and distribution of the early life stages of temperate reef fishes within their contemporary range, and tropical and subtropical reef fishes making poleward incursions. In the absence of suitable ecological conditions, disruptions to fish recruitment are likely, with implications for population replenishment of resident temperate reef fishes and colonization of higher-latitude reefs by range-expanding tropical and subtropical reef fishes. Factors such as larval supply, predator-prey interactions, and competition for resources will also play a role in determining reef fish recruitment success. However, we emphasize that understanding the relative importance of direct and indirect influences of temperature and habitat-mediated effects on juvenile fish distributions is critical for predicting how assemblages will evolve on tropicalized reefs in the future.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13484.

DATA AVAILABILITY STATEMENT
Additional details of the dataset and model results are provided in the supporting information. The data supporting the models and findings of this study are available in Dryad: https://doi.org/10.5061/dryad.66t1g1k39.

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BIOSKETCH

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