

Latitudinal patterns in trophic structure of temperate reef-associated fishes and predicted consequences of climate change

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Abstract

Some dramatic consequences of climate change are caused by shifting species interactions and associated changes to trophic structure and energy flow. In coastal ecosystems, the relative abundance of feeding guilds indicates dominant energy sources sustaining food webs. Here, we use a space-for-time substitution to investigate potential climate change impacts on trophic structure and energy flow in reef fish communities. We investigated latitudinal and seasonal patterns in the biomass distribution of five trophic groups across subtropical to temperate latitudes (29 to 44°S) in eastern Australia. Along western boundary currents, temperatures are increasing up to three times faster than the global average, making them ideal for studying climate change impacts. Using 10 years of Reef Life Survey data, we investigated potential determinants of fish biomass and community composition with generalized additive mixed models. Biomass decreased towards higher latitudes, from 220 g/m² in the subtropics to 13 g/m² in the south. Dominant trophic group also changed latitudinally, with herbivores and omnivores dominating lower latitudes (~30°S), zooplanktivores at mid-latitudes (~35°S) and benthic invertivores at higher latitudes (~40°S). Biomass varied seasonally, with lower latitudes experiencing a 3.2-fold increase between spring and autumn, while variation at higher latitudes was 1.9-fold. We found strong evidence that factors linked to latitude and seasonality are important determinants in the distribution of fish trophic structure. As climate-driven species redistributions accelerate in the 21st century, expected poleward shifts in trophic structure include overall increases in fish biomass linked to enhanced herbivory at mid-latitudes and increased planktivory at higher latitudes.

KEYWORDS

citizen science, planktivory, reef fish, Reef Life Survey, rocky reefs, trophic composition

1 | INTRODUCTION

Climate change has impacted all ecosystems on Earth, despite an average warming of only ~1°C so far (Pecl et al., 2017; Scheffers et al., 2016). One of the most widely documented impacts of warming

is the global redistribution of species (Parmesan, 2006; Poloczanska et al., 2013). To stay within their preferred thermal ranges, many species are moving towards the poles, to greater altitudes on land, and into deeper waters in the ocean (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013).

This redistribution of species is leading to new biological interactions between previously separated species, disrupting trophic structures and altering food webs (Scheffers et al., 2016).

Species redistributions are happening particularly fast in the ocean, with marine species shifting, on average, at least four times faster than on land (Poloczanska et al., 2013). These rapid shifts have already led to profound disruptions, especially on shallow temperate reefs, which are highly productive (some exceed $1,000 \text{ g C m}^{-2} \text{ year}^{-1}$ (Cebrian, 1999; Mann, 1973)) and have major economic and intrinsic benefits to their adjacent towns and cities (Bennett et al., 2016; Blamey & Bolton, 2018).

In coastal marine environments, the relative importance of herbivory and planktivory provides important information about dominant energy pathways (Morais & Bellwood, 2019; Truong, Suthers, Cruz, & Smith, 2017). Fish communities in temperate reefs are mostly underpinned by planktonic energy sources, with local benthic primary production being a minor contributor to local food webs (Truong et al., 2017). In these systems, seasonal fluxes of planktonic primary productivity can enrich sediments and fuel benthic food webs indirectly as excess organic material sinks to the seafloor (Heip, 1995; Parrish, Deibel, & Thompson, 2009; Wassmann, 1997). However, species redistributions due to climate change have increased the dominance of tropical species on temperate reefs, fundamentally altering species interactions and increasing the relative importance of herbivory (Vergés et al., 2016; Vergés, Steinberg, et al., 2014). It has been proposed that these climate-mediated shifts in energy flow from low to high herbivory can have important ecosystem function implications as a higher proportion of primary production is incorporated into higher trophic levels (Vergés et al., 2019). Such consequences of tropicalization, however, remain untested.

“Space-for-time” is a widely used approach to predict future trajectories of ecological systems based on present-day patterns, which is underpinned by the assumption that drivers of spatial gradients are similar to drivers of temporal changes (Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013; Elmendorf et al., 2015). These approaches often use latitudinal gradients to predict the effects of warming, as temperature is a key environmental variable that varies predictably with latitude (Wogan & Wang, 2018). Here, we examine latitudinal patterns in the trophic structure of fish communities and how reef fish functional biomass is spatially distributed to infer potential future changes in energy flow and fish biomass.

Previous studies measuring latitudinal patterns in reef-associated fish communities have tended to concentrate on specific trophic processes such as herbivory (Floeter, Behrens, Ferreira, Paddock, & Horn, 2005; Meekan & Choat, 1997) and predation (Barnes, Maxwell, Reuman, & Jennings, 2010; Freestone, Osman, Ruiz, & Torchin, 2011), while only a few have examined patterns in overall trophic structure (Floeter, Ferreira, Dominici-Arosemena, & Zalmon, 2004; Longo, Hay, Ferreira, & Floeter, 2019). Although zooplanktivores are the most speciose fish groups on many reefs (Bellwood, Streit, Brandl, & Tebbett, 2019; Morais & Bellwood, 2019) and can make up over 40% of fish biomass on temperate rocky reefs (Truong et al., 2017),

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we know little about large-scale latitudinal patterns of planktivory across the tropical to temperate interface of nearshore reefs. The distinct lack of studies may be partially attributed to the greater difficulty associated with observing zooplanktivores in situ (Bellwood et al., 2019).

Here, we use eastern Australia's temperate rocky reefs as a model system to uncover large-scale latitudinal patterns in trophic structure and total fish biomass, in a region strongly influenced by the East Australian Current (EAC; Suthers et al., 2011). Regions influenced by western boundary currents like the EAC, that is eastern Japan (Kuroshio Current), eastern United States (Gulf Stream), northern Brazil (Brazil Current) and south-eastern Africa (Agulhas Current), are climate change hotspots where waters are warming faster than the global average (Wu et al., 2012). Western boundary currents facilitate the poleward dispersion of warm water species (Vergés, Steinberg, et al., 2014) such as tropical herbivores (Figure 1),

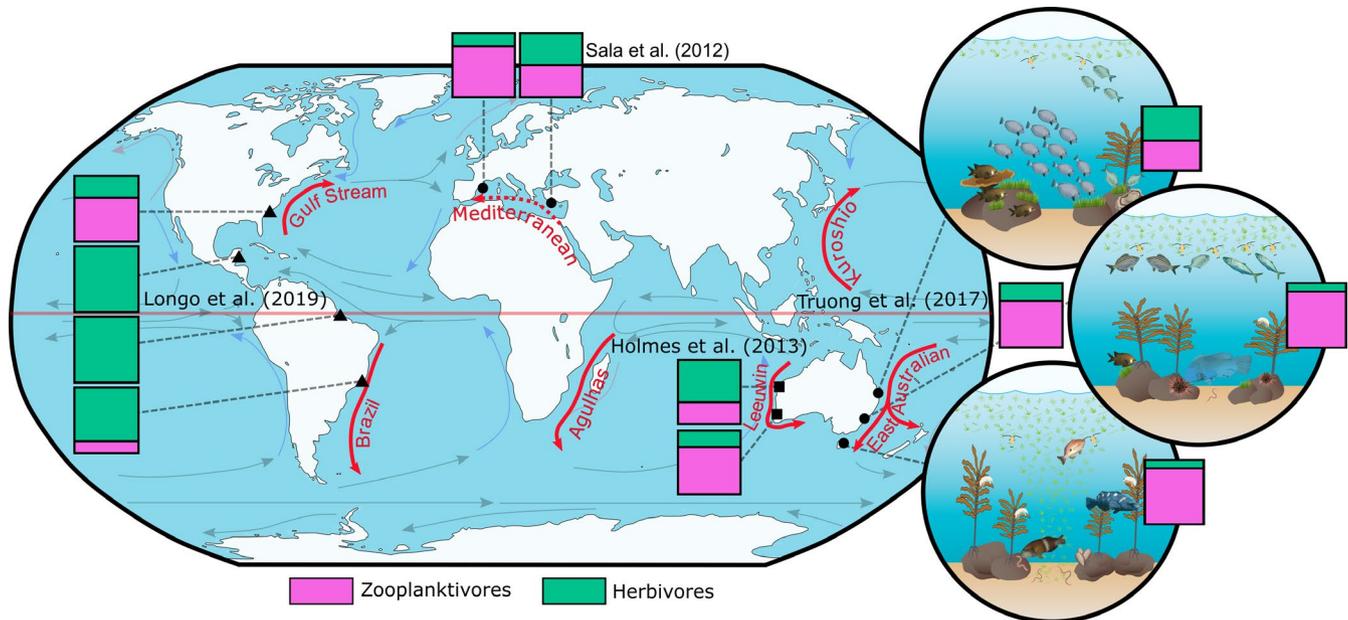


FIGURE 1 Variation in the proportional representation of herbivores and zooplanktivores (sum = 1) from select studies examining reef fish trophic structure along environmental gradients using three metrics: relative fish abundance (square symbols, Holmes et al., 2013), relative fish biomass (circle symbols, Sala et al., 2012; Truong et al., 2017) and relative feeding pressure (triangle symbols, Guilherme O Longo et al., 2019). Results from this study are presented on the far right. Major tropicalization gradients associated with boundary currents (solid red) and with invasion processes derived from the building of the Suez Canal (dashed red) are also indicated (methods in Appendix S1: Methods). Bubbles to the right of the map depict a conceptual model of temperate reef fish trophic group dominance and biomass distribution. The lower (most equatorial) latitude sites are dominated more by herbivores and omnivores and have high total biomass, low phytoplankton biomass and low zooplankton abundance. Mid-latitudes are dominated by zooplanktivores with high–moderate total biomass and productivity and the greatest zooplankton abundance, and high (more polar) latitudes are dominated by benthic invertivores with generally lower total biomass, while zooplankton abundance is low and much of phytoplankton productivity settles on the seafloor as a result of seasonal blooms

making them ideal sentinel ecosystems to understand and predict the impacts of climate change and associated poleward shifts in species distributions.

The dispersal of tropical fishes into temperate waters is not limited to western boundary currents and is occurring rapidly in other regions as well, leading to novel “tropicalization gradients.” For example, tropical herbivores have dispersed into the Mediterranean Sea from the Suez Canal and have established local populations, leading to a longitudinal gradient in herbivory (Vergés, Tomas, et al., 2014). The Leeuwin Current, an exceptional boundary current which flows poleward along the west coast of Australia, has also experienced recent tropicalization of fish communities in association with marine heat waves (Wernberg et al., 2013), affecting temperate ecosystems where planktivory may normally dominate.

We quantified how the biomass and structure of rocky reef-associated fish trophic groups vary over a latitudinal gradient across 1,800 km and 16° of latitude. Although latitude itself cannot be a causal factor shaping trophic structure, it indicates covarying environmental variables (such as temperature) that may be important determinants. We accounted for regional and local variables that may influence trophic structure and overall fish biomass by evaluating chlorophyll *a*, zooplankton abundance and

human population density, as well as non-dynamic variables such as depth. As temperature also shifts predictably with season and because seasonality is likely to be more influential at higher latitudes, we also quantified seasonal patterns in fish trophic structure and biomass.

We hypothesized that with increasing latitude, trophic composition would shift away from herbivore dominance in favour of trophic pathways that derive energy from plankton and benthic invertebrates (Figure 1). We predicted that these changes in trophic structure would be linked to lower overall fish biomass in higher latitudes, as a lower proportion of local benthic primary production is consumed (Vergés et al., 2019) and because of greater inter-seasonal variability in plankton production. At a regional level, we hypothesized that the amount of energy available as plankton would influence trophic group dominance, with the biomass of zooplanktivores linked positively to the abundance of zooplankton and/or phytoplankton. At a local level, we expected declines in the biomass of some trophic groups with high human population density (due to human impacts such as fishing) and we expected trophic group biomass to be linked to the depth of sites sampled. Finally, we discuss how climate-mediated poleward shifts of the observed distributions may alter the trophic ecology of temperate rocky reef communities during this century.

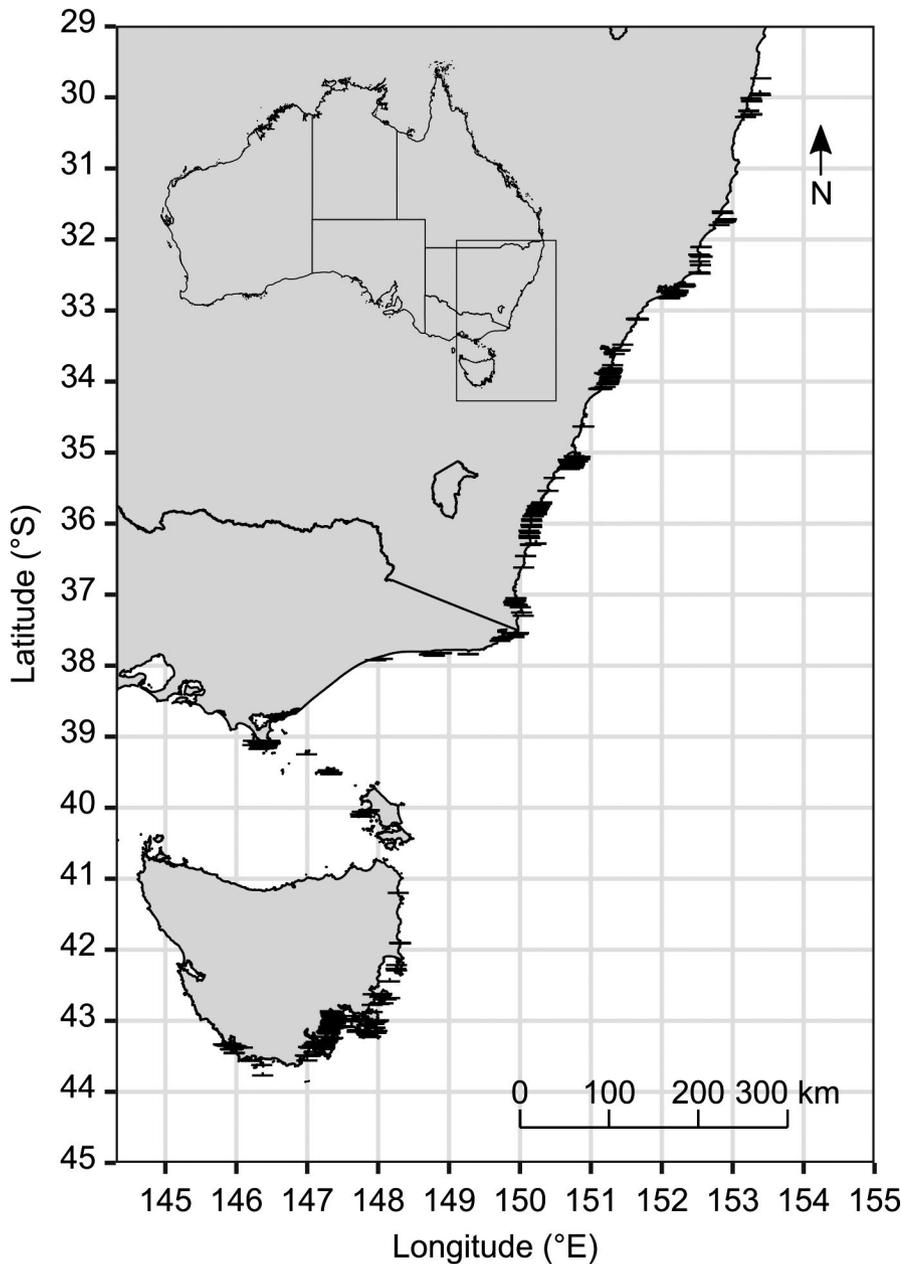


FIGURE 2 Chart of the south-east coast Australia, with black tick marks representing the 567 Reef Life Survey (RLS) sites

2 | METHODS

2.1 | Study region

Along the south-east coast of Australia, shallow rocky reefs range from urchin barrens to sponge gardens to outcrops dominated by dense stands of canopy-forming macroalgae (Bennett et al., 2016), particularly the laminarian kelp *Ecklonia radiata*, Lessoniaceae (Bennett et al., 2016; Wernberg et al., 2019). Collectively, these reefs combine to form a single entity spanning thousands of kilometres and connected by processes of the EAC (Roughan & Middleton, 2004; Suthers et al., 2011).

Water temperatures here can range from 10 to 27°C between the highest and lowest latitudes, respectively, generally peaking in March (early autumn) and reaching their minimum in September

(early spring). Current-driven localized upwellings are prevalent, particularly in spring and summer, facilitated by coastal winds (Roughan & Middleton, 2002, 2004). Upwelling events tend to be smaller and more episodic at lower latitudes and much larger at higher latitudes with the onset of spring (Everett, Baird, Roughan, Suthers, & Doblin, 2014). This spring upwelling is the driver of overall greater mean primary productivity at higher latitudes, despite the very low productivity of these waters in winter (Everett et al., 2014).

2.2 | Biomass of fish trophic groups

Fish count data were sourced from the Reef Life Survey (RLS) (reeflifesurvey.imas.utas.edu.au/portal/search, Accessed: 22/11/2017), a global

data set of systematic aquatic biodiversity surveys conducted by trained recreational divers in collaboration with experienced marine ecologists (Edgar & Stuart-Smith, 2014). The RLS follows a rigorous survey methodology globally, ensuring sites can be compared across large geographic and temporal extents. In this analysis, we combine RLS data with environmental and biological records across the same date range.

Survey data were collected from 3,032 RLS (between 01/2008 and 10/2017) across 567 sites (Figure 2). All sites were south of $\sim 29^{\circ}\text{S}$, across 16° of latitude, spanning the subtropical to temperate east coast of Australia, within an area commonly referred to as the "Great Southern Reef" (Bennett et al., 2016). Each survey consists of a single 50-m transect along a constant isobath. After laying the measuring tape along the transect, divers spend a few minutes preparing equipment (~ 5 min) providing an acclimation period for diver effects on fish to subside (Dickens, Goatley, Tanner, & Bellwood, 2011). Subsequently, two divers swim the length of the tape and record the identity, abundance and length class of all fishes observed within 5 m either side of the transect. Our analysis of these surveys was limited to non-cryptic teleost fishes, and to taxa observed in at least 5% of surveys. Fish biomass for each survey was calculated by RLS from fish counts, using observed fish total length and species-specific length-weight relationship variables available in FishBase (Froese & Pauly, 2009).

For the purposes of our analysis, it was essential that fish detectability remained consistent across latitude. The effects of divers on fish detectability have been studied in tropical (Dickens et al., 2011; MacNeil et al., 2008) and temperate systems (Edgar, Barrett, & Morton, 2004; Holmes et al., 2013; Watson & Harvey, 2007; Watson, Harvey, Anderson, & Kendrick, 2005). Although diver effects have been recorded for most families studied (Dickens et al., 2011), the fish most susceptible to variation in detectability generally include larger predators, chondrichthyans and cryptobenthic species (Brandl et al., 2019), which we have excluded from our analyses to avoid potential bias. Although large predators can dominate fish biomass at remote isolated reefs (Stevenson et al., 2007), their contribution to total fish biomass is often much less at reefs exposed to fishing and human disturbance (Valdivia, Cox, & Bruno, 2017), which are both prevalent factors along the heavily populated coastline of south-east Australia. Further, the primary reason for limiting our study to latitudes greater than 29 degrees south was to restrict our focus to only macroalgae-dominated rocky reefs and avoid the increased complexity of coral-dominated tropical sites. Therefore, we do not believe a latitudinal bias in detectability exists in the analysed data.

There are certainly sources of bias associated with underwater visual census that can affect the estimation of fish lengths, abundances and ultimately biomass (Edgar et al., 2004; Harvey, Fletcher, Shortis, & Kendrick, 2004). However, it is important to note that due to rigorous consistency in survey methods across the RLS programme, these biases should be consistent across locations and times. Our analyses were only concerned with comparisons of relative biomass, and as such, absolute biomass values were not necessary for survey results to be comparable.

To evaluate comparability of surveys across latitude and seasons, we compared site characteristics across our study domain. We tested whether survey depth, swell exposure or visibility, differed by season or four-degree latitudinal bin, using two-factor ANOVA (season and latitude bin) and Tukey's post hoc tests in R (R Core Team, 2018). Swell exposure was determined using the "dist2Line" function from the R package geosphere (Hijmans, Williams, Vennes, & Hijmans, 2019) to locate the nearest point to each site on a polygon shapefile of the Australian coast (Whiteway, 2009) and subsequently calculate the bearing between each point with its corresponding site. We then extracted mean wave direction per month by site coordinates from the Australian Wave Energy Atlas (Hemer, Pitman, McInnes, & Rosebrock, 2018) and rescaled their alignment with site aspect from 0 to 1, similar to Turnbull et al. (2018). Visibility data were diver estimates (in m) and were only available for 1,820 out of the 3,032 surveys. Although some pairwise differences in depth (max: 3.26 m), swell exposure (max: 0.07) and visibility (max: 3.48 m) were statistically significant, they were all very small and unlikely to be ecologically meaningful (Appendix S1: Table S1, Figure S1).

Photo quadrats, which contained 36 categories for benthic cover, were only available for 202 out of 567 sites. They were used to calculate a matrix of proportionate benthic cover using the R package vegan (Oksanen et al., 2013). These results were then compared visually with non-metric multidimensional scaling (NMDS) and bar charts (Appendix S1: Figures S2, S3), and statistically using the "adonis" function (Oksanen et al., 2013), which computes a two-factor permutational MANOVA, and post hoc comparisons of centroid distance were made using the "betadisper" function. As sites spanned $\sim 16^{\circ}$ of latitude, differences in benthic composition across latitude were to be expected (max: 0.18), while comparatively minimal variation across seasons was observed between winter and spring (max: 0.08) (Appendix S1: Table S1).

To further evaluate comparability of sites and surveys, we tabulated the number of surveys for each season and year by site (Appendix S1: Tables S2 and S3, respectively) and by one-degree latitudinal bands (Appendix S1: Figures S4 and S5, respectively). Besides apparent under-sampling between 38° and 39°S , and at latitudes higher than 37°S in winter and spring, there was no distinct seasonal bias to temporal survey distribution across the nearly ten-year period of survey data. This lack of winter and spring data precludes any seasonal conclusions for high latitudes. Most latitudes had regular survey coverage over the ten-year period, except for between 38° and 42°S , coinciding with the Bass Strait.

2.3 | Trophic classification

A species list of 163 fish species (all taxa observed in $\geq 5\%$ of surveys) and trophic group classifications was generated, with the use of data from FishBase (Froese & Pauly, 2009), Fishes of Australia (Bray & Gomon, 2018) and existing classifications made by Truong et al. (2017), using a similar methodology to Soler et al. (2015) which classified fishes into trophic groups for a global analysis of RLS data

(Appendix S1: Table S4). Taxa were allocated to one of five categories: zooplanktivores (feed primarily on zooplankton); herbivores (feed primarily on algae and/or seagrass); omnivores (have algae and/or seagrass as a minor component of their diet); benthic invertivores (carnivorous species that feed on zoobenthos but generally not fishes); and piscivores (carnivorous species that feed primarily on other fishes). This species list was then used to classify fishes in the biomass database, and biomass totals were summed among taxa to calculate the biomass in each trophic group for each survey.

2.4 | Characterising latitudinal trends

To examine generally how trophic composition varied across latitude, we analysed multiple metrics: total fish biomass, trophic group biomass and taxa-level biomass. We conducted linear regression to test whether total fish biomass broadly varied with latitude. The study region was then divided into 1-degree latitudinal bins, and mean observed total fish biomass per survey was calculated for each bin. Similarly, the mean proportion of biomass for each of the five fish trophic groups was calculated for each latitudinal bin, which was used to construct bar plots of biomass and trophic composition by latitude. The total number of surveys used in calculations was also tabulated and displayed with each bar plot for validation of spatiotemporal coverage.

To assess whether any seasonal variation in fish biomass was driven by growth or migration, we plotted length frequency distributions for each combination of season and four-degree latitudinal bin and calculated the median value for each distribution. Minimal variation in median length across seasons within latitude bins should indicate an effect of migration, rather than growth, on the total biomass of fish observed.

For a multivariate analysis of taxa-level biomass, Bray–Curtis dissimilarity was calculated from a matrix of 4th root-transformed mean biomass per site for the 163 fish species and visualized using non-metric multidimensional scaling (NMDS) with the R package “vegan” (Oksanen et al., 2013) in R (R Core Team, 2018). For a multivariate analysis of trophic group biomass, each site’s mean per-survey biomass of each trophic group was calculated, and these means were then summed for each site and used to calculate the proportionate biomass contribution for each of the five trophic groups. These proportions were used to calculate Bray–Curtis dissimilarity and visualized using NMDS. To determine which species and trophic groups were important in driving differences in biomass across latitude, trophic group loadings were generated using the `envfit` function in the “vegan” R package and overlaid on the trophic group proportion NMDS plot as vectors.

2.5 | Explanatory variables

2.5.1 | Zooplankton abundance

The Integrated Marine Observing System (IMOS) maintains a network of National Reference Stations (NRS) at strategic locations

around Australia. Regular zooplankton biomass surveys are conducted approximately bimonthly at NRS sites, and data were selected to span the same date range (09/2008–08/2017) as RLS data (01/2008–10/2017). Three reference sites (North Stradbroke Island: 27°S, Port Hacking: 34°S and Maria Island: 42°S) represent the northern, the middle and the southern extent of the RLS sites, respectively. Since zooplankton biomass and abundance are regularly measured simultaneously at these locations, these point location data were used to model the relationship between zooplankton abundance and biomass with linear regression, producing the following equation ($p < .001$, Adjusted $r^2 = 0.31$):

$$\text{Biomass} = e^{0.518 \cdot \ln \text{Abundance} - 1.57}$$

This relationship between zooplankton abundance and biomass suggested that continuous zooplankton abundance data from the IMOS Continuous Plankton Recorder (CPR) could also be used in our models. This assumes that the CPR over the continental shelf is representative of zooplankton abundance at our spatial scale. We extracted zooplankton abundance from CPR surveys between 03/2008 and 03/2017 and summed the abundance across each standardized 10 nautical mile section of CPR mesh (~19 km) for each voyage. We excluded all small zooplankton with a geometric mean size <0.6 mm diameter (Champion, Suthers, & Smith, 2015), to determine the mean zooplankton abundance for 0.5-degree latitudinal bins (~56 km each) for each of the four seasons. These bins were used for matching with RLS, which were conducted in the same season and latitudinal bin.

2.5.2 | Human population density

Human population density along the east coast was calculated in ArcGIS (ESRI, 2011) from Australian Bureau of Statistics Australian Population Grid 2016 (Australian Bureau of Statistics, 2017). A circular buffer with a 50 km radius was created for each RLS site in the analysis as in Bennett et al. (2016). The total number of people living within each 50 km radius was then calculated and applied to each site as a predictive variable in the full model. This variable is intended to represent potential human impacts such as fishing or urbanization near a site.

2.5.3 | SST and chlorophyll

Chlorophyll *a* concentration was used as a measure of phytoplankton biomass. Sea surface temperature (SST) and chlorophyll *a* concentration (Chl; using OC3 algorithm) were derived from Level-3 MODIS satellite data and were obtained from the IMOS Data Portal (<http://imos.aodn.org.au/imos/>) at daily 1-km resolution. The extent of the satellite data was limited to a 10 × 10 pixel grid (~100 km²) centred on each RLS site and bounded by the coast in order to maximize the data retrieval for each reef and minimize cloud interference. Seasonal means of SST and Chl (e.g., Spring, 2010) were calculated for each site for use in the modelling.

2.6 | Trophic group biomass modelling

To quantify whether latitudinal patterns in fish community composition were related to environmental drivers, generalized additive mixed models (GAMMs) were created for “trophic group biomass” and “trophic group biomass proportion” for four of the trophic groups (zooplanktivores, herbivores, omnivores and benthic invertivores) and total fish biomass. This was done using the R packages “GAMM4” (Wood & Scheipl, 2014). We did not model reef piscivores because they were absent from 38% of surveys and only contributed 4.8% to mean total fish biomass. Generally, underwater visual census is not an effective method for surveying piscivores and many of the larger species are shy of divers, particularly in areas where spearfishing is practised (Goetze et al., 2017; Gray et al., 2016; Kulbicki, 1998; Lindfield, McIlwain, & Harvey, 2014; Ward-Paige, Flemming, & Lotze, 2010).

The explanatory variables included in the full GAMM were “site latitude,” “month,” “mean zooplankton abundance,” “mean chlorophyll concentration,” “human population density,” plus “site” and “year” as random intercept factors. Site and year were included as random factors to account for residual spatial and temporal dependency in the response variable. Population density was included as a potentially explanatory variable because many factors that impact temperate reefs (e.g., fishing, pollution and urbanization) are correlated with human density (Brewer, Cinner, Green, & Pressey, 2013; Stallings, 2009) and there is an uneven distribution of people along the latitudinal coastline. Residual deviance was tested for spatial autocorrelation by applying Moran's I function from the R package “ape” (Paradis, Claude, & Strimmer, 2004) against an inverse distance matrix of projected site coordinates. Spatial and temporal patterns were modelled with a two-dimensional variable (tensor product) of site latitude and month (a cyclical variable). Sea surface temperature was examined but not included due to collinearity with site latitude ($r = 0.66$, $p < .001$). The percentage of surveys that recorded zero biomass for a trophic group ranged from 0.1% for benthic invertivores to 9.9% for omnivores; thus, the Tweedie distribution was selected as a family capable of modelling continuous non-negative data containing zeros (Foster & Bravington, 2013).

To model trophic group biomass proportion, the same response variable was used (each trophic group's biomass) but the model included the total observed fish biomass from each survey as a log-linear offset term. Including this offset standardized trophic group biomass to total biomass, that is a model of “trophic group biomass proportion.” There were thus nine response variables: the absolute and proportionate biomass observed for each of four trophic groups (zooplanktivores, herbivores, omnivores, benthic invertivores), and total fish biomass.

The full model calculated for each response variable was (in script notation; offset was only included for biomass proportion models):

$$\begin{aligned} \text{Response} &= t2(\text{SiteLat}, \text{Month}) + s(\text{Depth}) \\ &+ s(\ln(\text{MeanAbundZoo})) + s(\ln(\text{Chl})) + s(\ln(\text{Population})) \\ &+ (1|\text{Site}) + (1|\text{Year}) + \text{offset}(\ln(\text{Total Biomass})) \end{aligned}$$

where “s” indicates a penalized regression spline type smoother, and “t2” is a tensor product smooth. The Tweedie distribution parameter is specified when using the GAMM4 package, and this was found by fitting a GAMM without random effects in the “mgcv” R package (Wood, 2001). Residual plots and Q-Q plots were evaluated to ensure model assumptions were sufficiently met.

A model selection process was done to identify the most parsimonious model for each response. For each response variable, we applied the dredge function from R package “MuMIn” (Barton, 2009) to test every possible combination of variables. The model with the lowest Akaike information criterion (AIC) was selected as the best model.

Goodness of fit of the models was assessed using the percentage of explained deviance calculated without including the random effects. Response plots showing the relationship between response and covariate (holding all other covariates as constant) were used for visual interpretation of the effects for each variable.

2.6.1 | Model prediction

Predictions of the GAMMs of total fish biomass were used to visualize total fish biomass over a standard year for four latitudinal bins within the study area. Predicted biomass was calculated at each month, for four evenly spaced latitude bins, using mean values for depth, zooplankton abundance and population density within each bin. In some cases ($n = 3$), zooplankton data were unavailable, so the mean zooplankton abundance for the latitude bin was used and month was disregarded.

3 | RESULTS

3.1 | Broad latitudinal trends

Mean total fish biomass (\pm SE) decreased with latitude (slope = 19.4 g/m² per degree latitude, adj $r^2 = 0.16$, $p < .001$) and ranged from 220 ± 88 g/m² in the north (29.5°S) to 13 ± 1 g/m² in the south (43.5°S) (Figure 3a). Similarly, proportional composition by trophic group for the same 1-degree latitudinal bins (Figure 3b) indicated a shift in proportional dominance of trophic groups across latitude, with herbivores and omnivores dominating the lower latitudes, zooplanktivores dominating mid-latitudes and benthic invertivores dominating the higher latitudes.

There was also a seasonal component to these latitudinal trends (Figure 4). In the northern low latitudes (29°–33°S), there was a peak in biomass driven by omnivores, herbivores and zooplanktivores around late-autumn (282 ± 37 g/m² for May; Figure 4a). Further south (33 to 37°S) followed a similar trend, with observed biomass also peaking in late-autumn (211 ± 32 g/m² for May; Figure 4b) and a minimum at the end of spring (57 ± 7 g/m² for November). At 37° to 41°S, the maximum mean biomass was observed in mid-winter (281 ± 88 g/m² for July, based on only four surveys). At the most southern latitudes

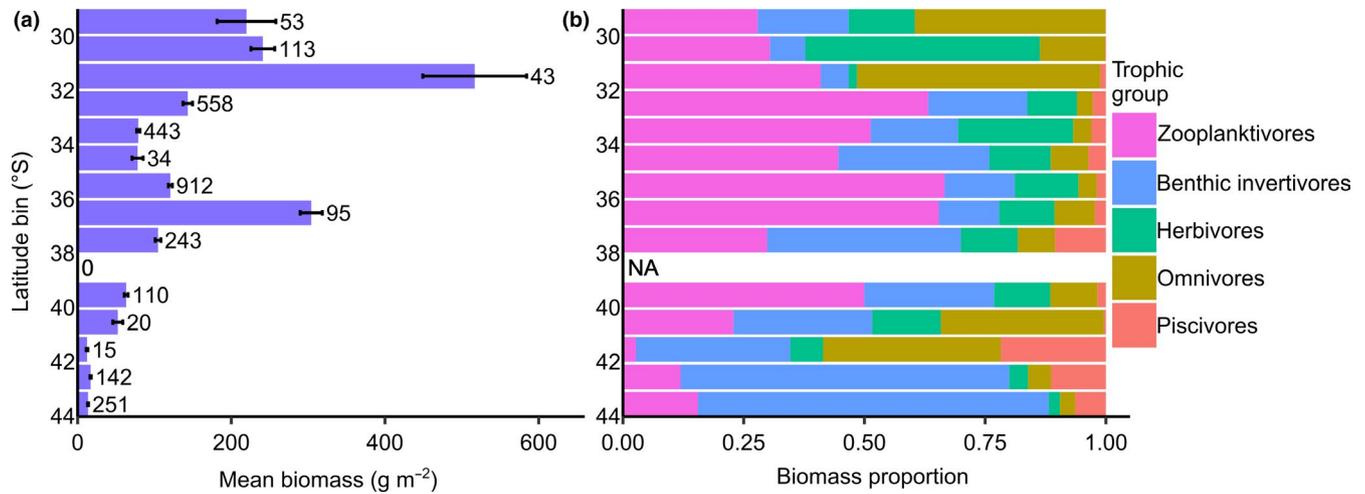


FIGURE 3 Mean biomass and biomass proportions across one-degree latitudinal bins, with (a) representing the mean observed biomass for all fish across fifteen one-degree bins from north to south. Error bars represent the standard error of the mean and (b) representing the mean proportionate biomass for each of the five trophic groups across the same bins. Numbers to the right of bars in (a) represent the number of unique surveys used to calculate both means and proportions

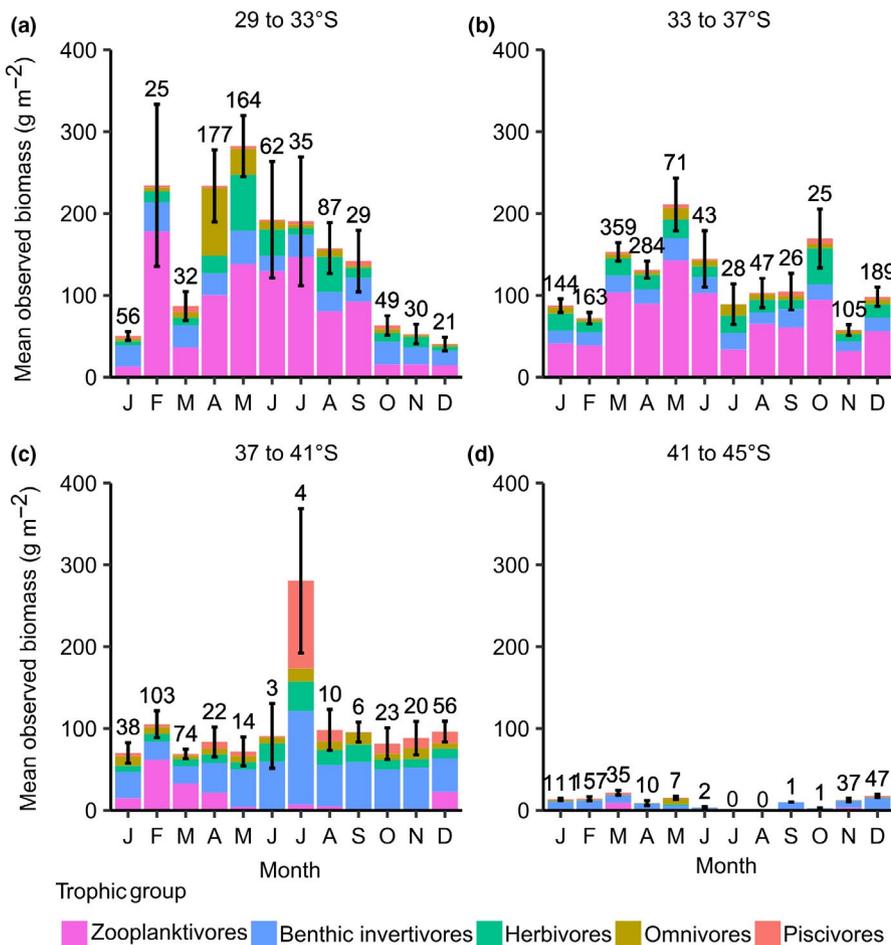


FIGURE 4 Mean monthly total fish biomass represented by the height of each bar. Stacked bars represent the proportionate contribution of each trophic group to the monthly mean total fish biomass. Error bars represent standard error of the mean for total fish biomass. Numbers above each error bar indicate the number of unique surveys used to calculate totals and proportions for each corresponding bar. Months where no data were available for a latitude bin are therefore represented with "0."

(41°–45°S), there was an order of magnitude lower fish biomass, although there were too few winter surveys to confirm seasonality for this region (Figure 4d). Some individual sites were only sporadically sampled across seasons. Therefore, to provide further validation to seasonal patterns, we examined a subset of five sites within a region

with very regular survey coverage and these seasonal patterns persisted (Appendix S1: Figure S6). Length frequency distributions indicated minimal variation in median length across seasons, suggesting that seasonal variation was likely more influenced by patterns in migration, rather than growth (Appendix S1: Figure S7).

3.2 | Multivariate latitudinal trends

As expected, there was clear latitudinal structure in the fish assemblage at the taxa level (Figure 5a) and based on proportional composition by trophic group (Figure 5b), with latitude associated most clearly with axis NMDS1. Sites occur along a gradient of samples dominated by zooplanktivores aligned with NMDS1, as shown by the trophic group loading vectors for the trophic proportion NMDS (Figure 5c), and predominantly at mid-latitudes (zoo: $r^2 = 0.97$, $p < .001$; with r^2 representing the squared correlation coefficient of each trophic group with their respective vector, and p representing the proportional rank of the statistic observed among those evaluated through 1,000 permutations). Those sites dominated by benthic invertivores (ben.inv: $r^2 = 0.97$, $p < .001$) aligned with NMDS1 in the higher latitudes, while herbivores and omnivores aligned with NMDS2 and contributed to community composition especially in the northern lower latitudes (herb: $r^2 = 0.46$, $p < .001$; omni: $r^2 = 0.37$, $p < .001$). The effect of piscivores was much weaker as they were never observed reliably in high abundance (pisc: $r^2 = 0.10$, $p < .001$). These distinct differences in trophic compositions with latitude are also evident in bar

plots of the proportional contributions to biomass across trophic groups and latitudinal bins (Figure 3b).

3.3 | Fish Biomass GAMMs—spatiotemporal effects

The model selection process resulted in the selection of five biomass models (Table 1), and in almost all cases, most of the variation in biomass was described by the tensor product smoother of month and site latitude (Appendix S1: Table S5). Moran's I statistics ranged from 0.03 to 0.14 across all models, and thus, residual spatial autocorrelation was not important. The results of calculating relative variable importance (RVI; 0–1) for each model and taking the mean of RVI scores across both sets of models suggest that the month–latitude tensor is the most influential explanatory variable, followed by depth and population density for the biomass and biomass proportion models, respectively (Appendix S1: Table S6).

There was clear spatiotemporal variation in fish biomass, shown in the contour plots of latitude by month tensor splines (Figure 6). Total fish biomass is generally higher at lower latitudes and in winter months (Figure 6e), which is a summation of the surfaces for the

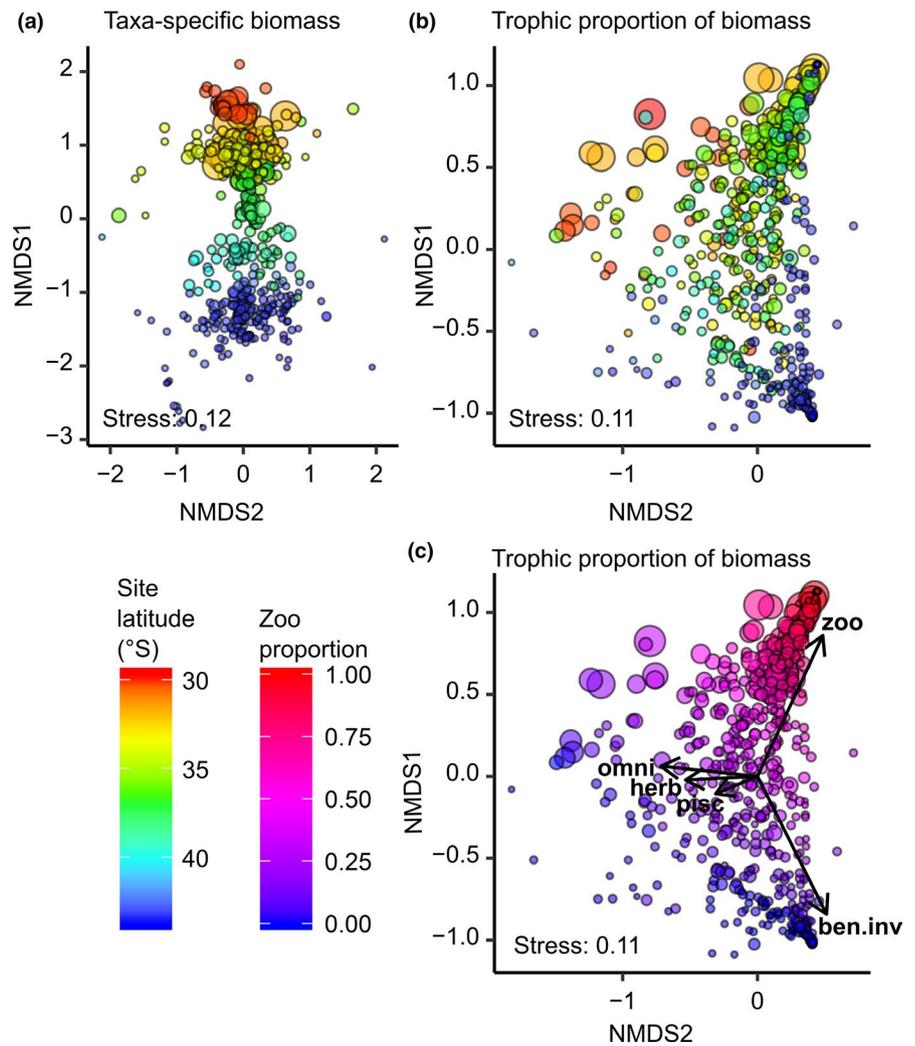


FIGURE 5 Non-metric multidimensional scaling (NMDS) plots displaying Bray–Curtis dissimilarity calculated across a matrix of mean observed biomass for individual taxa at RLS sites (a) and proportional mean biomass in each trophic group for each site (b and c). For (a) and (b), points are coloured by latitude, and for (c), points are coloured by the mean proportional biomass of planktivorous fishes for each site. Point sizes are scaled to the mean total fish biomass for each site. For (c), overlaid vectors indicate trophic group loadings for the corresponding groups: zoo = zooplanktivores; herb = herbivores; omni = omnivores; ben.inv = benthic invertivores; pisc = piscivores

TABLE 1 The final GAMMs generated through testing every possible combination of variables in the full model and selecting the model with lowest AIC score

Biomass						
Dependent variable	Parsimonious model terms (bold = significant effect)	Random effects	Deviance explained (%)	Parsimonious model p	Parsimonious model AIC	Full model Δ AIC
Zooplanktivores	SiteLat,Month + Depth +ln(MeanAbundZoo) + ln(Chl) + ln(Population)	SiteCode + Year	26.9	<0.001	57,796	0
Herbivores	SiteLat,Month + Depth +ln(MeanAbundZoo) + ln(Chl)	SiteCode + Year	30.1	<0.001	19,808.1	18
Omnivores	SiteLat,Month + Depth +ln(Population)	SiteCode + Year	44.5	<0.001	14,828.6	5.5
Benthic invertivores	SiteLat,Month + Depth +ln(Population)	SiteCode + Year	15.8	<0.001	21,324	6.8
Total fish	SiteLat,Month + Depth +ln(MeanAbundZoo) + ln(Population)	SiteCode + Year	25.7	<0.001	63,118.8	11.5
Biomass proportion						
Zooplanktivores	SiteLat,Month + Depth +ln(MeanAbundZoo) + ln(Chl) + ln(Population) + offset(TotalBiomass)	SiteCode + Year	26.8	<0.001	54,706.3	0
Herbivores	SiteLat,Month + Depth +ln(MeanAbundZoo) + ln(Chl) + ln(Population) + offset(TotalBiomass)	SiteCode + Year	22.6	<0.001	18,455.8	0
Omnivores	SiteLat,Month + Depth +ln(Population) + offset(TotalBiomass)	SiteCode + Year	15.1	<0.001	14,130.1	7.5
Benthic invertivores	SiteLat,Month + ln(MeanAbundZoo) + ln(Population) + offset(TotalBiomass)	SiteCode + Year	16	<0.001	20,592.3	7.3

Note: The AIC of the full model is given as AIC points greater than the selected parsimonious model. Variable codes are as follows: SiteLat = site latitude; Month = survey month; Depth = mean site depth; MeanAbundZoo = mean zooplankton abundance corresponding with survey season and latitude; Chl = chlorophyll concentration corresponding with survey season and latitude; Population = number of people living with a 50 km radius of a site. The biomass models model the per-survey biomass of each of the listed trophic groups, while the biomass proportion models model the biomass of each trophic group relative to the total fish biomass observed for each survey.

other trophic groups. The most variation among trophic groups was shown for zooplanktivores, which generally dominated total fish biomass (Figure 6a).

3.4 | Fish biomass GAMMs—environmental effects

At the regional level, one consistent finding was the minimal influence of phytoplankton density (chlorophyll *a*) on fish biomass or proportionate biomass across all groups, including zooplanktivores (Appendix S1: Figures S8 and S9). Total fish biomass and zooplanktivore biomass and proportional biomass showed a positive relationship with zooplankton abundance, although this had less influence than the month–latitude tensor or site depth. The biomass

proportion of benthic invertivores declined with increasing zooplankton abundance.

At the local level, the biomass of trophic groups was generally unimodal with site depth. The peak in herbivore biomass occurred at a shallower depth than for all other trophic groups, while omnivores peaked at deepest depths (Appendix S1: Figure S8b). Zooplanktivores and benthic invertivores showed low biomass at shallow sites and increasing variability with increasing site depth. As depth increased, the proportion of zooplanktivores and herbivores generally decreased, with a corresponding increase in omnivores (Appendix S1: Figure S9) (Parsons, Suthers, Cruz, & Smith, 2016). Responses for human population should be interpreted with caution due for the few surveyed sites with low covariate values; however, a general theme across omnivores, benthic invertivores and

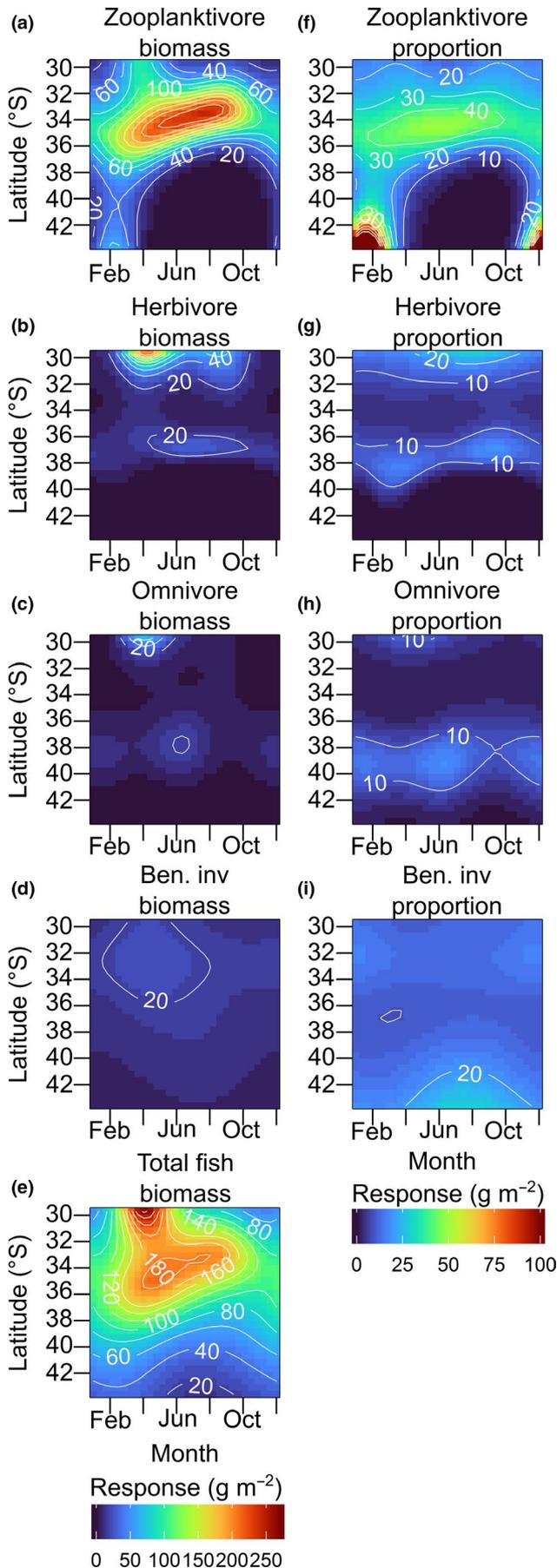


FIGURE 6 2d tensor contour plots showing fitted GAMM relationships with contours of trophic group biomass (in g/m²) by month (cyclical) and site latitude for (a) zooplanktivores, (b) herbivores, (c) omnivores, (d) benthic invertivores, (e) total fish biomass. The second row of contour plots (f, g, h and i) represents tensors from the corresponding biomass proportion models. Note the two different colour scales for the two columns of plots

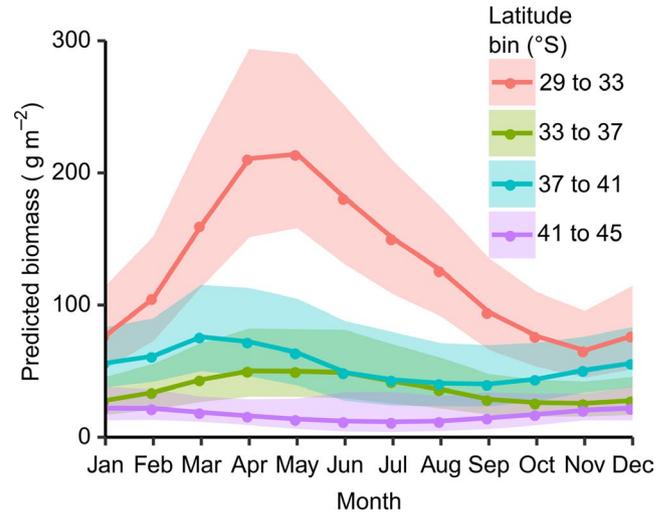


FIGURE 7 Predicted per-survey total fish biomass trajectories calculated by month and latitudinal bin using the total fish biomass GAMM. Confidence intervals for each latitudinal bin represent two times the standard error

total fish was a decline in biomass at high levels of human population density.

Across all models, the month–latitude tensors explained most of the variability in the data, and primary productivity (chlorophyll *a*) the least (Appendix S1: Table S6). The biomass proportion models showed a similar set of relationships (Appendix S1: Figure S9).

3.5 | Predicted fish biomass from the GAMM

There was a wide range of variability in the seasonal fluctuations of fish biomass observed at rocky reefs, with the greatest variability observed at the most northern latitudes of our study region (Figure 7). At this northern latitude bin (29°–33°S), the mean predicted biomass more than tripled from 66 to 214 g/m² (a 3.2-fold increase) between November and May. This region does contain an area of offshore islands within a marine reserve, but these patterns persisted when marine park sites were excluded. By comparison, predicted biomass at mid to high latitudes increased only ~1.8-fold between spring and autumn, although the highest latitudes have few winter surveys. Overall, predicted fish biomass was lowest in spring and generally peaked in autumn (Figure 7). Model prediction results are also reinforced by the monthly bar plots of mean observed biomass for each latitude bin (Figure 4).

4 | DISCUSSION

Along our “space-for-time” latitudinal gradient, we revealed some remarkable changes in fish biomass and trophic structure. Overall fish biomass declined over an order of magnitude from north to south, along with a dramatic shift in the trophic composition of fish assemblages associated with temperate rocky reefs. The relative biomass of zooplanktivores and benthic invertivores was the strongest drivers of assemblage composition across this range, with zooplanktivores dominating mid-latitudes and benthic invertivores dominating high latitudes. These observed differences in trophic structure over 16 degrees of latitude (Figure 1) reveal potential changes to the trophic structure of fish assemblages due to a warming ocean and species range shifts.

4.1 | Latitudinal gradients in trophic structure

Herbivores and omnivores made up the greatest proportion and the greatest total biomass in the lower latitude sites. Similar patterns were also described in the western Atlantic (Floeter et al., 2005), where herbivore abundance (Longo, Ferreira, & Floeter, 2014), plant-herbivore interactions (Longo et al., 2019) and herbivore biomass decrease towards higher latitudes, across both coral (Floeter et al., 2004) and rocky reef environments (Floeter et al., 2004; Morais, Ferreira, & Floeter, 2017).

We also observed a clear dominance of planktivory (>40% of the fish biomass) in the mid-latitudes between 31° and 37°S, confirming and extending earlier local studies (Kingsford & MacDiarmid, 1988; Parsons et al., 2016; Truong et al., 2017) despite the fact that planktonic primary production increases at higher latitudes (Everett et al., 2014). This is linked to the dominance of benthic invertivores at higher latitude sites where the contribution of benthic and detrital energy pathway is particularly important, based on infaunal (Gee, 1989) and epiphytic invertebrates (Poore & Steinberg, 1999), such as polychaetes, gastropods, bivalves, decapods, amphipods and echinoderms (Morton, Platell, & Gladstone, 2008). Higher latitudes are characterized by spring plankton blooms and very low winter zooplankton abundance (Harris, Nilsson, Clementson, & Thomas, 1987), and such seasonality could not support large year-round populations of zooplanktivores. Spring blooms enrich sediments as excess organic material sinks to the seafloor (Wassmann, 1997) and are associated with subsequent increased biomass and abundance of zoobenthic organisms (Heip, 1995; Parrish et al., 2009). This benthic enrichment coupled with high inter-seasonal variability in zooplankton abundance may favour benthic food webs and thus account for the dominance of benthic invertivores over zooplanktivores at higher latitudes.

4.2 | Disappearing fishes—winter declines in rocky reef-associated fish biomass

The strong seasonality in fish biomass was driven mostly by zooplanktivores but the reasons for these fluctuations were not clear.

There were also very few observations of large piscivores to account for the large reduction in fish biomass through winter and spring. Given that these seasonal increases in total fish biomass in the low to mid-latitudes were not accompanied by corresponding increases in median fish length, it is likely that these patterns were more a result of migration, rather than growth.

A plausible explanation is that during winter, zooplanktivores, which are dominated by yellowtail scad (*Trachurus novaezelandiae*, Carangidae), may migrate to access the East Australian Current, which is warmer offshore in winter (Suthers et al., 2011). Similar behaviour of offshore seasonal migration in response to declining bottom temperature was documented for Japanese horse mackerel (*Trachurus japonicus*, Carangidae) in the East China Sea (Sassa, Yamamoto, Tsukamoto, Konishi, & Tokimura, 2009). Although these pelagic zooplanktivores are not permanent reef residents, they have an important role in reef food webs through enriching detrital pathways with their faeces, and as prey (Morais & Bellwood, 2019; Pinnegar & Polunin, 2006; Robertson, 1982). In contrast to other regions, the higher latitudes were characterized by very low overall biomass of zooplanktivores although seasonal conclusions are not possible due to the lack of winter survey data.

4.3 | Dynamic temporal distribution—a means of managing predation?

Seasonal variation in mid-latitude sites was driven by variation in the biomass of zooplanktivores, as other groups fluctuated only slightly and followed no clear pattern. Such patterns were driven largely by *Trachurus novaezelandiae*, which can form large schools and regularly travel between the coast and deeper waters. These fish make large seasonal contributions to the trophic ecology of shallow temperate reefs, particularly for these mid-latitude sites (Deegan, 1993). For example, they make up the bulk of diet for piscivorous predators (Scharf, Buckel, McGinn, & Juanes, 2003) and the large-scale fluctuations in their biomass are almost certain to influence the suitability of reef habitats for piscivores as prey encounter rates are closely linked to prey capture rates (Breck, 1993). Therefore, it is possible that the seasonality of zooplanktivores may suppress the proliferation of their predators (Durant, Hjermann, Ottersen, & Stenseth, 2007).

In pelagic environments, zooplanktivores such as sardines and anchovies form large aggregations, which are generally separated by large distances, and predators must invest significant time and energy in their search for the next aggregation (Sims, Witt, Richardson, Southall, & Metcalfe, 2006). Therefore, while pelagic zooplanktivores manage predation through remaining spatially patchy, reef zooplanktivores may achieve a similar outcome through temporal patchiness.

4.4 | Climate change risks for temperate rocky reef communities

South-eastern Australia is a climate change hotspot, which is already experiencing substantial impacts (Sunday et al., 2015), with

many species shifting their distribution poleward (Champion, Hobday, Tracey, & Pecl, 2018; Champion, Hobday, Zhang, Pecl, & Tracey, 2019). Temperate reefs near the warm edge of their distribution are becoming "tropicalized," as many tropical species respond to warming by shifting their distribution towards these cooler, higher latitude regions (Vergés, Steinberg, et al., 2014). The latitudinal and seasonal patterns on trophic community composition and total fish biomass we have documented may also shift poleward with the cumulative range shifts of taxa. These shifting patterns will likely result in increased biomass of herbivorous and omnivorous fishes in high to mid-latitudes. In some regions, this has already led to overgrazing of seaweed forests and caused regime shifts as canopy-forming kelp declines towards low biomass turf-dominated habitats (Bennett, Wernberg, Harvey, Santana-Garcon, & Saunders, 2015; Filbee-Dexter & Wernberg, 2018; Vergés et al., 2016).

Expanded range and increased abundance of herbivorous fishes under climate change have been linked to macroalgae losses in several parts of the world, including Japan, Australia and the Mediterranean (Sala et al., 2012; Vergés, Steinberg, et al., 2014). However, there is evidence that existing macroalgae can also inhibit the spread of tropical fish species (Beck, Feary, Nakamura, & Booth, 2017). Thus, preventing further losses of macroalgae may be vital in slowing the poleward expansion of these tropical herbivores. Their influence may not be entirely negative however, as some range expanding herbivorous fishes, such as rabbitfishes in the Mediterranean, are already being exploited as new fisheries (El-Hawee, 2001). Further, as grazing by herbivores prevents the proliferation of macroalgae, their poleward expansion may facilitate a parallel expansion in habitat-forming corals (Booth & Sear, 2018; Cheal, Emslie, MacNeil, Miller, & Sweatman, 2013), which can shift poleward at rates of up to 14 km/year (Yamano, Sugihara, & Nomura, 2011). Climate-mediated changes in habitat composition and shifts in the distribution of foundation species such as kelp and corals can further influence and accelerate changes in fish community composition, as individual fish species lose or gain specific habitats used for settlement and recruitment, as refuge or as food (Vergés et al., 2019).

A poleward shift in the patterns observed could also lead to an increase in the influence of zooplanktivores in the Bass Strait and Tasmania. However, this space-for-time implication is dependent on specific changes in oceanography, as high biomass of zooplanktivores appears to be tightly linked to regions of regular upwelling, such as the separation zones of boundary currents (Bakun et al., 2015). As the East Australian Current strengthens (Ridgway, 2007) it is predicted that its separation zone could shift 100 km poleward by 2060 (Oliver & Holbrook, 2014), shifting patterns of nutrient enrichment to fish distribution along with it (Bakun et al., 2015).

Shifting oceanographic conditions, alongside milder winter water temperatures and more consistent planktonic primary production throughout the year, could facilitate subsequent increased abundances of planktivorous reef-associated fish at higher latitudes. In this case, increased direct consumption of planktonic primary production would reduce the proportion of organic matter reaching the

benthos, shifting trophic composition away from currently dominant benthic invertivores. This increased availability of smaller body size, highly abundant zooplanktivores would increase overall fish biomass at high latitude reefs and provide improved feeding opportunities for marine mammals, seabirds and piscivores (Kaschner, Karpouzi, Watson, & Pauly, 2006; Smith et al., 2011). This could be a net benefit for temperate reef ecosystems; however, trophic interactions are complex, and it is difficult to speculate on the full range of potential impacts. Clearly, further examination into how poleward shifts in such patterns would influence local conditions under multiple climate change scenarios would be useful for understanding potential future impacts for temperate rocky reefs. Ecosystem modelling could prove invaluable in this context.

5 | CONCLUSION

It is well established that species' distributions have begun shifting poleward due to climate change and that these redistributions will have significant implications for human systems (Pecl et al., 2017). Our work contributes critically by producing highly informed mechanistically based predicted changes in the latitudinal patterns of trophic structure and their potential consequences. The latitudinal patterns in trophic structure observed off eastern Australia in this study are relevant for other poleward-flowing boundary current systems (Figure 1; Vergés, Steinberg, et al., 2014). For example, reef fish communities in the western Atlantic, which are also influenced by poleward-flowing boundary currents, shift from being primarily dependent on low-energy food sources, such as algae and seagrass, to reliance on higher-energy foods, such as plankton and invertebrates, along the transition from tropical to temperate zones (Floeter et al., 2004). Herbivores that dominate near the tropics may also be expected to expand their distribution in both northern and southern poleward directions in the western Atlantic (Longo et al., 2019). Similarly, in south-eastern Japan the intensification of the Kuroshio boundary current has already been linked to the poleward expansion of tropical herbivorous fish (Kumagai et al., 2018). The observed patterns may also be relevant in the Mediterranean, where the arrival of tropical species from the Red Sea is initially facilitated by the Suez Canal and where the expansion of herbivorous fish is occurring longitudinally in a western direction as this basin continues to warm (Azzurro, Franzitta, Milazzo, Bariche, & Fanelli, 2017).

Many questions surrounding the tropicalization of rocky reefs remain against a backdrop of urbanization and invasive species on temperate coasts. Our results suggest that overall herbivorous and planktivorous fish biomass at these reefs will increase, which could lead to subsequent losses of macroalgae in lower latitudes and a shift towards more direct planktonic trophic pathways at higher latitudes. More generally, the large latitudinal differences in the trophic composition and ecology of fishes observed in our study highlight the future of valuable, temperate rocky reefs under climate change.

The observed patterns in total fish biomass do not match latitudinal gradients in planktonic primary productivity, which are greatest in higher latitudes (Everett et al., 2014), suggesting that other drivers such as temperature are important in determining total fish biomass and trophic structure. However, there was a positive relationship between zooplankton abundance and total fish and zooplanktivore biomass, indicating that low inter-seasonal variability in zooplankton may be a vital factor driving the structure of reef-associated fish assemblages. It could also be that the on-reef abundance of zooplankton is influenced by fine-scale processes not apparent in our estimate of zooplankton abundance, and studies that sample coastal zooplankton abundance at a finer spatial resolution are necessary to quantify the dynamic importance of zooplankton biomass to reef-associated fish assemblages. Regardless of the root cause driving these patterns, it is likely that the relative contribution of planktonic subsidies to both tropical (Morais & Bellwood, 2019) and temperate (Truong et al., 2017) reefs has been greatly underestimated.

Due to the dependence of numerous predators on zooplanktivores, it is also important to consider the root causes of these seasonal migrations. These seasonal abundances and paucities of fish biomass would undoubtedly impact the behaviour of mobile piscivorous predators and make large contributions to reef energy flow (Pinnegar & Polunin, 2006; Robertson, 1982); however, we do not at this stage understand what is causing them. Our along-shore analysis indicates the need for more research into these cross-shelf seasonal movements and what drives them.

Finally, it is important to acknowledge that climate-driven re-distributions of species will continue to lead to novel species interactions, changes in foundation species and the emergence of no-analogue communities, that is communities that are compositionally unlike any found today (Williams & Jackson, 2007). Therefore, while we can learn much about trophic structure and energy pathways from contemporary distributions, we should also expect and be prepared for early detection of ecological “surprises” in coming decades (Lindenmayer, Likens, Krebs, & Hobbs, 2010).

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CONFLICT OF INTEREST

We have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All data used in this analysis are freely available from The Australian Ocean Data Network (<https://portal.aodn.org.au>). Reef Life Survey data, which include fish lengths for generating biomass estimates, are available by request from enquiries@reeflifesurvey.com.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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