














Spatial compositional turnover varies with trophic level and body size in marine assemblages of micro- and macroorganisms

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Abstract

Aim: Spatial compositional turnover varies considerably among co-occurring assemblages of organisms, presumably shaped by common processes related to species traits. We investigated patterns of spatial turnover in a diverse set of marine assemblages using zeta diversity, which extends traditional pairwise measures of turnover to capture the roles of both rare and common species in shaping assemblage turnover. We tested the generality of hypothesized patterns related to ecological traits and provide insights into mechanisms of biodiversity change.

Location: Temperate pelagic and benthic marine assemblages of micro- and macroorganisms along south-eastern Australia (30–36° S latitude).

Time period: 2008–2021.

Major taxa studied: Bacteria, phytoplankton, zooplankton, fish, and macrobenthic groups.

Methods: Six marine datasets spanning bacteria to fishes were collated for measures of “species” occurrence, with a 1° latitude grain. For each assemblage, ecological traits of body size, habitat and trophic level were analysed for the form and rate of decline in zeta diversity and for the species retention rate.

Results: Species at higher trophic levels showed two to three times the rate of zeta diversity decline compared with lower trophic levels, indicating an increase in turnover from phytoplankton to carnivorous fishes. Body size showed the hypothesized unimodal relationship with rates of turnover for macroorganisms. Patterns of bacterial turnover contrasted with those found for macroorganisms, with the highest levels of turnover in pelagic habitats compared with benthic (kelp-associated) habitats. The shape of retention rate curves showed the importance of both rare and common species in driving turnover; a finding that would not have been observable using pairwise (beta diversity) measures of turnover.

Main conclusions: Our results support theoretical predictions for phytoplankton and macroorganisms, showing an increase in turnover rate with trophic level, but these

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predictions did not hold for bacteria. Such deviations from theory need to be investigated further to identify underlying processes that govern microbial assemblage dynamics.

KEYWORDS

benthic, biodiversity, compositional turnover, fish, latitude, microbial communities, pelagic, species retention, zeta diversity

1 | INTRODUCTION

Spatial gradients in environmental conditions can cause profound changes in biodiversity, and ecologists have long sought to explain variation in species identity and richness across space and time, known as turnover (Fischer, 1960; MacArthur, 1965; Pianka, 1966). Measurement of spatial turnover in biodiversity was enabled initially by the development of alpha and gamma diversity (MacArthur, 1965) and their relationship, beta diversity (Whittaker, 1972). Many broad patterns central to ecology and environmental management have been identified based on these parameters, such as changes in biodiversity along latitudinal gradients, whereby temperate realms are associated with higher spatial turnover and lower richness than tropical environments (Gaston & Blackburn, 2000). Environmental heterogeneity often produces dissimilarity in species composition between sites (i.e., turnover). Temperate marine habitats are often described as relatively homogeneous environments and are thus predicted to show lower turnover than freshwater or terrestrial realms (Soininen, 2010). At smaller spatial scales, however, general drivers of turnover become less clear (Lawton, 1999). Despite an increasing number of studies measuring beta diversity across a range of habitats, empirical data across multiple, co-occurring assemblages are rare, presenting a barrier for effective management of biodiversity (McGill et al., 2015).

To achieve an ecosystem-level understanding of turnover, it is important to test the generality of patterns of turnover across assemblages and how these relate to function (Seibold et al., 2018). For assemblages inhabiting the same space, differences in turnover can

be associated with characteristics of the organisms themselves (i.e., “ecological traits”), such as body size (and thereby adult dispersal ability), habitat use and trophic position (Nekola & White, 1999; Soininen et al., 2007) (Figure 1). Body size is a trait associated with all living organisms and is correlated with range size [in both passive (e.g., plankton) and large-bodied active dispersers], generation time (Villarino et al., 2018), and many other life-history traits that can influence distribution (Stearns, 1992). Theory predicts a concave relationship between body size and turnover; small, passive dispersers, such as plankton, cover wide ranges owing to wind and oceanographic processes, whereas active, large-bodied organisms possess large home ranges, hence turnover is anticipated to be low at the extreme ends of the size ranges (Barneche et al., 2019). Organisms of intermediate size possess greater site affinity and are expected to be more patchily distributed, resulting in comparatively high turnover (Soininen, 2010) (Figure 1a).

When considering the influence of habitat characteristics on turnover at local scales, benthic organisms are predicted to occur in patchier distributions than pelagic organisms, as supported by previous work showing higher temporal turnover in the benthos than in plankton (Korhonen et al., 2010) (Figure 1b). Organisms occupying higher trophic positions are likely to have more specialized diets, which might explain their relatively steeper turnover in species composition, independent of body size, compared with producers or first-order consumers (Hillebrand, 2004) (Figure 1c). Comparing turnover among ecological traits, in addition to measuring changes in overall species composition of assemblages, might provide an effective surrogate for ecosystem productivity and resilience (Coleman et al., 2015; Díaz & Cabido, 2001), but tests within and across co-occurring assemblages are lacking.

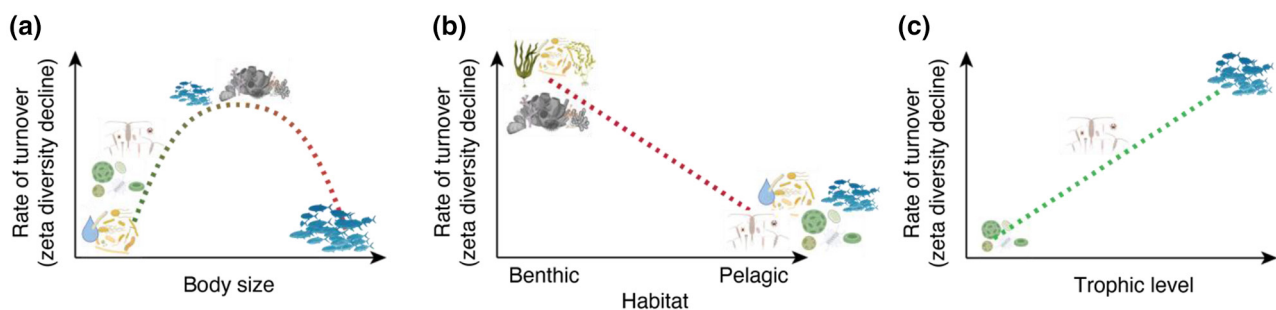


FIGURE 1 Conceptual representation of predicted changes in the rate of zeta diversity decline (i.e., spatial turnover) across the following ecological traits: (a) body size; (b) habitat; and (c) trophic level. Specific predictions for New South Wales datasets are as follows: (a) rate of turnover is expected to show a unimodal relationship with body size, initially increasing with body size among assemblages that are mainly passive and decreasing for larger, actively mobile assemblages; (b) assemblages occupying benthic assemblages should show greater patchiness and therefore greater spatial turnover compared with more widely distributed, pelagic assemblages; and (c) rate of turnover should increase with assemblage trophic position. Predictions and figure are adapted from Soininen et al. (2007)

Here, we seek to test whether patterns of turnover are generalizable within and across assemblages that co-occur along a latitudinal gradient, and are predictable and consistent with expectations based on their ecological traits. To assess the contribution of the full complement of common to rare species, we used zeta diversity measures. Zeta diversity is a recently developed metric for continuous compositional turnover that quantifies the shared number of species across any combination ($n = i$) of sites (Hui & McGeoch, 2014). Zeta extends previous pairwise measures of beta diversity ($n = 2$ sites) that emphasize the contribution of rare species to turnover (McGeoch et al., 2019), in order to compare similarity in species occurrence across multiple combinations of sites simultaneously (Figure 2a). Zeta diversity can be applied to many ecological questions, including the identification of potential key drivers of turnover in native versus alien species (Latombe, Richardson, et al., 2018), or to assess the efficacy of management protection on community stability (Pettersen et al., 2021). Zeta diversity can provide additional information on turnover compared with beta diversity, but to our knowledge it has yet to be used to test hypotheses of multiple assemblage turnover directly.

Using the east Australian coastline, a sampling region spanning 800 km or 6° of latitude, we measured two key aspects of turnover across different taxa, from microorganisms to fish, in marine assemblages: (1) zeta diversity decline, which provides an overall indication of the form and rate of change in species composition across space; and (2) species retention rate, which determines the relative role of rare to common species in driving spatial variation in assemblage composition. To assess the importance of considering

the contribution of rare to common species for unveiling patterns of turnover and the drivers of assemblage composition, we also compared beta and zeta diversity estimates of turnover. In an attempt to avoid confounding patterns of spatial turnover among taxa with underlying differences across geographical ranges (Koleff et al., 2003; Rodríguez & Arita, 2004; Soininen et al., 2007), we used datasets of co-occurring assemblages spanning the same latitudinal gradient, with a similar distance (c. 1° intervals) between sites. This approach aimed to facilitate direct comparisons of spatial turnover across marine assemblages to test existing predictions regarding ecological traits of body size, habitat and trophic level.

2 | METHODS

2.1 | Study area

Spatial turnover for rare to widespread genetically distinct organisms (species, operational taxonomic units and groups) was quantified in New South Wales (NSW; 30°0'36"–36°53'60" S), along the south-east coast of Australia, spanning 816 km. The NSW coastline encompasses dynamic oceanographic systems, including the southern section of the poleward-flowing East Australian Current and the eddy field it produces (Suthers et al., 2011). These oceanographic processes modulate the climate of the region, in addition to the biodiversity and functioning of marine ecosystems (Coleman et al., 2011). Over the next century, temperate regions of Australia are forecast to warm more than any other area in the Southern Hemisphere (Cai

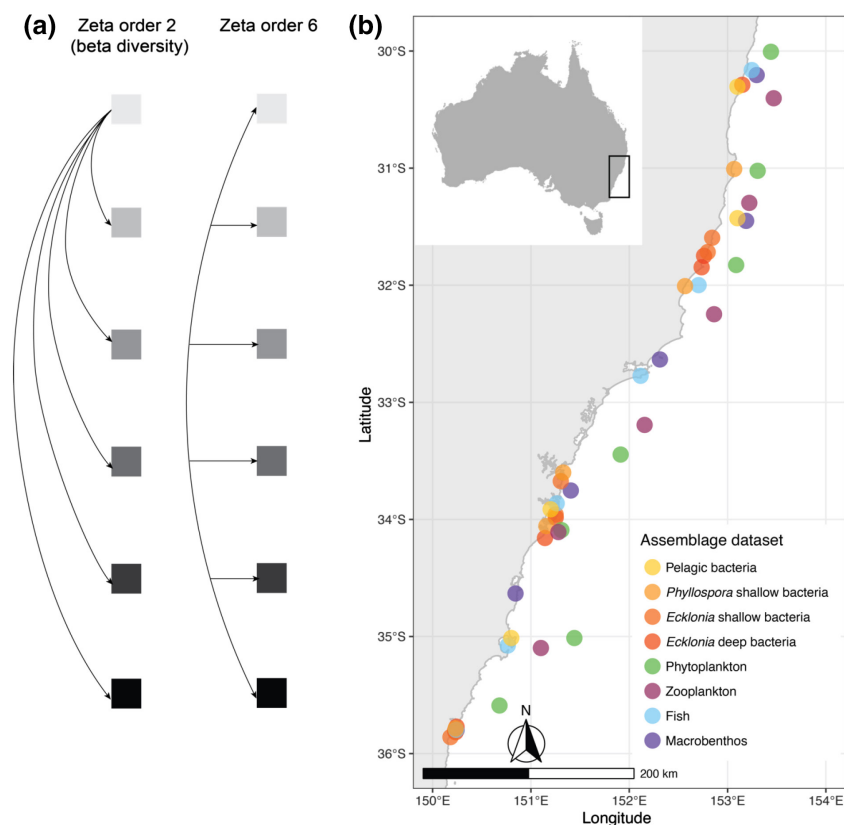


FIGURE 2 (a) Conceptual figure of zeta diversity across varying orders (i.e., combinations of sites along latitudinal gradients), illustrating the shared number of species between pairs of sites (beta diversity; i.e., zeta 2) and the shared number of multiple sites (in this example, six sites, simultaneously; i.e., zeta 6). For visual clarity, only pairwise values for beta diversity between the first site and all other sites are shown. The full measure of beta diversity would incorporate all possible pairwise combinations across the six sites. (b) Map of marine co-occurring assemblage sites sampled along the coast of New South Wales, Australia. Each point represents a site sampled within each dataset

et al., 2005), hence ongoing monitoring and a greater understanding of processes affecting the biodiversity of this region are key conservation priorities (Figure 2b).

2.2 | Marine assemblage datasets

We investigated zeta diversity relationships across six marine assemblages: (1) fishes; (2) benthic macroorganisms; (3) zooplankton; (4) phytoplankton; (5) kelp-associated (and thus benthic) microorganisms; and (6) pelagic microorganisms. Here, we define an “assemblage” as a group of organisms in a sample that may or may not interact, but are often taxonomically close, and we use the term “community” as a general term to describe “a group of interacting species populations occurring together in space” (Stroud et al., 2015). All assemblages were measured at the level of species except for macrobenthic (see details below) and bacterial assemblages, for which there is no generally accepted species concept (Achtman & Wagner, 2008) and which were therefore described by the commonly used denoised amplicon sequence variants (ASVs) that represent genetically distinct organismal entities or zero-radius operational taxonomic units (Callahan et al., 2016; Edgar, 2018). The ASVs were identified based on sampling of the 16S rRNA gene (details below), which mainly targets bacteria and some archaea; however, hereafter we refer to these samples more generally as ‘microorganisms’. Benthic macroorganisms were identified to the highest taxonomic resolution and are referred to hereafter as “groups”. Species/ASV/group-level incidence (presence/absence) data were collated from several datasets, for which sampling occurred at 1° latitude intervals across a 6° latitudinal range (c. -30 to -36°, with consistent longitude c. 150–151°; Table 1). In these datasets, presences were recorded between 2008 and 2021 (Table 1). To account for any potential within-level temporal variation driving among-level differences in zeta diversity, we analysed zeta diversity measures across multiple time points in datasets for which temporal replication was available (kelp-associated bacteria, phytoplankton, zooplankton and fishes). Before analysis, abundance data were converted to occurrence (i.e., presence = 1/absence = 0) data. All data handling and analysis was conducted in R v.4.0.3 (R Core Team, 2020).

2.2.1 | Fish

Fish species abundance data were sourced from the Reef Life Survey (RLS), which is a global dataset for monitoring rocky and coral reef ecological communities, with the extract including data collected between February 2008 and March 2021 (Edgar & Stuart-Smith, 2021). In brief, surveys involved a visual census of fish species by SCUBA along a 50m transect line (mean ± SD depth: 7.97 ± 3.9 m). Fish within 5 m of the transect line were recorded, and multiple transects were generally sampled at each site (mean = 2.8 ± 1.2). For details on the RLS standard method, see Edgar & Stuart-Smith (2014) and Edgar et al. (2020). A total of 613 fish species were identified in rocky reef

TABLE 1 Summary of datasets used across six co-occurring marine assemblages

Level	Unit of diversity (total number)	Latitudinal range (°)	Longitudinal range (°)	Sampling period	Mean number of samples per degree latitude (±SD)	Sampling protocol	Source
1. Fish	Species (n = 613)	-30.01 to -35.99	150.16 to 153.27	February 2008–March 2021	210 (151)	SCUBA survey of rocky reefs c. 8 m in depth	RLS
2. Macrobenthos	Groups (n = 94)	-30.2 to -35.8	150.2 to 153.3	August 2012–November 2012	142 (49)	AUV images of rocky reefs 25–50 m in depth	IMOS
3. Zooplankton	Species (n = 298)	-30.01 to -37.00	150.18 to 153.82	June 2009–November 2019	94 (13)	Plankton sampler towed at 7 m depth	AODN
4. Phytoplankton	Species (n = 160)	-30.01 to -36.71	150.23 to 153.82	June 2009–November 2019	91 (37)	Plankton sampler towed at 7 m depth	AODN
5. Kelp-associated bacteria	ASVs (n = 8,582–13,104)	-31.70–35.8	150.2 to 152.8	April 2011–January 2012	5 (0)	Swab surface of kelp at shallow (c. 1 m) and deep (c. 10 m) depths	<i>Ecklonia radiata</i> : Marzinelli et al. (2015); <i>Phyllospora comosa</i> : E. M. Marzinelli and N. L. R. Williams (unpublished observations)
6. Pelagic bacteria	ASVs (n = 34,733)	-30.3 to -36.9	150.2 to 152.8	June 2011–April 2012	3 (0)	Surface water samples	Williams et al. (unpublished observations)

Note: Latitude is in decimal degrees. Sampling period and frequency (mean number of samples taken at each latitudinal gradient per year) are given in parentheses.

Abbreviations: AODN, Australian ocean data network; ASV, amplicon sequence variant; AUV, autonomous underwater vehicle; IMOS, integrated marine observing system; RLS, reef life survey.

sites located along the NSW coast. Commonly occurring species included *Atypichthys strigatus*, *Cheilodactylus fuscus*, *Notolabrus gym-nogenis*, *Ophthalmolepis lineolatus*, *Parma microlepis* and *Trachinops taeniatus*, and rare species included species within the *Bodianus*, *Eviota*, *Naso* and *Valenciennesa* genera (many tropical vagrants). Fish species were categorized based on traits that contribute to the ecological position of species in the ecosystem: body size, habitat and trophic level (Stuart-Smith et al., 2013). Body size [maximum length (ML)] included small to medium-sized (<30 cm; $n = 308$ species) and large (≥ 30 cm; $n = 258$ species) fishes. Habitat categories were benthic ($n = 118$ species), demersal ($n = 360$ species), pelagic site attached ($n = 51$ species) and pelagic non-site attached ($n = 37$ species). Fish species were also categorized into their trophic position as herbivores ($n = 110$ species), planktivores ($n = 70$ species), invertivores ($n = 305$ species) and carnivores ($n = 81$ species). Species were assigned ecological traits [body size (i.e., species ML), habitat and trophic group] based on data from FishBase (<http://www.fishbase.org/>) and combined expert knowledge (Parravicini et al., 2020; Stuart-Smith et al., 2013).

2.2.2 | Macrobenthos

Autonomous underwater vehicles (AUVs) were deployed along the south-eastern Australian coast as part of the Integrated Marine Observing System (IMOS; <https://imos.org.au>) long-term benthic monitoring programme. For details on sampling design, see Ferrari et al. (2018). Briefly, surveys were conducted on rocky reefs at 25–50 m depth during August–November 2012. Within General Use Zones (Marine Protected Area sites were excluded from the dataset), seven sites were selected, and three to seven 25 m \times 25 m plots of rocky reef were surveyed within each site. Images (1.5 MP) of the benthos were obtained at intervals of c. 0.5 s. For each plot, 50 images, each covering an area of c. 2 m², were randomly selected, and taxa were identified on 25 random points that were overlaid on each image. CORAL POINT COUNT software with EXCEL extensions (Kohler & Gill, 2006) and the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) v.1.2 (Althaus et al., 2015) were used to identify and categorize taxa to the highest possible taxonomic resolution. In total, 94 taxonomic groups were identified. Common groups included macroalgae (turf, encrusting, branching and filamentous) and sponges (encrusting and massive/erect forms), whereas ascidians, anemones (colonial and tube), corals (octocoral branching and stony), crustaceans (barnacles) and molluscs (chitons) were relatively rare.

2.2.3 | Zooplankton

Plankton (zooplankton and phytoplankton) species abundance data were downloaded from the Australian Ocean Data Network (AODN) Open Access to Ocean Data portal (<https://portal.aodn.org.au>). The Australian Continuous Plankton Recorder (AusCPR) survey is part of

the largest plankton monitoring programme in the world (Richardson et al., 2006). The East Australian Current route extends along the east coast of Australia, with surveys conducted every 2 months. The data used for our analyses were sampled along the Brisbane–Sydney (BRSY) and Sydney–Melbourne (SYME) routes, between June 2009 and November 2018. The plankton recorder samples water at a fixed depth of 7 m. Water enters through a square 1.27 cm \times 1.27 cm aperture and flows down, continuously filtering zooplankton and phytoplankton onto a 270 μ m silk filtering mesh before preserving the samples in formalin. The silk is cut into 5 cm segment “samples” representing approximately five nautical miles of towing distance. The mesh size captures copepods, Cladocera, pteropods and chaetognaths, where all organisms <2 mm total length within each sample are identified and counted. We used data at 1° intervals along NSW, resulting in a latitudinal gradient of c. 6° (Table 1). A total of 191 species were identified, consisting largely of copepods ($n = 173$), including *Temora turbinata* and *Oncaea venusta*, but also the cladoceran *Pleopis polyphemoides*.

2.2.4 | Phytoplankton

Phytoplankton were identified in water samples collected from surveys along the BRSY and SYME routes, between June 2009 and November 2018, by the AusCPR (see details in section 2.2.3 Zooplankton). A total of 73 phytoplankton species were identified. Common species included diatom (e.g., *Climacodium frauenfeldianum*), dinoflagellate (e.g., *Noctiluca scintillans* and *Tripoceratium concilians*) species.

2.2.5 | Kelp-associated bacteria

Bacterial assemblages on the surface of two kelp species, *Ecklonia radiata* and *Phyllospora comosa*, were sampled consistently at nine sites in NSW during April 2011–January 2012. Both species were sampled in shallow (c. 1 m) water, and *E. radiata* microbial assemblages were also sampled in deep (c. 10 m) water. To characterize microbial communities associated with kelp-surface tissues across species, season and depth, an area of 20 cm² on the middle section of a secondary lamina was swabbed with sterile cotton swabs for 30 s. DNA was extracted from each swab, and 16S rRNA gene amplicon sequencing was used to generate a dataset of relative abundances of ASVs per sample. For methodological details, see Marzinelli et al. (2015) and Thompson et al. (2017).

The bioinformatic analysis was done through R using the software USEARCH v.11.0.667 (Edgar & Flyvbjerg, 2015), unless specified otherwise. Sequenced data were quality trimmed using the software TRIMMOMATIC v.36 (Bolger et al., 2014) to remove 3' end low-quality bases (Q score < 20; minimum length = 100; sliding window = 4:20). Trimmed sequences were merged (minimum length = 250 and maximum length = 550), quality filtered (maximum expected error threshold of one) and dereplicated. All reads were denoised into ASVs to acquire the maximum possible biological

resolution (Edgar, 2016). Chimeras were removed *de novo* within the UNOISE3 algorithm followed by UCHIME2 (Edgar et al., 2011) and using SILVA 132 SSU Ref NR99 as a reference database (Quast et al., 2012). Quality-filtered sequences were subsequently mapped back onto ASV sequences to calculate the relative abundance in each sample.

An initial taxonomic assignment of ASVs was performed using the Bayesian Lowest Common Ancestor (BLCA)-based taxonomic classification method (BLCA; in the *conda* environment using PYTHON v.3.9; Gao et al., 2017) and the SILVA database (Quast et al., 2012). Through this first taxonomic assignment, chloroplasts and mitochondria were identified and removed from the dataset before further statistical analysis. A similar taxonomic assignment was done using the Genome Taxonomy Database (GTDB; Parks et al., 2020) with the filtered dataset, which provides a higher resolution for cultured and uncultured microbial taxa in comparison to SILVA. After removal of low-occurring ASVs [$<0.05\%$ sample abundance across all samples that were likely to be errors; (Reitmeier et al., 2021)], the final total number of ASVs was 10,073 for *E. radiata* shallow samples, 13,104 for *E. radiata* deep samples and 8,582 for *P. comosa*.

2.2.6 | Pelagic bacteria

Seawater samples were taken from five sites along the NSW coast (Table 1; Figure 2) using tinted, pre-bleached drums. Water samples were filtered through a $.22\mu\text{m}$, 47mm disk filter (Millipore, DURAPORE PVDF .22UM WH PL) using a peristaltic pump. Filters were then kept on dry ice for the duration of sampling, transported to the laboratory and stored at -80°C until being processed. Microbial DNA was obtained by genomic DNA extraction using the PowerWater DNA isolation Kit (QIAGEN) in accordance with the manufacturer's instructions. The DNA quantity and purity were then evaluated using a Nanodrop-1000 spectrophotometer. To characterize bacterial community composition in samples, the V3-V4 region of the bacterial 16S rRNA gene was amplified using the 341f/805r primer set (Takahashi et al., 2014), with the following cycling conditions: 95°C for 3 min, followed by 25 cycles of: 95°C for 30 s, 55°C for 30 s and 72°C for 30 s, then 72°C for 5 min, with a final hold at 4°C (Illumina, 2013). The same primer was used as for kelp-associated microorganisms (detailed above). Amplicons were sequenced subsequently using the Illumina MiSeq platform (300bp paired-end analysis at the Ramaciotti Institute of Genomics, University of New South Wales). Sequence data were converted into ASV tables as for kelp-associated microorganism samples detailed above, resulting in a final total number of 34,733 ASVs.

2.3 | Zeta diversity analysis

We computed zeta (ζ) diversity, the shared number of species across multiple combinations of assemblages, to evaluate differences in

patterns of compositional turnover across taxonomic groups. By considering different combinations of sites (from two to n sites; the order of zeta; Figure 2a), zeta diversity captures the contribution of rare (shared by few sites) to common (shared by many sites) species. As the zeta order increases, the zeta values (ζ_i) decrease, and the shape of the decline captures the rate of species turnover. For each dataset, we analysed the following parameters: (1) the form of zeta diversity decline; (2) the rate of zeta diversity decline; and (3) the species retention rate, computed as the ratio of zeta values divided by zeta values at the lower order (ζ_i/ζ_{i-1}), as used previously by Pettersen et al. (2021). Zeta diversity was calculated for all orders (combinations of latitudes) using the *zetadiv* package (Latombe, McGeoch, et al., 2018). To account for differences in mean species richness (i.e., alpha diversity) and provide output that was comparable among datasets, the decline in zeta diversity was calculated for both raw values and Simpson-normalized richness-independent zeta using the *Zeta.decline.mc* function (Latombe, McGeoch, et al., 2018).

For each dataset, we tested three key hypotheses. First, the form of zeta diversity decline will be fitted best by a power law function, indicative of underlying environmental drivers of turnover across all taxonomic groups. The decrease in the shared number of species with increasing number of sites (zeta diversity decline) is generally fitted best by either exponential or power law functions [the two most common forms of zeta diversity decline (Hui & McGeoch, 2014; McGeoch et al., 2019)]. Comparing the form of zeta diversity decline can provide insights into the likely drivers of species turnover. Exponential patterns of turnover are indicative of underlying stochastic processes, whereas power law functions suggest that deterministic processes, such as common environmental variables, are responsible for the rate of turnover among sites. We compared the goodness-of-fit for exponential versus power law functions by comparing values of the Akaike information criterion (AIC) (Akaike, 1998). Second, the rate of zeta diversity decline will show a unimodal relationship with body size (Figure 1a), which is higher in benthic compared with pelagic groups (Figure 1b) and shows a positive relationship with trophic level (Figure 1c). The rate of zeta diversity decline, computed as the exponent of the fitted parametric form, represents the magnitude of compositional turnover. Third, the species retention rate will vary among taxonomic groups, reflecting the complexity of rare versus common species in driving turnover. We calculated the ratio of species, ASVs or groups retained with increasing zeta order (the species retention rate) that quantifies the relative rate of turnover for low-occurrence (rare) to high-occurrence (common) members of the assemblages. The shape of the retention rate gives a more precise measure of the order at which the majority of community members (e.g., species) are retained, and therefore the role of rare to common species in driving patterns of turnover. Rare species are present in only a small number of combined sites; hence, retention rates that approach one at low orders of zeta suggest that rare species have greater influence on overall turnover. In contrast, common species present across a large number of sites are particularly important in assemblages with retention rates approaching one at high orders of zeta. Finally, to

determine the relative contribution of rare and common species to diversity (as measured by zeta diversity), compared with traditional pairwise measures of turnover that account mainly for the contribution of rare species (beta diversity), we compared estimates of turnover across these two metrics.

3 | RESULTS

3.1 | The form and rate of decline in zeta diversity

Across all marine assemblages, zeta diversity decline was best fitted by power law (rather than exponential) functions ($\Delta\text{AIC} > 2$; Table S1), which is consistent with niche processes (i.e., physical/environmental factors and/or ecological interactions) as the likely primary drivers of turnover (McGeoch et al., 2019). Overall, we found that average assemblage member (species/ASV/group) richness (i.e., alpha diversity, ζ_1) was approximately two orders of magnitude higher in pelagic and kelp-associated microorganism assemblages compared with macroorganism assemblages (Table 2). Yet, average species richness did not appear to drive the rate of decline in zeta diversity; pelagic microorganisms showed the highest rate of turnover [zeta diversity decline exponent = -0.94 , 95% CI: $(-1.17, -0.71)$], while kelp-associated microorganisms were intermediate compared with other types of marine assemblages, which were lower [zeta diversity decline exponent range $\in (-0.41, -0.10)$]. There was also no clear trend between sampling effort (Table 1) and decline in zeta diversity. Phytoplankton and zooplankton assemblages showed the shallowest turnover overall, possessing a greater proportion of shared species across latitudinal gradients [zeta diversity decline exponent range $\in (-0.15, -0.08)$]. Fish species showed intermediate turnover [zeta diversity decline exponent = -0.31 , 95% CI: $(-0.35, -0.27)$], and benthic groups [zeta diversity decline exponent = -0.59 , 95% CI: $(-0.59, -0.58)$] showed a high level of spatial turnover, suggesting that underlying drivers of turnover are likely to be decoupled across benthic and pelagic assemblages (Figure 3).

When comparing the rate of zeta diversity decline, expressed as the magnitude of the power law relationship exponent across ecological traits, we found that the relationship between body size and turnover was unimodal for macroorganism assemblages (Figure 4a). Conversely, turnover in microorganisms spanned a large range of values and deviated from the expected pattern. Turnover increased initially with body size rank, from phytoplankton to benthic groups, before declining in large fishes. Across body size categories, small to medium-sized fishes (< 30 cm in ML) showed significantly shallow turnover compared with large species (≥ 30 cm in ML). We found no clear pattern regarding the rate of zeta diversity decline and whether assemblages were benthic or pelagic (Figure 4b). The phytoplankton and zooplankton assemblages showed relatively shallow turnover, while benthic groups did not show significantly higher turnover compared with pelagic fish assemblages. Contrary to prediction, pelagic microorganisms showed significantly higher turnover than benthic (kelp-associated) microorganisms. Across fish habitat groups, the magnitude of zeta diversity decline was greatest overall for

pelagic, non-site-attached species (e.g., open water *Carangid* and *Seriola* spp.), and lowest for demersal and benthic species (Table 2). Spatial turnover was positively correlated with trophic position, from phytoplankton to fishes (Figure 4c). Within the fish dataset, we observed significant differences in spatial turnover across trophic groups; carnivores showed twice the rate of turnover compared with herbivores, benthic invertivores and planktivores (Table 2).

Within kelp-associated microorganisms, the rate of turnover did not exhibit a statistically significant difference between the host species *E. radiata* or *P. comosa*, or between shallow versus deep *E. radiata* samples; however, microbial assemblages on kelp at 10 m depth showed a trend for lower species richness (i.e., zeta 1) and steeper decline (Table 2). Seasonal comparisons revealed highest turnover of both host species during spring and winter; however, this trend was significant only for microorganisms associated with shallow *E. radiata* and *P. comosa* samples when compared with summer samples, which showed relatively low turnover (Table S2).

There was considerable variation in species turnover across sampling years, but this was non-significant, and no clear temporal trend was evident in species turnover for phytoplankton, zooplankton and fish assemblages spanning 2008–2019 (Table S3).

3.2 | Species retention rate

Zeta ratio-based retention rates varied among co-occurring assemblages (Figure 5). Species retention rates showed four key trends. First, phytoplankton and zooplankton retention rates increased in a similar manner and stabilized close to one at zeta order 2.

Second, pelagic and shallow kelp-associated ASV retention rates also increased, and reached one at zeta order 5. In these assemblages, common species were sampled consistently across latitudinal gradients, and therefore did not contribute to turnover. In contrast, rare species made a disproportionately greater contribution to turnover observed in phytoplankton, zooplankton and the pelagic and shallow kelp-associated microbial assemblages.

Third, the zeta ratio of pelagic ASVs, deep kelp-associated ASVs and benthic groups continued to increase with zeta order, while remaining below one. Increasing retention rates suggest that all assemblage members, from common to rare, contributed to turnover. It is therefore likely that more sites need to be sampled in order to capture the full spectrum of commonness (which would be the case if stabilization of retention rate was observed) for these assemblages.

Fourth, fish species showed a slightly unimodal retention rate. This suggests that common species were also being lost with the addition of new sites (i.e., increasing orders of zeta). In this case, all species (both rare and common) contributed to turnover, and therefore there were likely to be fewer common species in the fish species assemblage, compared with assemblages that showed stabilizing retention curves (e.g., phytoplankton, zooplankton, kelp-associated ASVs). Despite the novel trend for fishes, the decline in retention rate was relatively low, such that 94% of species were retained within three orders of zeta (i.e., the average of three site combinations).

TABLE 2 Zeta diversity (orders 1–5) and zeta diversity decline across six co-occurring marine assemblages

Ecological trait	Zeta diversity (\pm SD)					Zeta diversity decline (raw) [exponent (95% CI)]	Zeta diversity decline (Simpson normalized) [exponent (95% CI)]
	Order 1	Order 2	Order 3	Order 4	Order 5		
1. Fish							
All species	195 (83)	106 (41)	77 (24)	63 (12)	54 (6)	$\zeta_5 = 2.27i^{-.78}$ (-.85, -.70)	$\zeta_5 = -0.01i^{-.31}$ (-.35, -.27)
Small size (<30 cm)	94 (52)	47 (25)	32 (14)	24 (7)	21 (2)	$\zeta_5 = 1.95i^{-.91}$ (-1.02, -.81)	$\zeta_5 = -0.01i^{-.24}$ (-.28, -.20)
Large size (\geq 30 cm)	90 (30)	54 (16)	41 (10)	34 (6)	31 (4)	$\zeta_5 = 1.94i^{-.67}$ (-.72, -.62)	$\zeta_5 = -0.00i^{-.36}$ (-.40, -.32)
Benthic	35 (16)	18 (8)	12 (4)	10 (2)	9 (1)	$\zeta_5 = 1.50i^{-.77}$ (-.96, -.58)	$\zeta_5 = -0.04i^{-.16}$ (-.34, .02)
Demersal	124 (57)	69 (27)	51 (15)	42 (8)	36 (4)	$\zeta_5 = 2.08i^{-.74}$ (-.82, -.67)	$\zeta_5 = 0.00i^{-.28}$ (-.32, -.24)
Pelagic (site attached)	17 (7)	9 (4)	6 (3)	4 (2)	3 (1)	$\zeta_5 = 1.28i^{-1.15}$ (-1.43, -.87)	$\zeta_5 = 0.05i^{-.71}$ (-1.01, -.41)
Pelagic (non-site attached)	9 (5)	5 (2)	3 (1)	2 (1)	2 (0)	$\zeta_5 = 0.95i^{-.88}$ (-1.00, -.76)	$\zeta_5 = -0.01i^{-.42}$ (-.51, -.32)
Herbivore	37 (18)	20 (10)	14 (6)	10 (4)	8 (2)	$\zeta_5 = 1.57i^{-.94}$ (-.96, -.92)	$\zeta_5 = -0.01i^{-.24}$ (-0.28, -.20)
Planktivore	22 (12)	11 (5)	8 (3)	6 (1)	5 (1)	$\zeta_5 = 1.31i^{-.84}$ (-.98, -.70)	$\zeta_5 = -0.01i^{-.26}$ (-.29, -.24)
Benthic invertivore	103 (42)	58 (21)	44 (12)	37 (7)	33 (3)	$\zeta_5 = 1.99i^{-.69}$ (-.79, -.59)	$\zeta_5 = -0.01i^{-.23}$ (-.30, -.17)
Higher carnivore	22 (9)	12 (5)	8 (3)	6 (2)	5 (1)	$\zeta_5 = 1.35i^{-.96}$ (-.98, -.93)	$\zeta_5 = -0.00i^{-.45}$ (-.46, -.44)
2. Macrobenthos							
	27 (7)	15 (4)	10 (3)	8 (2)	7 (1)	$\zeta_5 = 1.42i^{-.84}$ (-.87, -.81)	$\zeta_5 = -0.00i^{-.59}$ (-.62, -.56)
3. Zooplankton							
	94 (6)	78 (4)	71 (3)	67 (2)	64 (2)	$\zeta_5 = 1.97i^{-.24}$ (-0.26, -.23)	$\zeta_5 = -0.00i^{-.21}$ (-.21, -.21)
4. Phytoplankton							
	25 (7)	19 (4)	17 (3)	15 (2)	14 (2)	$\zeta_5 = 1.40i^{-.35}$ (-.39, -.32)	$\zeta_5 = -0.01i^{-.10}$ (-.13, -.08)
5. Kelp-associated bacteria							
<i>Ecklonia radiata</i> (deep)	2,181 (1,391)	995 (656)	635 (405)	465 (277)	370 (202)	$\zeta_5 = 3.33i^{-1.10}$ (-1.13, -1.06)	$\zeta_5 = -0.01i^{-.37}$ (-.41, -.33)
<i>Ecklonia radiata</i> (shallow)	2,772 (1,205)	1,497 (801)	1,031 (591)	779 (452)	620 (350)	$\zeta_5 = 3.45i^{-.94}$ (-.99, -.90)	$\zeta_5 = -0.03i^{-.23}$ (-.35, -.10)
<i>Phyllospora comosa</i> (shallow)	2,241 (658)	1,347 (658)	1,038 (360)	866 (314)	749 (278)	$\zeta_5 = 3.34i^{-.68}$ (-.71, -.65)	$\zeta_5 = -0.03i^{-.27}$ (-.38, -.15)
6. Pelagic bacteria							
	3,390 (341)	1,953 (429)	1,257 (313)	870 (200)	630 (200)	$\zeta_5 = 3.71i^{-1.04}$ (-1.28, -.80)	$\zeta_5 = 0.03i^{-.94}$ (-1.17, -.71)

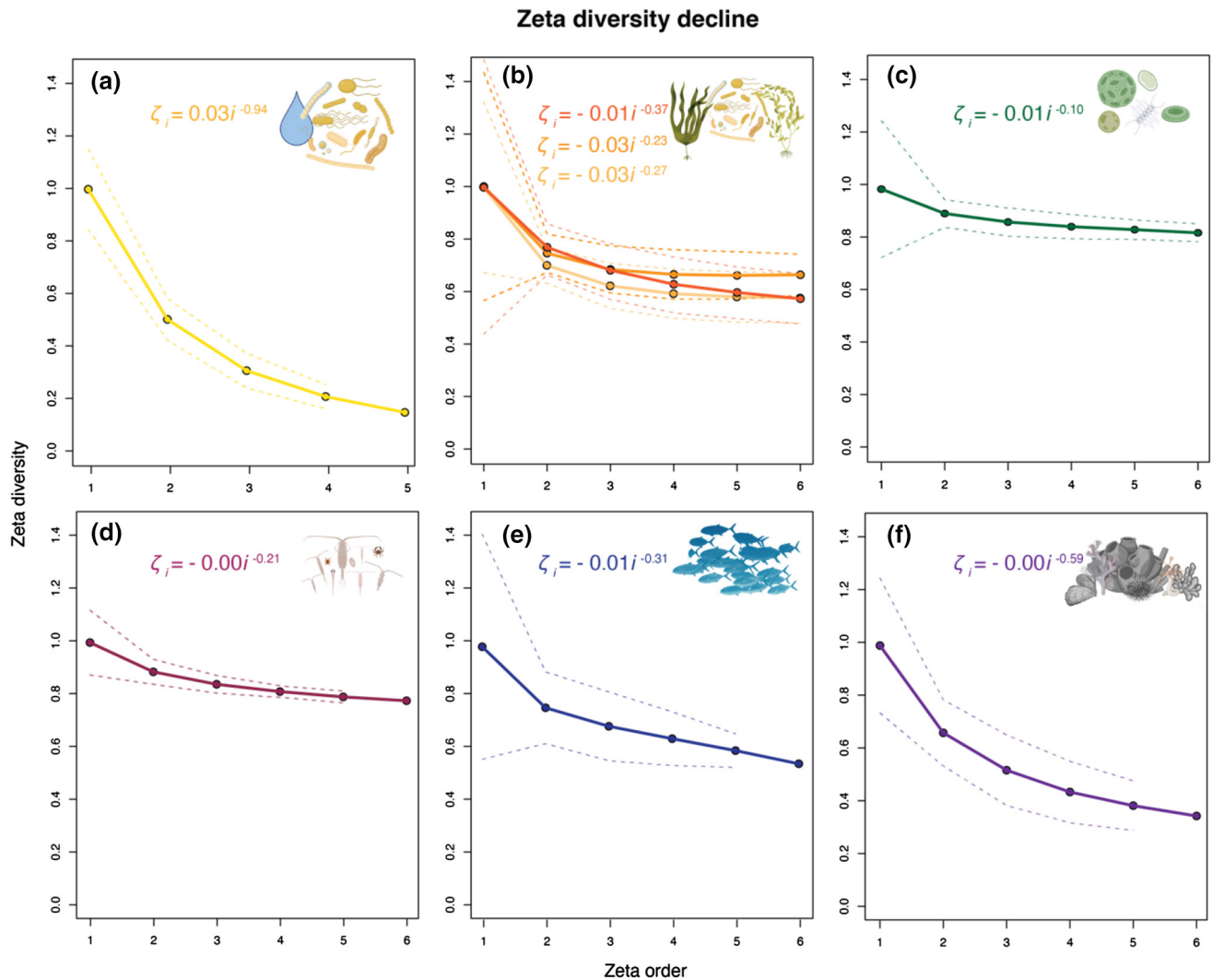


FIGURE 3 Zeta diversity decline (Simpson normalized) for six marine co-occurring assemblages sampled at 1° intervals along the coast of New South Wales, Australia (from -30 to -36° latitude). Zeta diversity [the average shared number of assemblage members; e.g., species/amplicon sequence variants (ASVs)/groups] was calculated with increases in zeta order (number of combinations of sites) for the following: (a) pelagic bacteria ASVs; (b) kelp-associated bacteria ASVs (yellow = shallow *Phyllospora comosa*; light orange = shallow *Ecklonia radiata*; dark orange = deep *Ecklonia radiata*); (c) phytoplankton species; (d) zooplankton species; (e) fish species; and (f) macrobenthic groups

3.3 | The relative importance of rare to common assemblage members in driving turnover

The rank order of turnover varied according to whether measures of beta (i.e., zeta order 2) or zeta diversity were used (Figure 6). Beta diversity was significantly but not strongly correlated with the slope of zeta diversity decline ($F_{1,16} = 26.44$, $p < .0001$, $R^2 = .60$). More importantly, differences in beta diversity between co-occurring assemblages were small compared with the slopes of zeta declines, hence significant differences found through use of zeta diversity shown in Figure 3 would not have been observable using only pairwise measures. For example, pelagic (site-attached) fishes showed significantly higher zeta diversity decline compared with benthic fish species, yet this result was not apparent through measures of beta diversity that are largely driven by differences in rare species. Our observed differences in the magnitude of turnover across trophic levels also

depended on whether pairwise (beta) or all (zeta) site comparisons were used. Carnivorous fish showed significantly higher zeta but not beta diversity compared with lower trophic levels, demonstrating the importance of measuring the full complement of compositional change when quantifying patterns of turnover.

4 | DISCUSSION

4.1 | Spatial turnover across macroorganisms is correlated with trophic position and body size

Compositional turnover in communities has been measured for decades, yet still little is known of the intrinsic characteristics (e.g., traits) that best describe biodiversity patterns common to a vast range of taxonomic groups and ecosystem components, particularly

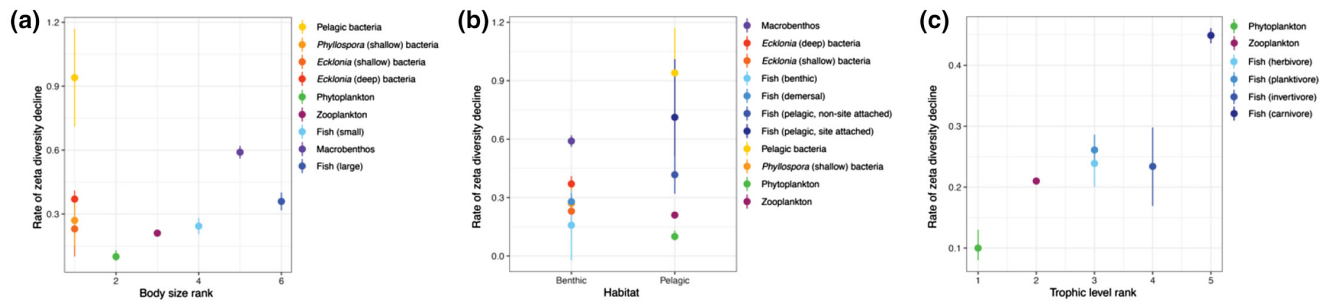


FIGURE 4 Summary results of spatial turnover (calculated as the inverse of Simpson-normalized exponent for zeta diversity, $\pm 95\%$ CI). (a) Excluding bacteria, the relationship between body size and turnover followed a predicted unimodal function, with turnover increasing with body size (Figure 1) in organisms exhibiting relatively passive distribution from phytoplankton species to macrobenthic groups, then decreasing for larger, actively mobile fishes. (b) Benthic habitats did not show greater turnover compared with pelagic habitats, as expected. (c) Turnover increased with trophic level from phytoplankton to carnivorous fishes, following the predicted theory. Macrobenthic and bacterial assemblages were excluded from trophic-level comparisons, owing to a lack of data on feeding and predation activity for these groups. Results for pelagic bacteria, *Phyllospora comosa* (shallow) bacteria and *Ecklonia radiata* (shallow, deep) bacteria did not align with predictions for macroorganisms (i.e., Figure 1). Small-sized bacteria showed relatively high turnover compared with larger-bodied organisms, and pelagic bacteria showed higher turnover than benthic (kelp-associated) bacteria

in marine ecosystems (MacArthur, 1965; Tittensor et al., 2010). Incorporating a multitrophic approach can reveal important insights into ecosystem processes (Seibold et al., 2018). Through investigating zeta diversity among co-occurring assemblages spanning a consistent latitudinal range, we found that trophic position provided a clear indicator of relative spatial turnover in and among temperate marine assemblages that would otherwise not have been evident through use of pairwise (beta diversity) measures of turnover alone (Figure 6). Among assemblages, the steepness of the decline in zeta diversity increased with trophic level, indicating that turnover was threefold higher in fishes than in phytoplankton. Our finding of low turnover in phytoplankton is consistent with studies by Soininen et al. (2018) and Soininen et al. (2007), that found lowest turnover in passively dispersed organisms and aquatic diatoms (autotrophs), respectively, compared with other habitat groups. We found the same trend for fishes; higher carnivores showed almost twice as much turnover as lower trophic levels. This overall pattern was evident within two orders of zeta, with higher beta diversity (and therefore elevated turnover) in carnivores compared with herbivores, planktivores and invertivores. Our findings support the notion that organisms with a high trophic position show strong turnover (gradients) in alpha diversity than those in low trophic positions (Hillebrand, 2004).

Body size is a universally important trait that is linked to many ecological processes, including predation, competition, dispersal potential and the strength of contributions by an individual or species to various ecosystem functions (Azovsky et al., 2020; Peters, 1983). Notwithstanding microorganisms, the relationship between turnover and body size followed theoretical predictions across co-occurring assemblages. We found that the rate of spatial turnover increased with body size from phytoplankton to benthic groups, before declining in large fishes. Our observed unimodal pattern was driven by the macrobenthic assemblage, which showed turnover intermediate of small and large fish, hence caution should be exercised when interpreting conclusions regarding

body size and turnover more generally. Nevertheless, this finding is consistent with a prediction by Soininen et al. (2007) and subsequent studies supporting a unimodal relationship between body size and beta diversity via an initial, positive trend in “passively” distributed organisms (e.g., phytoplankton, zooplankton and benthic groups), followed by a negative correlation for large-bodied, actively dispersing organisms, such as larger fish species (Barneche et al., 2019; Soininen et al., 2018). The mechanisms underlying the relationship between body size and turnover are not fully resolved; however, dispersal capacity and site affinity might produce size-dependent effects on the distribution of species in marine environments (Azovsky et al., 2020; Shanks, 2009). For example, fish larvae can exhibit site affinity and possess the behavioural potential to position themselves according to a specific niche, more so than zooplankton or phytoplankton (Levin, 2006). Larval behaviour can slow dispersal by $\leq 10,000$ times in comparison to that expected for a passive particle (Siegel et al., 2003), which might explain reduced homogeneity and thus relatively higher turnover in fishes. Although direct measures of spatial turnover in small marine organisms, such as plankton, are rare (reviewed by McManus & Woodson, 2012), the movement of phytoplankton is generally limited to vertical migration, with little capacity to control distribution on a broad scale (McManus & Woodson, 2012). Compared with larger organisms, phytoplankton can also occupy a relatively broad fundamental niche, including low-nutrient regimens, which might facilitate a wide distribution, hence low compositional turnover (Brun et al., 2015).

4.2 | Spatial turnover in bacterial communities deviates from ecological trait predictions

Although microorganisms form the majority of the world's biodiversity, a conceptual understanding of the spatial scaling of microbial

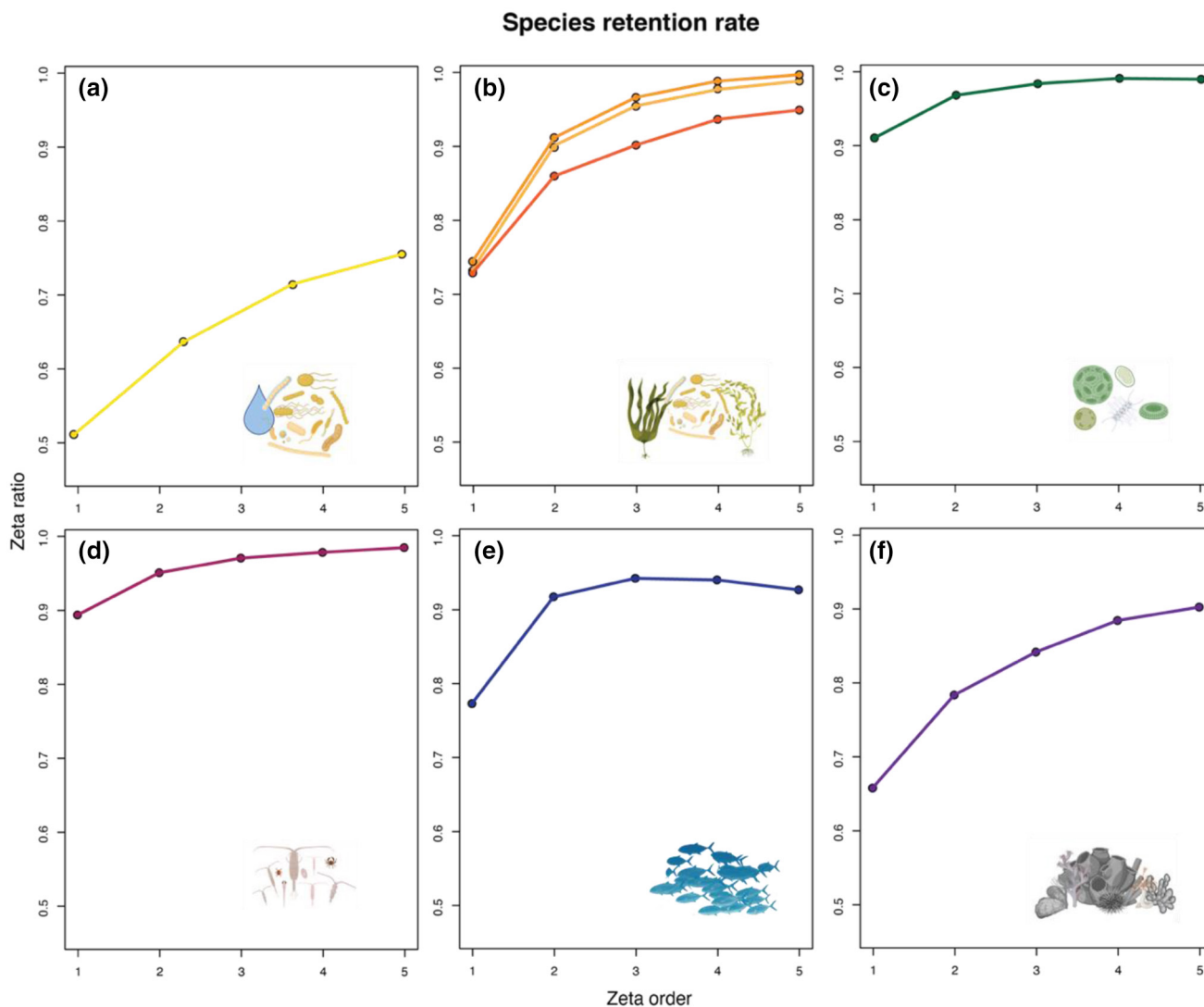


FIGURE 5 Species retention rate (Simpson-normalized) curves for six marine co-occurring assemblages sampled at 1° intervals along the coast of New South Wales, Australia (from -30 to -36° latitude): (a) pelagic bacteria amplicon sequence variants (ASVs); (b) kelp-associated bacteria ASVs (yellow = shallow *Phyllospora comosa*; light orange = shallow *Ecklonia radiata*; dark orange = deep *Ecklonia radiata*); (c) phytoplankton species; (d) zooplankton species; (e) fish species; and (f) macrobenthic groups. The zeta ratio shows the degree to which common species are more likely to be retained with the addition of sites, compared with rare species, with increasing zeta order. Most groups show the zeta ratio reaching an asymptote at high orders of zeta (c. zeta order 5), suggesting that common species (those shared at higher orders of zeta) are driving patterns of turnover, whereas fishes show a retention rate stabilizing at zeta order 3 before a slight decline at orders 4–5, indicating that rare species are influencing community composition, relative to other assemblages

diversity is lacking (Green & Bohannan, 2006). We found a clear discrepancy between our expectations (which were based on macroorganisms) and our findings, with respect to rates of turnover in bacterial assemblages. Both pelagic and kelp-associated bacteria did not align with existing predictions of turnover rates based on macroorganisms. According to predictions for body size, we anticipated that ASV turnover rate would be lowest for microorganisms. Nevertheless, pelagic and benthic (kelp-associated) bacteria showed relatively high and intermediate levels of spatial turnover, respectively. Although technical advances have allowed for detailed examination of spatial turnover in microbial communities only in recent times, studies of beta diversity, and therefore turnover, in free-living microbial eukaryotes (e.g., protozoa and microalgae) support

a complex biogeography similar to that found for macroorganisms (Noguez et al., 2005). Our study supports emerging evidence that microorganisms have highly structured ASV assemblages, and therefore high levels of turnover, as shown by a relatively steep decline in zeta diversity (Hillebrand et al., 2001). The underlying drivers of bacterial assemblage composition, and whether they are correlated with ecological traits applicable to macroorganisms, remain unclear.

Contrary to expectation from theory based on macroorganisms, we observed greater turnover in pelagic compared with benthic (i.e., kelp-associated) bacterial assemblages. One potential explanation for the observed patchiness in microbial ASVs through space is the highly dynamic environment experienced by free-living/planktonic microorganisms in shallow waters, even across microspatial

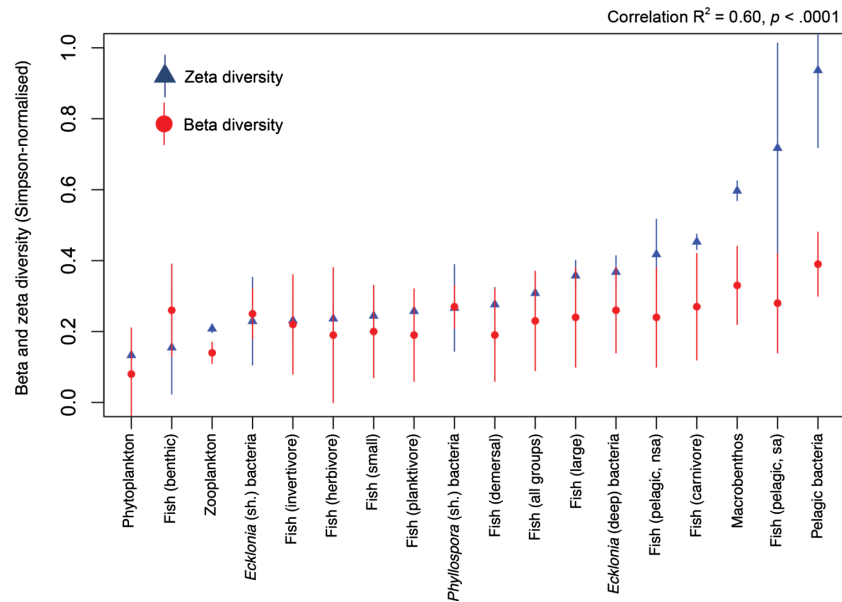


FIGURE 6 Comparison of Simpson-normalized beta diversity [i.e., zeta order 2 (\pm SD; red circles)] and zeta diversity (\pm SD; blue triangles), ranked by zeta diversity, for co-occurring marine assemblages across the six New South Wales datasets (nsa = non-site attached; sa = site attached). The correlation between beta and zeta diversity is significant, but they are not equivalent ($R^2 = .60$). Zeta diversity captures turnover across the entire range of rare to widespread species (represented by low and high orders of zeta, respectively), whereas beta diversity mainly captures the contribution of rare species shared by combinations of pairwise sites. Given that beta diversity captures only part of the species turnover, it can lead to a failure to detect differences in turnover between assemblages (i.e., type II errors)

scales (Stocker, 2012). Environmental fluctuations can shape the behaviour, ecology and evolution of microorganisms; hence, the occurrence of genetically distinct planktonic microorganisms might be a direct product of high variation in local oceanographic processes (Nguyen et al., 2021). In contrast, the microbial diversity associated with the surface of kelp is likely to be the product of selection for a specific function determined by the host. Regardless of whether the presence of a particular host is patchy, healthy kelps generally host a similar variety of functional groups, which are likely to reflect similarities in their genetic diversity (Marzinelli et al., 2015; Qiu et al., 2019; Roth-Schulze et al., 2016; Song et al., 2021). At the level of microorganisms, host-associated environments are likely to be more stable than the surrounding environment and might explain, at least in part, the discrepancy in rates of turnover between pelagic and benthic microbial assemblages (e.g., Egan et al., 2013).

4.3 | The role of rare to common species in shaping spatial turnover

We found that rare species, present in relatively fewer sites, served a disproportionately greater role in species turnover in phytoplankton, zooplankton and pelagic, and shallow kelp-associated bacterial assemblages, as shown by asymptotic zeta ratio-based retention rate curves (McGeoch et al., 2019). Evidence that environmental (rather than stochastic) processes are likely to underlie patterns of spatial turnover in these assemblages suggests that rare species are also likely to be specialists, associated with habitats within their narrow

realized ecological niche (Lazarina et al., 2019). Although the sampling region of the east coast of Australia is dominated by rocky reef habitats, it hosts a suite of biotic and abiotic gradients, including temperate to sub-tropical thermal niches. Given the importance of rare species in shaping turnover in planktonic and kelp-associated microbial organisms, focus on the response of rare, habitat-specialist species to environmental change might lead to insights regarding ecosystem function and are therefore a potential conservation priority (Stuart-Smith et al., 2021).

The observation of a unimodal retention rate, exclusive to the fish assemblage, supported the importance of the contributions of both rare and common species to turnover. Between zeta orders 1 and 3, rare species were increasingly being retained; however, with the addition of sites beyond zeta order 3, common species were being lost. This small but abrupt shift might have been driven by large, pelagic and/or predatory fishes that are more patchily distributed than the pomacentrids, wrasses and other families that dominate NSW reef habitats (Edgar et al., 2020). In contrast, the increasing retention rates with order of zeta observed for deep kelp-associated ASVs and benthic groups suggest that some species are so common that their contribution to turnover becomes trivial and highlight the difference between the concept of commonness for this functional group compared with others. More sites might therefore be needed to capture adequately the common species driving turnover for these assemblages. These findings demonstrate the importance of zeta ratio retention rates both for distinguishing patterns of turnover and for assessing the extent of sampling needed to capture these trends adequately across the full range of rare to common species.

4.4 | Implications of varying spatial turnover for the management of marine communities

Temperate marine ecosystems have often been viewed as relatively stable, homogeneous environments. Multiple lines of evidence suggest that spatial turnover is lower in the oceans compared with freshwater and terrestrial ecosystems, and furthermore, of all global regions, beta diversity is lowest in the Pacific Ocean (Clarke, 1992; Soininen et al., 2007). Yet, measures of species turnover are often limited to measures of single trophic levels or taxonomic groups of macroorganisms. Our comparative data for assemblages of micro- to macroorganisms occupying the same spatial/latitudinal extent showed significant differences in spatial turnover within and across marine assemblages. Through measures of continuous compositional change—zeta diversity, we found that turnover rates were greatest for pelagic microorganisms and large-bodied fishes. To adequately capture biodiversity in marine systems, conservation monitoring efforts need to reflect this spatial variation.

The clear disconnect between patterns of turnover observed in macroorganisms versus microorganisms showcases a key knowledge gap in our understanding of microbial community assembly and variation through space. At the scale of microorganisms, the ocean is highly heterogeneous. Microbial indicators are increasingly being used as a management tool to infer the environmental state of ecosystems (Glasl et al., 2019; Saxena et al., 2015), yet to use these metrics effectively, a clearer understanding of the underlying processes that govern microbial assemblage dynamics is needed. Given that microorganisms underpin the functioning of marine ecosystems, monitoring efforts that align with the rate of spatial turnover are needed to capture biodiversity adequately at this level (Stocker, 2012).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data and code have been made available for peer review on the Open Science Framework: https://osf.io/xcsaj/?view_only=7c503004f943473da464659af1b91e1a.

Sequence data for unpublished pelagic microorganisms have been submitted to the BioProject database under ID number PRNJNA776096: <http://www.ncbi.nlm.nih.gov/bioproject/776096>.

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BIOSKETCH

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