

Tropicalization unlocks novel trophic pathways and enhances secondary productivity in temperate reefs

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Funding information

Australian Research Council, Grant/Award Number: DP170100023, DP190100058 and DP190102030; Holsworth Wildlife Research Endowment

Handling Editor: Scott Burgess

Abstract

1. The structure of ecological communities is rapidly changing across the globe due to climate-mediated shifts in species distributions, with novel ecosystem states emerging as new species become dominant. While it is clear that such changes restructure habitat properties and their associated assemblages, how new nutritional resources and consumers may affect the ecosystem trophic structure and energetic dynamics remains poorly resolved.
2. Here, we investigate how the reconfiguration of tropicalized reefs—that is, temperate ecosystems receiving an influx of tropical species—affects the availability of nutritional resources and energy flow through herbivore-based trophic pathways. To do so, we quantified changes in algal and detrital resources along a tropicalization gradient in eastern Australia. We also estimated energy flow towards herbivorous fishes by quantifying their standing biomass (kg/ha), productivity (kg ha⁻¹ day⁻¹), and biomass turnover (% day⁻¹), using an individual-level modelling approach that combines estimates of fish growth rates and mortality.
3. Along the gradient, tropicalized reefs had relatively higher amounts of palatable algal turfs and detrital particulates compared to non-tropicalized sites. Feeding intensity by herbivorous fishes was also c. 400 times higher on tropicalized reefs, with tropical turf-cropping surgeon fishes being responsible for >98% of the feeding rates.
4. Turf-driven trophic pathways underpinned virtual all (>99%) of the biomass produced by tropical fishes, which contributed up to 63% of the total herbivorous fish standing biomass and 86% of the productivity despite only representing 35% of the abundance. Turfs also fuelled most of the secondary productivity of tropical fishes on tropicalized reefs across Australia's western tropical-temperate transition zone, although their overall productivity was ~5 times lower. This is possibly due to turfs there containing elevated sediment loads, which dilute the nutritional quality of turf-based resources, as well as other differences in the biogeographical context.
5. We propose that algal turfs are central drivers of ecosystem energetic shifts on temperate reefs as they become tropicalized because they support novel algal

and detrital trophic pathways that enhance secondary productivity and biomass turnover. Our results also suggest that turf characteristics such as organic content or sediment load may emerge as increasingly important drivers of energy flow in temperate locations where turfs dominate benthic cover.

1 | INTRODUCTION

The global redistribution of life on Earth under climate change is reshaping the structure and functioning of ecosystems at previously unseen rates (Beaugrand et al., 2015; Pecl et al., 2017). Local species declines and losses are driving functional changes in equatorial regions (Beaugrand et al., 2015; Morais et al., 2020), while migrant warm-affinity species play increasingly important roles in temperate and polar biomes (García Molinos et al., 2016; Pessarrodona et al., 2018; Vergés, Steinberg, et al., 2014). The irreversibility of some of these changes has prompted for a reconsideration of how we understand the functioning of ecosystems (Hobbs et al., 2006; Hughes et al., 2017), as well as their governance, management, and conservation (Bellwood, Pratchett, et al., 2019; Hobbs et al., 2009). A key challenge as ecosystems become increasingly modified by human actions is unpacking the new dynamics that govern their functioning, as well as harnessing the novel services they can provide. Central to this challenge is understanding how ecosystem restructuring affects trophic pathways and energetic dynamics, which are crucial for providing resources to human societies.

Temperate reefs across the globe are rapidly transitioning into novel configurations, with climate change emerging as the principal driver of ecosystem change in most regions (Mieszkowska et al., 2014; Wernberg et al., 2019). Underwater forests formed by large canopy-forming seaweeds are the biological engine of temperate reefs, providing habitat and nursery for many associated species (Teagle et al., 2017), and supporting food webs and carbon cycling (Truong et al., 2017; Wernberg et al., 2019). Yet, the poleward migration of species is fundamentally transforming these underwater habitats, which are increasingly dominated by warm-affinity canopy-forming species (Tanaka et al., 2012), or transitioning into deforested states dominated by sea urchins and/or low-lying turf algae (Filbee-Dexter & Scheibling, 2014; Filbee-Dexter & Wernberg, 2018; Vergés, Steinberg, et al., 2014). While we are beginning to understand how such climate-driven changes in benthic structure affect functions such as primary productivity or habitat provision (Pessarrodona et al., 2018; Teagle et al., 2018), their cascading effects to higher trophic levels (e.g. secondary productivity) remain poorly resolved, limiting our understanding of how energy flow changes at the ecosystem level. This is particularly true for mobile taxa such as reef fishes, which are key conduits of energy, but often show mixed, species-specific, responses to shifts in habitat structure (Pratchett et al., 2008; Smith et al., 2021).

Gradual warming, intensifying poleward subtropical boundary currents, and/or marine heatwaves facilitate the range expansion of tropical fishes and other species into temperate regions (Horta

e Costa et al., 2014; Vergés, Steinberg, et al., 2014; Wernberg et al., 2016)—a phenomenon known as tropicalization. Many tropical herbivorous fishes have expanded their ranges and successfully established in temperate reefs (Vergés et al., 2016), resulting in increasing abundance and functional diversity of the herbivore assemblage (Vergés, Steinberg, et al., 2014), as well as total fish biomass (Holland et al., 2020; Smith et al., 2021). These fishes also increase seaweed consumption and can lead to overgrazing (Vergés et al., 2016), thereby playing a key role in shifting benthic composition from canopy to turf algae as the dominant providers of habitat (Bennett et al., 2015; Vergés, Tomas, et al., 2014). Tropical herbivores are thus central drivers of shifts in energy flow and can drive changes in biomass production in fish assemblages (Smith et al., 2021). Yet, insights into how energy flow changes under tropicalization have so far been based on latitudinal space-for-time substitutions (Holland et al., 2020) and/or relied on measurements of fish standing biomass (Smith et al., 2021), which show a limited correlation with secondary productivity (i.e. how much fish biomass is produced per area per day)—a more dynamic measure of energy flow (Morais & Bellwood, 2019). Although traditionally a challenging metric to quantify, recent methodological developments have made it relatively straightforward to robustly estimate secondary productivity from field data (Morais & Bellwood, 2020). These methods remain, however, to be applied in temperate locations and within the context of tropicalization.

Importantly, we also lack a mechanistic understanding of what trophic pathways may underpin tropicalization-driven energetic shifts. Examining how the different nutritional components of the benthos (e.g. algae, detritus, and invertebrates) are affected by tropicalization may provide strong insights on how the main energetic pathways shift. The nutritional resources exploited by nominally herbivorous fishes (i.e. fishes consuming algal-based resources, hereafter referred to herbivorous fishes) vary considerably. Broadly speaking, fishes exploit two main herbivory pathways: 'browsers' feed primarily on canopy-forming seaweeds, while 'grazers' target the various nutritional resources contained within the algal turf matrix (e.g. algae, detritus and microbes). The morphological, physiological and/or behavioural traits of herbivorous fishes accessing those resources varies across groups, and so does their ecosystem function (Bellwood, Streit, et al., 2019). Importantly, as these groups are more diversified in tropical areas, their intrusion into temperate reefs results in increases in the diversity, intensity, and spatial extent of herbivory functions (Zarco-Perello et al., 2020). Energy flow can thus be expected to shift depending on the relative abundance of tropical and temperate herbivores, as well as the different functional groups they belong to.

In the present work, we aim to understand how tropicalization affects the rate and pathways of energy flow at the ecosystem level. We first investigate how this phenomenon affects nutritional resources available to herbivorous fishes by quantifying the (a) relative availability of organic (detritus, algae) and inorganic (sediment, calcified algae) matter and (b) herbivore feeding interactions, along an inshore–offshore tropicalization gradient at the Solitary Islands region (eastern Australia). Using these mechanistic insights, we then investigate how different herbivorous trophic pathways at tropicalized sites affect the overall production and turnover of fish biomass. To examine whether the detected patterns are consistent across different biogeographical regions, we also compare our findings to tropicalized reefs in western Australia, where a shift from canopy kelp to turf has also occurred. The insights obtained here are key to understand how the energy dynamics of temperate ecosystems will change as they become increasingly dominated by tropical species, and constitute one of the first attempts at quantifying fish secondary productivity and turnover on temperate reefs.

2 | MATERIALS AND METHODS

2.1 | Study regions

Our studies were conducted in the temperate–tropical transition zones of the east and west coasts of the Australian continent (Figure 1), where the warm range edge of the dominant habitat-forming temperate kelp *Ecklonia radiata* lies. Within these transition zones, kelps have recently disappeared or experienced steep declines coinciding with climate-driven increases in ocean temperatures; the frequency of heatwaves; and the arrival of tropical herbivorous fish, which have increased consumer pressure on kelps (Vergés et al., 2016; Wernberg et al., 2016).

2.2 | Tropicalization effects on algal resources and herbivorous fish productivity

In eastern Australia, sampling was conducted at the same depth range (6–12 m) on reefs along an inshore–offshore gradient in the Solitary Islands region (Figure 1a). This tropical–temperate transition zone constitutes a valuable natural laboratory to study the effects of tropicalization as offshore reefs feature higher mean and maximum temperature (Malcolm et al., 2011), tropical fish abundance (Malcolm et al., 2010), and turf and coral cover (Harriott et al., 1994), despite being relatively close (1–3 km apart) to inshore reefs dominated by kelp forests and temperate fishes (Malcolm et al., 2010; Figure 1b,c; Figure S1). Kelp was originally present in many offshore reefs, but gradually declined and eventually disappeared by 2009 coinciding with an increase in herbivory and tropical herbivores (Vergés et al., 2016). These inshore–offshore differences are thus consistent with the expectations of tropicalization, while the close proximity and shared latitude of sites minimize the influence of other factors

such as differences daylength and seasonality. Nevertheless, any conclusions driven from this inshore–offshore gradient need to consider the possible influence of factors other than temperature operating across the shelf (e.g. such as riverine influence).

2.3 | Benthic structure and organic matter availability

To examine how benthic nutritional resources vary across the tropicalization gradient in the Solitary Islands region, we surveyed the benthic composition, algal structure, and relative availability of organic matter. Sampling was conducted at three shallow (6–12 m) inshore sites (0.2–1 km from the coast), which are presently dominated by kelp forests and were considered to represent non-tropicalized states (hereafter control sites; Table S1); and, four offshore sites (2.2–4.5 km to coast; Table S1) where temperatures are ~0.5–1°C higher on average (Malcolm et al., 2011), tropical herbivores have increased in abundance (Smith et al., 2021), and kelp loss has occurred in recent years (Vergés et al., 2016), thus representing a tropicalized state (hereafter tropicalized sites).

To characterize the benthic composition at each site, we recorded the percentage cover of the main benthic habitat-forming organisms along seven 25 m transects during March 2019 (austral autumn). Images of the benthos (6–12 photoquadrats) were taken approximately every 2.5 m along the transect line c. 60 cm away from substrate. Twenty-five points were then randomly laid in each image and assigned to one of the following categories (kelp, turf algae and CCA, hard coral, sponges and tunicates, other macroalgae, other live organisms or sand) in CoralNet (UCSB). Turf algae and CCA were considered in the same category as very small filamentous algae that often grew on some of the CCA across the tropicalized sites was not visible on the photos (A. Pessarrodona, pers. obs.).

We also surveyed the algal assemblage composition, structure, and the relative availability of organic matter at each site by collecting benthic samples from 5 to 9 quadrats placed haphazardly and at least 5 m apart along the benthos during March 2019. The number of quadrats varied due to weather conditions and limited dive times. To standardize accumulation of benthic particulates across substrates, suitable sampling surfaces were flat (<30° from horizontal) areas on bedrock or large boulders (>10 m wide) without any large sediment-retaining pits. To begin sampling, SCUBA divers randomly placed a 400 cm² quadrat over the substrate and estimated the height of the algal vegetation at five randomly selected points within the quadrat with a ruler. Subsequently, all the non-encrusting algae and benthic particulates within the quadrat were collected using a Venturi suction sampler, with all the materials accumulating in a 63-µm mesh bag attached to the end of the sampler. Benthic particulates contain a mixture of inorganic sediments and detrital organic aggregates (including non-living algal organic matter and numerous associated microbial groups such as diatoms, bacteria, and dinoflagellates; Wilson et al., 2003). The biomass of kelp plants across control sites could not be collected using this method and was derived

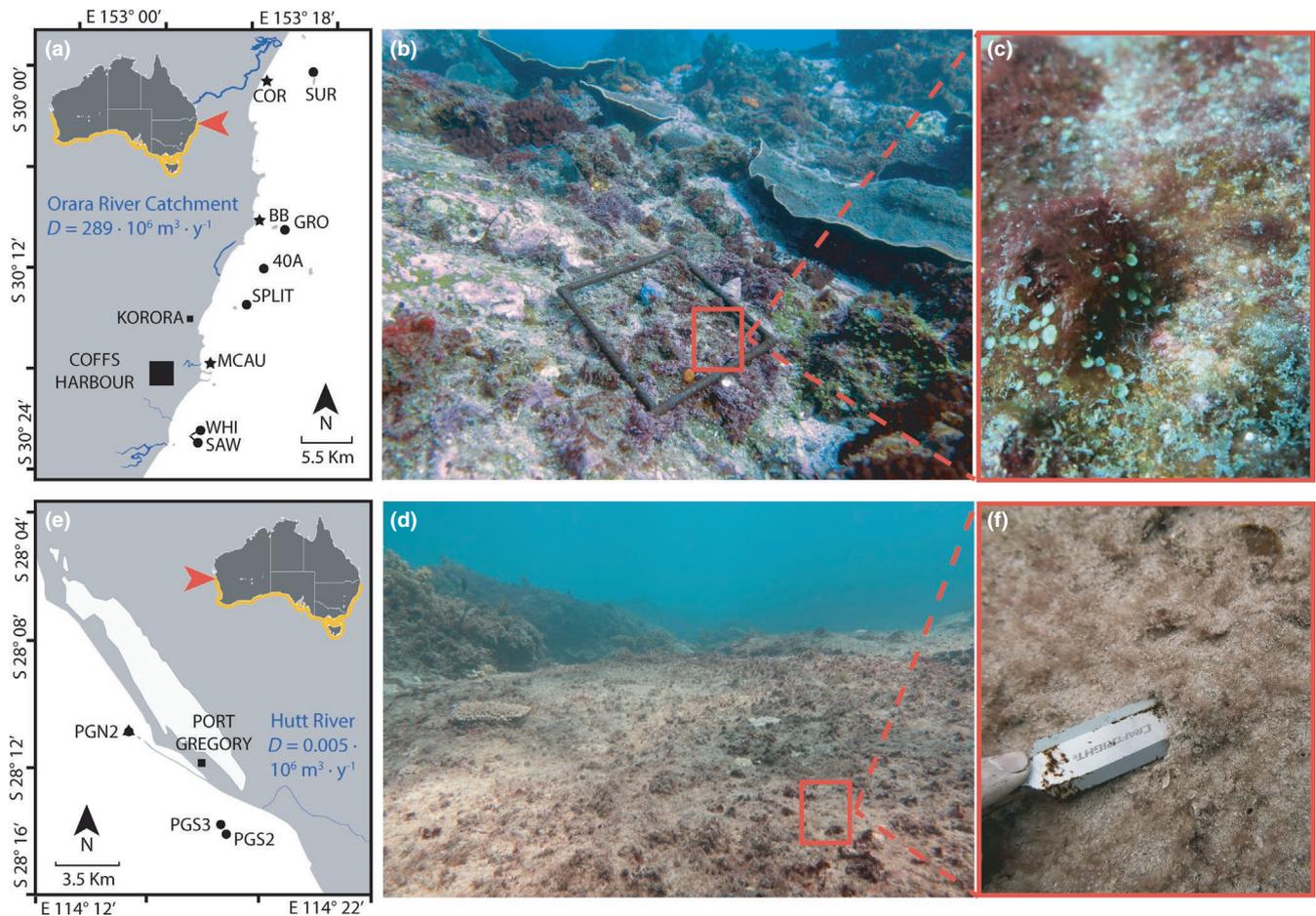


FIGURE 1 Map of study locations in eastern (a) and western (e) tropical-temperate transition zones of Australia. The position of the study locations within the distribution of the golden kelp *Ecklonia radiata* (yellow line) is indicated by a red arrow. Control sites are indicated by a star, while tropicalized sites are indicated by a dot. Squares denote an urban nucleus. The annual discharge (D ; 10-year mean) of rivers near study sites (in blue) is indicated in $10^6 \text{ m}^3/\text{year}$. Typical tropicalized reefs from eastern and western Australia are shown in (b) and (d) respectively, with details of the algal community shown in (c) and (f). Photographs by A. Vergés (b) and A. Pessarrodona (c, d, f). See Table S1 for details of sampling sites

from a previous survey in the study area (Bare Bluff and Corindi, ten 0.25 m^2 quadrats randomly placed at each site; 8.2 ± 2.2 individuals/ m^2 , $0.86 \pm 0.05 \text{ kg DW}/\text{m}^2$; means \pm SE; M. Langley and A. Vergés, 2018, unpubl. data). All collections for this study were conducted under permit P13/0007-2.0 (NSW Department of Primary Industries).

Samples were frozen within 6 hr of collection and transported to the laboratory and processed as per Pessarrodona, Filbee-Dexter, et al. (2021). Briefly, we separated the benthic particulates and algal components which were grouped into algal functional groups (filamentous, foliose, corticated, leathery and articulated coralline algae) following Steneck and Dethier (1994). The particulate component of the samples ($63\text{--}2,000 \mu\text{m}$) was then thoroughly washed with fresh water through a sieve stack and dried to yield the size-particle distribution and total benthic particulate load. Samples were bleached with 30% hydrogen peroxide (H_2O_2) for at least a week to remove any organic matter, with regular stirring and fresh solution being added until no bubbles were produced. After bleaching, samples were rinsed with fresh water to remove salts and reweighed to yield

total organic and inorganic loads, as well as the percentage of organics in benthic particulates.

Once all the samples were processed, we estimated the average biomass (kg dry weight, DW) of the inorganic and organic benthic components at control and tropicalized locations to yield insights about the quantity and availability of nutritional resources to consumers. In this analysis, we did not include corals, tunicates, sponges and other live organisms such as urchins as our study was primarily concerned with nominally herbivorous fishes. Inorganic matter consisted of the inorganic fraction of the benthic particulates (i.e. the sediment) plus the calcified biomass of articulated coralline algae. Organic mass included the detritus (organic load) in the benthic particulates as well as algae from the algal assemblage and kelp surveys. As organic mass inside coralline algae is unavailable to most fish consumers in our study area (parrotfishes are scarce in the Solitary Islands; Smith et al., 2021), it was categorized in a separate 'unconsumable organic matter' component. To determine the relative organic and inorganic mass of calcified algae, we dried and weighed individuals of the dominant coralline algae *Arthrocardia wardii*

($n = 8$) and *Amphiroa anceps* ($n = 10$), exposed them to 5% hydrogen chloride until no bubbles were produced and then re-dried and re-weighed the remaining material. The relative organic percentage value (10.3%) was then applied to the coralline algae weights from all our samples to yield the organic and inorganic weights. All weights were standardized to m^2 to match the scale of kelp measurements.

2.4 | Herbivory intensity

To examine how the benthic feeding intensity by different herbivorous fishes differed along the inshore-offshore tropicalization gradient, we quantified the interactions (number of bites) between nominally herbivorous fishes and the seafloor using video cameras (GoPro). Cameras ($n = 3-6$, as some failed to record) were deployed at nine sites (five control and four tropicalized; Table S1) for two consecutive days, between November 2012 and April 2013, with recordings lasting 72–249 min (169 ± 54 ; mean \pm SD) as part of an experiment to examine consumption rates on kelp tethers and the benthos (for details, see Vergés et al., 2016). Kelp tethers were small subadult plants (47 ± 14 cm length) and were always deployed on open areas. In the control sites, tethers were deployed on large canopy gaps ($>4 m^2$) or at the edge of kelp forests to minimize the effects of surrounding canopies. The identity of herbivores biting on either the kelp assays or the benthos did not differ across our sites (Vergés et al., 2016), suggesting minimal effects of the kelp tethers on benthic feeding. Only bites on the benthos were used in our analysis, with bites being standardized to area ($1 m^2$) and time (60 min). A total of 21 and 25 replicates were obtained at the control and tropicalized sites respectively (>70 hr of footage). We assumed benthic composition during 2012–2013 was broadly representative to the one encountered in 2017–2019 (A. Vergés, unpubl. data).

2.5 | Herbivore biomass, secondary productivity and turnover

To investigate how the different herbivorous trophic pathways affect the wider energetics of tropicalized reefs, we evaluated the standing biomass (in kg/ha), the net secondary productivity (the amount of fish tissue accumulated by a fish assemblage minus the losses due to mortality; in $kg ha^{-1} day^{-1}$), and the biomass turnover (the flow rate of biomass, defined here as the quotient between net productivity and standing biomass; in $\% day^{-1}$) of the herbivorous fish assemblage in reefs that underwent tropicalization. All of these metrics were obtained by surveying the abundance and body size of fishes and modelling their biomass, growth and mortality using the approach developed by Morais and Bellwood (2020). As we were interested in how different nutritional components of the benthos and the different trophic pathways they underpin affect the flow of energy, herbivorous fish species were grouped into four groups based on (a) their temperature affinity (temperate or tropical) and (b) the main trophic pathways they exploit (canopy- or turf-driven

pathways; Table S2). Fishes exploiting canopy-forming algae often feed on erect macroalgae (e.g. kelps, *Sargassum* spp.) and included species traditionally classified as macroalgal browsers (e.g. *Kyphosus* spp.). Fishes exploiting turf-driven pathways included algal farmers (e.g. *Parma* spp., *Stegastes* spp.), and fishes feeding on various components of the turf algal matrix including croppers (e.g. *Prionurus* spp.), scrapers (e.g. *Scarus* spp.) and others.

The standing biomass of each group was estimated from fish surveys conducted in spring yearly from 2017 to 2019 at three tropicalized reefs in the Solitary Islands region. At each site, eight 25×5 m belt transects were swum to obtain fish size and abundance data (total transects $n = 64$, as surveys were not able to be completed in one of the sites in 2018; Table S1). Multi-year surveys were used to provide an average overview of the fish assemblage structure, as certain tropical species can be highly abundant in certain years and very rare in others and the presence of schooling species is also highly variable. A SCUBA diver swum at a constant pace (~ 2 min per transect) using a diver-operated stereo video (stereo-DOV) consisting of two GoPro cameras inwardly converged at c. 8 degrees to provide a standardized field of view and accurate length measurements. The system was calibrated before each survey following the methods outlined in Boutros et al. (2015) using the CAL software (SeaGis). Video footage was analysed using the software 'EventMeasure Stereo' (SeaGis) to identify fish species and measure individual fork length. Biomass of fish individuals was obtained using standard length–weight relationships, with parameters obtained from Fishbase (Froese & Pauly, 2021). Species with missing information were assigned parameters from a closely related species.

To estimate the secondary productivity and turnover of each herbivore fish group, we used the individual age framework recently developed by Morais and Bellwood (2020) and the accompanying R package `RFISHPROD` to calculate the underlying framework equations and parameters. Briefly, this approach combines information on fish body size, with species-specific life-history traits to predict the age, growth and natural mortality rates of individuals. For the model, we used information on the mean sea surface temperature of our locations (NOAA), maximum lengths, diet and position in the water column obtained from Fishbase and the database provided in Morais and Bellwood (2018). These data were then used to calculate K_{max} —a standardized growth parameter under a von Bertalanffy growth model (VBGM), which represents the rate at which a fish with a given length would approach its species' maximum length (Morais & Bellwood, 2020). K_{max} can be predicted with relative accuracy for unsampled species using body size and the ecological trait information above (Morais & Bellwood, 2018). To calculate the expected net biomass production by a given individual in a day, the observed fish weight (obtained using the length–weight coefficient) from our surveys was subtracted from the modelled weight obtained for that fish under a day of growth. A size- and species-specific mortality risk was then derived and applied it to our dataset to estimate which individuals from our data would stochastically perish after a day. To do so, the empirical relationships derived by Pauly (1980) and Gislason et al. (2010)

were implemented within following Morais and Bellwood (2020). These equations consider VBGM parameters, sea surface temperature and an exponential negative relationship between mortality risk and size. Finally, we summed the individual estimates of fish biomass growth for each group to obtain the produced biomass. The biomass turnover was then calculated as the quotient of produced biomass and standing biomass.

2.6 | Biogeographical patterns

To explore whether the patterns documented were consistent across different biogeographical contexts, we compared the benthic structure and herbivorous fish productivity on tropicalized reefs across Australia's western tropical-temperate transition zone. Sampling was conducted on the coastal sandstone reefs off Port Gregory (Figure 1e; Table S1), located in Western Australia. Reefs in this region were historically dominated (c. 70% cover; Bennett et al., 2015) by kelp and other canopy-forming species (mainly *Sargassum* spp.), which declined or disappeared completely and became dominated by algal turfs after a marine heatwave in 2011 (Figure 1d-f), with tropical herbivores also increasing in abundance (Bennett et al., 2015).

The composition of the fish assemblage at three tropicalized reefs in that region was obtained between 2017 and 2019 following the protocols described for eastern Australia (i.e. eight transects at each site every year, $n = 71$ transects in total). Benthic cover at each site was quantified on October 2019 along four transects ($n = 10$ photoquadrats), while algal assemblages were sampled March 2019 following the methods described but using a 100 cm² quadrat ($n = 10$) as it was an area visually greater than the structural pattern of the algal assemblage. The mesh bags used were also coarser (125 μ m). For comparison purposes, only algae and particulates sieved into 125–2,000 μ m size classes were used for sediment biomass estimates, which were standardized to kg DW/m². This was anticipated to have minimal effects in the comparison as sediments across the two study areas are skewed towards medium grain sizes (A. Pessarrodona, unpubl. data). All collections were conducted under permit FT61000345 (WA Department of Biodiversity, Conservation and Attractions).

2.7 | Statistical analyses

To visualize the composition of algal assemblages between control and tropicalized sites in eastern Australia, we used a non-metric multidimensional scaling (NDMS) analysis based on Bray–Curtis distances of square-root transformed biomass data (wet weight). Kelp was not included in the analysis as described above. The effects of tropicalization status (fixed factor; control vs. tropicalized) were then examined using a permutational multivariate analysis of variance (PERMANOVA) with 9,999 permutations under a reduce model using PRIMER 7.0 with the PERMANOVA

+ add-on (Anderson et al., 2008). Site was included as a random factor nested within tropicalization status, to account for the hierarchical nature of the data ($n = 3$ and 4, for control and tropicalized states). To examine data dispersion, we conducted permutational analysis of multivariate dispersion (PERMDISP) to determine whether within-group variation differed between levels of each factor. Finally, similarity percentage analysis (SIMPER) was used to identify which species/taxa were responsible for the similarity between reef states.

Comparisons among tropicalization status were made using generalized linear mixed models (GLMMs) within the R statistical environment using the GLMMTMB package (Brooks et al., 2017). In all models, tropicalization status (two levels, control vs. tropicalized) was considered a fixed effect, while site was considered as a random effect nested within tropicalization status (seven sites) as we considered sites to be random from a pool of potential sites within each tropicalization status. GLMMs were fitted with a gamma (particulate and organic load), or tweedie (mean algal height and algae biomass) distribution and a log-link, as exploration of the residuals revealed heteroscedasticity of the residuals and non-normality. The distribution used on all our models depended on the data type and model fit as assessed by QQ plots and residual dispersion, Kolmogorov–Smirnov, and outlier tests with the DHARMA package (Hartig, 2020). For the response variable 'Species richness', we used a Poisson distribution as data were counts, while for the variables 'Proportion of organic matter in the particulate load' we used a beta error distribution due to the proportional nature of the data. To test for differences in herbivory intensity (bites/m²) across tropicalization states we used a GLMM with a zero-inflated negative binomial distribution as data were counts and highly zero skewed (>60% replicates with the absence of bites). Filming duration (minutes) was included as a covariate while site (nine sites) was included as a random effect within tropicalization status (fixed effect, two levels).

To compare the benthic structure between tropicalized reefs in eastern and western Australia, we used GLMMs with coast as a fixed effect (two levels) and site (seven levels) as a random effect nested within coast. For the response variables 'Mean algal height' and 'Particulate load' we used a gamma error distribution, while for the variables 'Proportion of organic matter in the particulate load' and 'Algae biomass' we used beta and tweedie distributions respectively based on the reasoning above. Finally, we compared the standing herbivorous fish biomass (kg 100 m⁻²) and productivity (kg ha⁻¹ day⁻¹) between coasts (two levels), trophic pathways (two levels, canopy or turf driven) and temperature affinities (two levels, temperate or tropical) using GLMMs fitted with a gamma error distribution and the variables sampling year (three levels) and site (three levels) specified as random effects. As some trophic pathways were absent in some coasts inflating the data with zeroes, we modelled those absences depending on the factors and their interactions. Model convergence issues due to large eigenvalues meant we could not estimate the variance of the triple interaction in all models and the Coast:Affinity interaction in the productivity model.

3 | RESULTS

3.1 | Benthic structure

Benthic cover was dominated by kelps in control sites and turfs at tropicalized sites (Figure S1). The understory/turf algal communities of control and tropicalized sites in the Solitary Islands were significantly different (PERMANOVA: Pseudo $F_{1,37} = 2.68$, $p = 0.01$; Figure 2a). Control sites were dominated by coralline algae, with *Arthrocardia wardii* and *Amphiroa anceps* being the most abundant (84% of average biomass; Table 1). The composition of tropicalized sites on the other hand was more variable, from relatively barren sites

with few species present in low biomass, to more diverse sites featuring similar richness and abundances to the control sites. *Amphiroa anceps*, *Zonaria turneriana*, *Lobophora variegata*, *Dictyota* sp. and a red filamentous algae contributed 90.3% of the average biomass in tropicalized sites. There was significant heterogeneity between tropicalized and control sites (PERMDISP, $p < 0.05$), potentially due to our unbalanced design (Anderson & Walsh, 2013). Randomly removing a tropicalized site resulted in non-significant PERMDISP but a significant effect of tropicalization status in PERMANOVA, suggesting that there was a 'true' tropicalization status effect in our original analysis.

Overall, algal vegetation in the tropicalized sites was significantly shorter (1.1 ± 1.3 cm; $p < 0.05$; Table S3; Figure 2b), with understory/

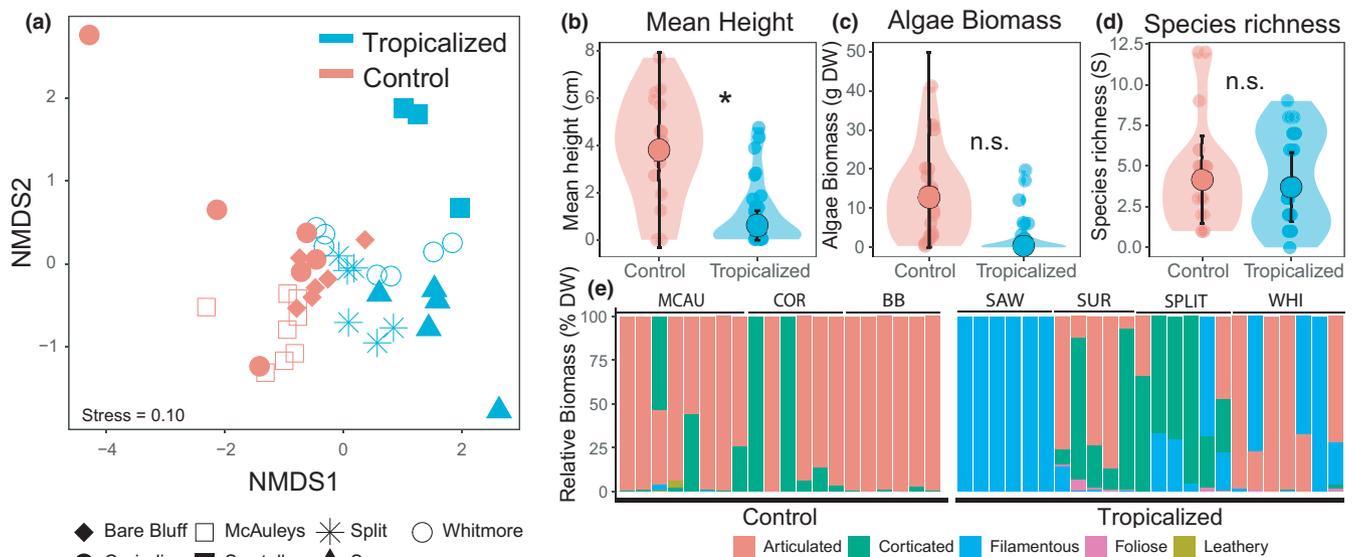


FIGURE 2 Algal assemblage structure at control and tropicalized sites in the Solitary Islands region. Note that kelps were not sampled. (a) NMDS plot showing similarities in the algal assemblages based on square-root transformed biomass data. Symbols depict sampling sites. (b–d) Mean algal height (mean of five measurements), total algae biomass (dry weight; DW) and species richness of samples (400 cm²). Small dots inside the violin indicate the replicate-level values, while larger dots and error bars denote the predicted mean and 95% confidence interval from the model. *Indicates significant differences at $\alpha < 0.05$, while n.s. indicates non-significant differences. (e) Differences in relative abundance (DW) of different algal functional groups within the turf community at control and tropicalized sites; each bar depicts a sample

TABLE 1 Breakdown of average dissimilarity between control and tropicalized reefs in the Solitary Islands region contributed by each algal taxa; taxa are ordered in decreasing contributions. Only taxa contributing at least 3% are included. The total average dissimilarity between reef states was 88.6%. Note the abundances were square-root transformed for analysis

Species	Control	Tropicalized	Average dissimilarity	Dissimilarity SD	% Contribution	Cumulative %
	Average abundance	Average abundance				
<i>Arthrocardia wardii</i>	2.8	0.00	28.6	1.1	32.2	32.2
<i>Amphiroa anceps</i>	2.2	1.2	20.0	1.2	22.4	54.6
<i>Peyssonnelia</i> sp.	0.6	0.0	7.3	0.5	8.2	62.8
Filamentous turf	0.1	0.4	4.5	0.8	5.1	67.9
<i>Jania rosea</i>	0.4	0.2	4.3	0.8	4.8	72.7
<i>Zonaria turneriana</i>	0.1	0.5	4.2	0.4	4.7	77.4
<i>Lobophora variegata</i>	0.0	0.3	3.0	0.5	3.4	80.8
<i>Curdiea crassa</i>	0.1	0.0	2.7	0.2	3.0	83.4

turf vegetation in control sites averaging 3.9 ± 2.3 cm. It is important to note, however, that our surveys in control sites deliberately did not capture kelp plants, which form tall canopies and would have further significantly increased the vegetation height. Total understory/turf standing algal biomass (DW) in the tropicalized sites was ~ 4.5 times lower on average, although differences were not significant (GLMM, $p > 0.05$; Table S3; Figure 2c). Understorey/turf assemblages between control and tropicalized sites also did not differ in terms of species richness (Figure 2d) but were markedly different in terms of the dominant functional groups (Figure 2e). Articulated coralline algae dominated at the control sites, while a wide range of functional forms dominated the tropicalized sites.

Total benthic particulate loads were not significantly different along the tropicalization gradient (Figure S3a), although loads varied substantially among sites, as reflected by high random effect variance. Loads varied from 1.71 ± 0.43 g 400 cm $^{-2}$ (means \pm SD) at Sawtell, a tropicalized site, to 38.11 ± 11.33 g 400 cm $^{-2}$ at a control site, Bare Bluff. The organic loads contained within the particulates were also not different along the gradient (Figure S3b). The particulates deposited on tropicalized sites contained, however, a significantly higher portion of organics relative to the total particulate mass ($p < 0.05$; Figure S3c). Organic content ranged from 0% to 13%, with the highest mean content ($7.43 \pm 2.88\%$) found in the particulate loads of tropicalized sites (Whitmore), and the lowest ($2.2 \pm 1.0\%$) at a control site (Bare Bluff). There was no relationship between the percentage of organics or silicates and the total particulate load (Figure S4).

3.2 | Organic matter availability

The biomass of organic and inorganic benthic components differed along the tropicalization gradient. On average, almost 60% of the

total benthic biomass in the control sites was in the inorganic compartment (sediment and calcium carbonate), with most of the organic biomass being in kelp plants (Figure 3). Overall, detritus and algal organic matter represented comparatively minor compartments (5.5%) with a substantial fraction of the turf organic matter (57%) being in articulated coralline algae, and therefore not available to primary consumers. Total benthic biomass was lower and still dominated by the inorganic compartment in the tropicalized sites, although most of the organic biomass in those sites was in algal turfs. More algal matter within that compartment was consumable in tropicalized sites (79%), with detritus also being more available (Figure 3).

3.3 | Herbivory intensity

Feeding interactions between herbivorous fishes and the benthos were dominated by tropical species on both control and tropicalized sites. Interactions were almost negligible in control sites, varying from 0 to 47 bites m $^{-2}$ hr $^{-1}$, and substrate bites being registered in 23% of the samples. Feeding interactions on the tropicalized sites were significantly higher ($400 \pm 1,891$ bites m $^{-2}$ hr $^{-1}$; GLMM, $p = 0.01$, Table S3, Figure 3), but also very variable, ranging from 0 to an estimated 12,000 bites m $^{-2}$ hr $^{-1}$ (by a large school of approximately 200 individuals). Feeding was entirely dominated by schooling subtropical surgeonfishes (*Prionurus* spp.), with 44% of the samples registering substrate bites.

3.4 | Herbivore biomass, secondary productivity and turnover

Across the tropicalized reefs in the Solitary Islands region, average herbivorous fish abundance and biomass ranged between 43–49

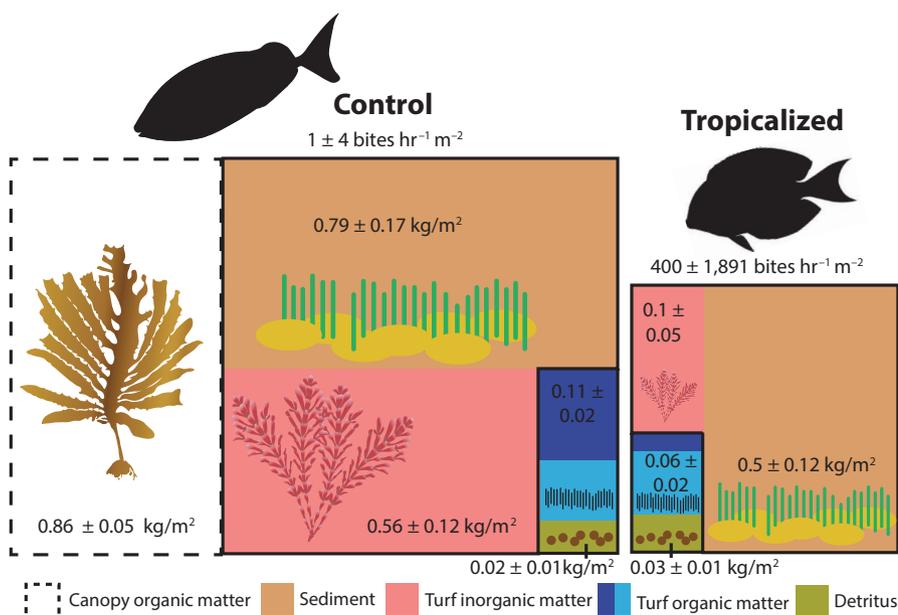


FIGURE 3 Conceptual diagram showing the average biomass (kg dry weight/ m^2) of inorganic sediment, turf inorganic matter (CaCO_3), canopy, turf and detrital organic matter in the benthic particulates in control and tropicalized sites (means \pm SE) in the Solitary Islands region. Consumable algae organic matter is shown in light blue, while unconsumable algae organic matter (i.e. inside calcified algae) is shown in dark blue. The mean fish bite rates on the EAM are shown above the boxes. The area of the boxes comprising each benthic component is scaled to represent their study wide averages

individuals 100 m^{-2} and $5.5\text{--}6.2\text{ kg }100\text{ m}^{-2}$. Herbivore abundance was dominated by temperate damselfishes (30.4 ± 2.27 individuals 100 m^{-2} , mean \pm SE; 65% of herbivorous fish), whilst herbivore biomass was dominated by tropical turf-cropping surgeonfishes ($3.68 \pm 1.3\text{ kg }100\text{ m}^{-2}$; Figure 4a, GLMM, $p < 0.001$; Table S4). Browsers accounted relatively little to herbivore fish abundance or biomass (0.5% and 1% respectively). Most of the herbivorous fish in this location therefore relied on turf-driven trophic pathways, with tropical herbivorous fish contributing to 34.5% (16.11 ± 5.6 individuals 100 m^{-2}) of the total herbivorous fish abundance and 63% of the total herbivorous biomass on average. The total reef-scale herbivorous fish productivity was $0.89 \pm 0.3\text{ kg ha}^{-1}\text{ day}^{-1}$ (Figure 4b). Tropical fishes produced between 0.58 and $1.08\text{ kg ha}^{-1}\text{ day}^{-1}$ ($0.74 \pm 0.25\text{ kg ha}^{-1}\text{ day}^{-1}$; dominated by cropping surgeonfishes), while the production of temperate herbivores was comparatively minor ($0.14 \pm 0.01\text{ kg ha}^{-1}\text{ day}^{-1}$). Macroalgal browsers had negligible production ($0\text{--}0.01\text{ kg ha}^{-1}\text{ day}^{-1}$).

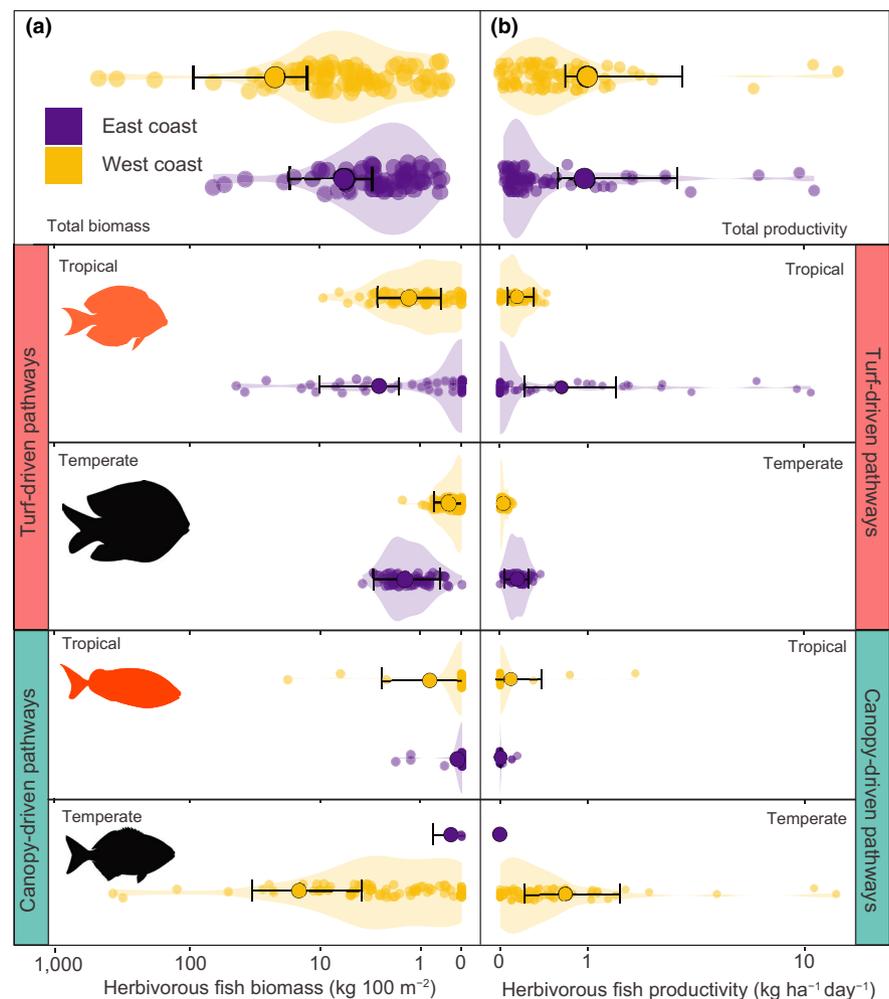
3.5 | Biogeographical patterns

At tropicalized reefs in western Australia, herbivore fish abundance and biomass ranged between 15–28 individuals 100 m^{-2} and

$8.7\text{--}26.3\text{ kg }100\text{ m}^{-2}$. Tropical fishes exploiting turf-driven pathways were also widespread in this region, representing between 13% and 25% of all herbivores. Herbivorous fish abundance and biomass was dominated, however, by browsers exploiting canopy-driven pathways (mostly *Kyphosus* spp., positive Coast-Pathway interaction, GLMM, $p < 0.001$; Table S4), which comprised 51% and 87% of abundance and biomass respectively (10.6 ± 2.35 individuals and $15.6 \pm 6.6\text{ kg }100\text{ m}^{-2}$; Figure 4a). Fish exploiting turf-driven pathways had an average standing biomass of $1.8 \pm 0.32\text{ kg }100\text{ m}^{-2}$, with scraping parrotfishes contributing between 83% and 99% of that biomass across sites (Figure S5). The reef-scale productivity of herbivorous fishes in western Australia totalled $0.99 \pm 0.3\text{ kg ha}^{-1}\text{ day}^{-1}$, the majority of production being from macroalgal browsers ($0.82 \pm 0.25\text{ kg ha}^{-1}\text{ day}^{-1}$; Figure 4b). Tropical fishes exploiting turf-driven trophic pathways produced between 0.11 and $0.15\text{ kg ha}^{-1}\text{ day}^{-1}$ ($0.13 \pm 0.01\text{ kg ha}^{-1}\text{ day}^{-1}$; dominated by scrapers). Temperate algal farmers produced an average of $0.14 \pm 0.01\text{ kg ha}^{-1}\text{ day}^{-1}$.

Tropicalized reefs in western Australia were also dominated by turfs (Figure S2) but featured conspicuously longer, sediment-laden turfs compared to eastern Australia. Algal biomass was an average of five times lower on the east coast (Figure 5a), with turfs also being c. 1 cm shorter on average (Figure 5b), albeit those differences were

FIGURE 4 Herbivorous fish biomass (a) and total secondary productivity (b) at tropicalized sites in eastern (purple) and western (yellow) Australia. The first two top panels show the total values of the herbivorous fish assemblages, while the rest of the panels depict groups exploiting turf- or canopy-seaweed-driven trophic pathways. Groups are split by temperature affinity: tropical (orange silhouette) or temperate (black). Small dots show the individual transect-level biomass and productivity values, while larger dots and error bars denote the predicted mean and 95% confidence interval from the model. In some cases errors bars are too small to be visible. Silhouettes represent some of the dominant species in each pathway



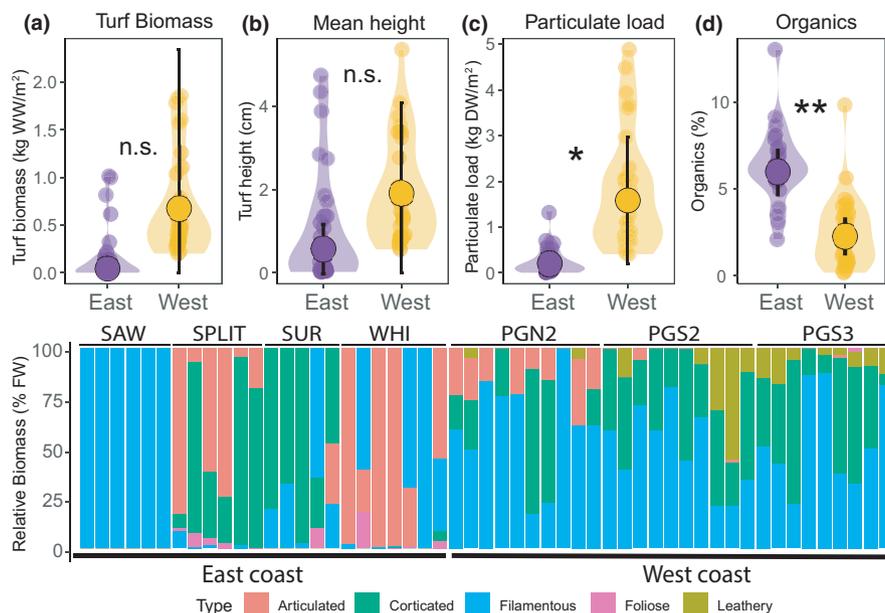


FIGURE 5 Turf assemblage structure and characteristics of its associated particulates in eastern (four sites) and western (three sites) Australia. (a) Turf algal biomass (wet weight; WW), (b) mean turf height (cm), (c) benthic particulate load (kg dry weight; DW; 125–2,000 μm), (d) relative percentage of organic material in the benthic particulates. Small dots show the individual transect-level biomass and productivity values, while larger dots and error bars denote the predicted mean and 95% confidence interval from the model. In some cases error bars are too small to be visible. (e) Differences in relative abundance (wet weight; WW) of different algal functional groups within the turf community; each bar depicts a sample. *Indicates significant differences at $\alpha < 0.05$, $**\alpha < 0.01$, while n.s. indicates non-significant differences

not significant (GLMM, $p > 0.05$; Table S3). Turf particulate loads on western reefs were >7 times higher (1.8 ± 0.2 and 0.25 ± 0.06 kg/m², respectively, GLMM, $p < 0.001$; Table S3; Figure 5c). Particulate loads were, however, significantly organically enriched on the east compare to the west ($5.6 \pm 2.4\%$ and $2.5 \pm 2.0\%$ respectively; Figure 5d; GLMM, $p < 0.001$; Table S3). Filamentous algae were the dominant algal component of turfs at all sites in western Australia, while turfs in eastern Australia were dominated by a wide range of forms depending on the site (Figure 5e).

4 | DISCUSSION

The composition and structure of temperate reefs is rapidly changing across the globe, with warm-affinity species playing increasingly dominant roles in ecosystem function (Pessarrodona et al., 2018; Tanaka et al., 2012; Vergés, Steinberg, et al., 2014). While we are beginning to unravel the ecological implications of such compositional shifts, little is known about how they affect energy flow through higher trophic levels and the wider ecosystem. Tropicalized temperate reefs offer a unique opportunity to study climate-driven changes in energy flow as they often feature habitat and nutritional resource shifts coupled with mixtures of temperate and tropical species performing novel functions (Vergés et al., 2019). Along an inshore-offshore tropicalization gradient in eastern Australia, we found that tropicalization results in dominance by fast-growing turfs and a relatively higher availability of palatable algae and detrital particles. Locations that experienced tropicalization exhibited a

higher intensity of feeding by herbivorous fishes than control sites, with the majority of grazing activity on the benthos being driven by tropical fishes exploiting turf-driven pathways. These fishes also dominated the production and turnover of biomass in the herbivorous fish assemblage, suggesting that they are key drivers of energy flow through the food web. A transcontinental comparison with Australia's western tropical-temperate transition zone revealed that turf-grazing tropical fishes also contributed substantially to the total herbivore biomass produced on tropicalized reefs. We thus posit that the rise of turfs and tropical herbivores on tropicalized reefs enables higher herbivore productivity by strengthening two trophic pathways: algivory and detritivory.

On average, the benthos of tropicalized sites experienced 400 times more bites by herbivorous fishes, suggesting higher herbivory than inshore control sites. It has been hypothesized that a strengthening of herbivory is one of the possible causes behind the increase in fish abundance and biomass that has occurred at the studied eastern Australian reefs following their tropicalization, although the mechanisms fuelling such increases have not been established (Smith et al., 2021). Here, we found that the availability of palatable algal organic matter and its consumption was higher in sites that experienced tropicalization compared to control sites, offering one potential mechanism. Tropicalized sites were dominated by filamentous, foliose and corticated turf-forming algae, which are generally considered to be nutritionally superior and less defended compared to the algae that dominated control forested sites (kelps and articulated coralline algae). For example, turf algae generally have higher energetic content (e.g. lipids, carbohydrates and proteins; Montgomery &

Gerking, 1980; Paine & Vadas, 1969; Table S5) and are preferred by most herbivores (Littler et al., 1983; Montgomery & Gerking, 1980).

Turf algae are also faster growing than coralline algae or kelps, and can sustain higher yields to herbivores (e.g. some filamentous algae can completely regrow after 4 days of grazing, Bonaldo & Bellwood, 2011). It is thus likely that a greater portion of the algal productivity is readily consumed in turf-dominated tropicalized reefs, directly fuelling fish biomass. Indeed, large kelp plants and coralline algae are only consumed by a few specialized organisms (Andrew & Jones, 1990; Nicholson & Clements, 2020; Table S5), their productivity being largely exported to other habitats as detritus (Krumhansl & Scheibling, 2012). For instance, the skeleton of coralline algae makes them relatively unpalatable and very well-defended, with few herbivore species being able to feed on them even in areas with diverse herbivore assemblages (Longo et al., 2015).

Tropicalization also appears to unlock benthic detrital pathways. Benthic particulates were significantly more enriched (higher detritus content) in tropicalized sites, suggesting they had a higher nutritional value. This agrees with observations from tropical reefs, where turfs constitute a main source of detritus to the benthos (Hansen et al., 1992; Wilson et al., 2003). The availability of that detritus to consumers depends on the amount of inorganic sediments mixed within the benthic particulates (Gordon et al., 2016), but also on the relative abundance of other benthic components. Detrital particles constituted a similar fraction (c. 35%) of the total consumable organic matter in the understory/turf layer at control and tropicalized locations, but this organic matter was additionally diluted by relatively larger quantities of inorganic algae (i.e. CaCO_3) as well as inorganic sediments at control sites.

Together, these findings suggest that tropicalization enhances the resource base available to primary consumers of temperate reefs, fuelling herbivorous fish biomass production. While the nature of our study design could not resolve temporal changes arising from tropicalization at the offshore sites, previous studies have shown that total fish biomass at offshore sites has increased following tropicalization (i.e. loss of kelp cover and increase in tropical species; Smith et al., 2021). In particular, fishes exploiting turf-driven pathways have experienced the largest biomass gains ($\Delta 371$ g FW per individual) of any fish species, consistent with the observations made here and suggesting that they may have been particularly benefited by the expansion of turfs after kelp decline (Smith et al., 2021). Still, other factors (e.g. riverine input, sediments, wave energy or predator abundance) varying along the inshore–offshore gradient examined in this study could have confounded some of patterns observed. For instance, high sediment loads could be inhibiting herbivory and turf productivity at our inshore sites (Tebbett et al., 2018), while lower predator abundances offshore could result in higher benthic feeding pressure. While we cannot discount the influence some of these factors may have contributed to our observations, we found that total benthic sediment loads did not significantly vary across tropicalized and control sites (Figure S3), and no differences in predator abundance have previously been found across the studied gradient (Malcolm et al., 2010).

At our study sites in eastern Australia, tropical fishes obtaining nutrition from turf-derived pathways were central drivers of energy flow, producing $83 \pm 4\%$ of the daily herbivorous fish biomass despite only comprising $35 \pm 5\%$ of the abundance and $64 \pm 6\%$ of the standing biomass. This is likely to represent a major fraction of the overall fish productivity of the reef, as herbivores make up a 43% of total fish biomass alone (S. Smith, unpub. data). The high rates of productivity of tropical fishes are likely due to their higher biomass turnover (i.e. production efficiency), as they generally produced more biomass per unit of standing stock biomass than their temperate counterparts (Figure S6). These differences may be explained by how fishes utilize turfs. Tropical fishes are turf-cropping roaming herbivores (e.g. *Prionurus* spp.) with high metabolic demands that exert intense feeding pressure (Basford et al., 2016; Vergés et al., 2016), while temperate fishes exploiting turfs are algal farmers (*Parma* spp.) with relatively low feeding rates (Saunders, 2011). The increase in tropical fishes in reefs under tropicalization thus represents a major shift in fish energetic dynamics, with more energy being derived from turf resources and high rates of secondary productivity.

Our surveys in western Australia revealed that tropical fishes exploiting turf-driven pathways are widespread in tropicalized reefs, reaffirming that turfs are important drivers of the shifts in biomass production and energy flow caused by tropicalization more globally. Indeed, more than 90% of the secondary productivity of tropical herbivores was fuelled by turf-driven pathways. Herbivore groups and the overall contribution of turf-driven pathways to total herbivore biomass and secondary productivity, differed, however, between the two biogeographical contexts. In eastern Australia, secondary productivity and grazing pressure was dominated by turf-cropping herbivores (*Prionurus* spp., >98% of the bites)—which have steadily increased in abundance and biomass in sites where kelp declined (Smith et al., 2021; Vergés et al., 2016). In western Australia, secondary productivity was dominated by herbivores targeting canopy-forming macroalgae (*Kyphosus* spp.), while fish exploiting turf-driven pathways were relatively less important and dominated mostly by turf-scraping herbivores (*Scarus* spp. Figure S5). Some of the patterns documented here will be undeniably influenced by filters acting at large biogeographical scales, such spatial connectivity, phylogeny, and physiological constraints related to temperature (Ferreira et al., 2004), coupled with other finer scale filters such as the availability and quality of food resources. For example, the scarcity of surgeonfishes—which have high rates of secondary productivity and biomass turnover—in western Australia may also explain some of the observed differences. Additionally, despite kelps largely disappearing from reefs in the western temperate–tropical transition zone, other canopy-forming algae such as *Sargassum* spp. are present (Figure S2). *Sargassum* spp. may thus constitute an important resource for temperate and tropical browsers, continuing to fuel fish productivity as opposed to tropicalized eastern Australia reefs, where *Sargassum* spp. and other erect algae are scarcer (Figures S1 and S2).

The comparatively lower secondary productivity of fish exploiting turf-driven pathways in western Australia could also partially be

explained by a lower energetic yield of turf and detritus to fishes in this region. In coral reefs, the nutritional value of turfs and its yield to herbivorous fishes is influenced by sediment loads (Tebbett et al., 2018), with precipitous declines in the primary productivity of turfs and the relative value of its associated particulates beyond sediment loads of 0.1 kg/m² (Tebbett & Bellwood, 2020). Turfs in western Australia contained an average of 1.8 ± 0.25 kg/m² of inorganic sediment, seven times more than those on the east and one of the highest loads reported in the subtidal literature (Pessarrodona, Filbee-Dexter, et al., 2021; Tebbett & Bellwood, 2019). This diluted their organic quality and likely their nutritional yield to herbivorous fishes in the region (scrapers and sediment suckers), which ingest sediment while feeding and are therefore likely susceptible to high sediment loads and reduced organic content (Gordon et al., 2016).

Overall, these findings point to the importance of considering the biogeographical context and the characteristics of turfs and their particulates when predicting consequences of tropicalization on energy flow. Defining trophic pathways and guilds based on strictly discrete categories is always complex, as these may vary across ontogeny, space, and time (Parravicini et al., 2020). Some of these nuances therefore may not have been captured by our functional classification approach. For example, range-expanding herbivores may exploit novel resources in temperate reefs (Miranda et al., 2019), and examining the exact pathways exploited by each fish in a novel environment will require a more thorough analysis of their diet. Further research is also needed to understand the effect of other fine (e.g. site) and larger (e.g. biogeography) spatial scale factors in shaping herbivory dynamics. Similarly, the role of turfs as a trophic resource for benthic invertivorous fish, which often derive an important fraction of energy from the fauna living among turfs (Kramer et al., 2013), requires future exploration.

As humans are transforming Earth's ecosystems at an increasing rate, there is a pressing need to understand and empirically measure the functional role of organisms in novel ecosystem configurations. As tropicalization continues to reshape temperate reefs, an imminent challenge is understanding how organisms that are dominant in tropical locations (e.g. turfs, surgeonfishes and parrotfishes) transform energy flow (Vergés et al., 2019). Here, we show that corticated and filamentous turfs support novel trophic pathways and directly channel more energy towards consumers. This energetic rerouting manifests in higher biomass production by herbivores, which is predominantly driven by tropical species. The characteristics shaping the nature of algal turfs (e.g. particulate load, organic content), and its interactions with herbivorous fishes, thus emerge as important drivers of overall ecosystem function in temperate reefs as these become tropicalized. In particular, inorganic sediments bound within algal turfs may play an increasingly important role in shaping reef-scale trophodynamics, and the secondary productivity of fish.

ACKNOWLEDGEMENTS

This manuscript was substantially improved after incorporating feedback and comments from an anonymous reviewer and Renato Morais. The authors are also grateful for the support of

Derrick Cruz, Heather Denham and Erin McCosker during fieldwork. A.P. acknowledges support from the Australian Government International Research Training Program and the Holsworth Wildlife Research Endowment. T.W. and A.V. are grateful for support from the Australian Research Council DP170100023 (T.W., A.V.), DP190100058 (T.W.), and DP190102030 (A.V.). This work was also supported by a New South Wales Environmental Trust grant to A.V.

CONFLICT OF INTEREST

Adriana Vergés is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper. The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.P. conceived the idea and designed the research, collected and processed the turf samples, assisted in fish and herbivory data collection, analysed the data and drafted the manuscript; A.V. and T.W. provided input to the research idea, with A.V. assisting in turf sample collection in eastern Australia; A.V., N.E.B., S.B., M.P.S. and S.S. collected the fish and herbivory data; N.E.B. provided input to the data analysis; all authors commented on the manuscript draft; A.P., A.V. and T.W. provided funding.

DATA AVAILABILITY STATEMENT

All data and scripts that support the findings of this study are openly available in the Figshare repository <https://doi.org/10.6084/m9.figshare.16850803.v3> (Pessarrodona, Vergés, et al., 2021).

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How to cite this article: Pessarrodona, A., Vergés, A., Bosch, N. E., Bell, S., Smith, S., Sgarlatta, M. P., & Wernberg, T. (2022). Tropicalization unlocks novel trophic pathways and enhances secondary productivity in temperate reefs. *Functional Ecology*, 36, 659–673. <https://doi.org/10.1111/1365-2435.13990>