

ARTICLE

Coastal and Marine Ecology

Refining the trophic diversity, network structure, and bottom-up importance of prey groups for temperate reef fishes

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Abstract

Marine fish communities are highly diverse and contribute significantly to ecosystem processes. However, understanding their specific functional roles and the importance of different prey groups for sustaining fish communities has been limited by the historical classification of fishes into a few coarse trophic guilds. Using diet information to perform a high-resolution trophic classification of 298 temperate reef fish species distributed across south-western Australia, we built metacommunity and subregional trophic networks to evaluate the most important trophic relationships and energy pathways in temperate reefs. We identified 26 specialized trophic guilds within the groups of herbivores, zoobenthivores, zooplanktivores, piscivores, and cleaners. Zoobenthivorous fishes had the highest species richness and trophic diversity with 191 species in nine guilds. Consumers of crustaceans showed greater species redundancy at the metacommunity level. In contrast, a low redundancy of echinodermivores could represent a risk to local capacity for top-down control of sea urchins across the region. Finer scale analysis of prey at the family level showed that piscivorous guilds may influence different trophic pathways, with some guilds consuming other piscivorous fishes, while others consume lower trophic levels, particularly crustaceavores. Evidence of predation on herbivorous guilds was only found for turf grazers, suggesting that fish herbivory might not function as a major direct link between primary producers and higher trophic levels. Among the prey consumed by fishes, micro-crustaceans and decapods accounted for 33% of all diet proportions. The importance of macrophytes to the fish community likely resides indirectly through the trophic pathway of herbivorous and detritivorous invertebrates, particularly crustaceans, which are more consumed by fishes than macrophytes themselves. Comparison of trophic networks in the region showed that warmer locations had higher species redundancy per node and higher strength in trophic interactions. Yet, all networks had structural properties consistent with the

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meta-network regarding the importance of prey groups and modularity. Considering high-resolution predator-prey interactions enhances our understanding of the blue-print of ecosystem functions in shallow marine systems. Identifying the specific trophic significance of different consumers and prey groups is important for ecological forecasting and the prioritization of conservation and resource management regulations in our current fast-changing world.

KEY WORDS

diet, ecological network, ecosystem function, feeding ecology, functional groups, Great Southern Reef, herbivory, kelp forest, predation, rocky reefs, top predator, trophic guild

INTRODUCTION

The trophic interrelationships between species are a core determinant for broader ecosystem functions. Variations in the diversity or abundance of species can have repercussions across entire trophic networks, resulting in trophic cascades (Pace et al., 1999). Redundancy in trophic interactions is important to maintain trophic links and energy flow in ecosystems in the face of disturbances. Groups of species can be classified in trophic guilds according to their diet similarity (Burns, 1989). The more species in a trophic guild, the higher the redundancy of trophic linkages, and the lesser the ecological consequences if one species decreases in abundance or disappears entirely (Sanders et al., 2018). Therefore, detailed knowledge of trophic interactions is necessary to understand the ecological role and mortality risks of individual species, define trophic guilds, and assess the resilience of ecosystems to disturbances (Geary et al., 2020).

In marine ecosystems, teleost and chondrichthyan fishes are major drivers of top-down forcing. They compose trophic guilds across all levels of consumers, maintaining the flow of energy across trophic networks, and influencing the habitat structure of ecosystems. For instance, herbivorous fishes can be the dominant consumers of macroalgae in coral reefs, facilitating the proliferation of scleractinian corals (Smith et al., 2010). Mesopredator fishes consume smaller fishes and macro-invertebrates and can mediate trophic interactions in the benthic space, such as reducing the herbivory by sea urchin populations and helping maintain high abundances of kelp forests in temperate reefs (Hamilton & Caselle, 2015). The trophic impact of large-ranging top predators, such as sharks, is challenging to define as direct evidence of predation rates is difficult to obtain, and results of correlative studies of prey-predator abundances are sometimes contradictory (Sandin et al., 2022). However, it is likely that under high abundances, they can act as agents of natural selection and significantly

regulate the populations of mesopredators, with cascading effects to lower trophic levels (Heupel et al., 2019).

Despite the high diversity of fishes in shallow marine ecosystems, such as coral reefs or kelp forests, the description of their trophic diversity has remained limited to a few broad trophic guilds (Raymundo et al., 2009). Lack of empirical information can lead to trophic classifications based on expert opinion, which can result in uncertain and simplistic groupings (e.g., herbivores, omnivores, zoobenthivores, or piscivores). Quantitative analyses can be more accurate in assigning trophic membership but also have resulted in coarse classifications. For instance, global analyses summarizing hundreds of different prey items have classified hundreds of reef fishes into 7–11 trophic guilds (Halpern & Floeter, 2008; Mouillot et al., 2014; Parravicini et al., 2020). However, other studies with narrower taxonomic and geographical scopes have found a similar trophic diversity. For instance, in the temperate reefs in eastern Australia, 70 species were classified into 10 trophic guilds (Bulman et al., 2001). In Pattani Bay, Thailand, 29 estuarine species were classified into five trophic guilds, including specializations such as “shrimp-fish feeder” or “polychaete feeder” (Soe et al., 2021). While on the Great Barrier Reef, eight trophic specializations were recognized among members of the family Labridae (Bellwood et al., 2006). Indeed, herbivorous species alone can be classified into at least five trophic groups when feeding differences are considered in more detail: scrapers/excavators, grazers, macroalgae browsers, seagrass browsers, and detritivores (Halpern & Floeter, 2008; Zarco-Perello et al., 2020). Thus, given the diversity of prey available to reef fishes (including extremely diverse primary producers, sessile and mobile invertebrates, and vertebrates), the diversity of fish species, and their morphological feeding adaptations, the trophic diversity of reef fish communities is likely much higher than recognized by any of the existing classification systems. Their functional roles in the ecosystem must therefore also vary in ways we do not yet understand.

High-resolution trophic classifications are needed to better understand the importance of certain species as top-down enforcers and, equally importantly, to identify key prey groups that drive bottom-up forcing. Coarse trophic classifications can be practical for identifying general flows of energy (Fulton et al., 2003), but they are of limited use for understanding ecological interactions and interdependencies in the ecosystem. This includes bottom-up energy flow in predator-prey interactions, which have received considerably less attention than top-down effects in trophic studies of marine systems. While primary productivity has been researched widely, less focus has been given to the trophic groups that link primary producers and top predators (Smith et al., 2010). Although specific prey groups are described in diet analyses for individual species (Behrens & Lafferty, 2012), the precise identification of prey importance has rarely been considered at the community level (Stål et al., 2007). This disparity is illustrated by the fact that while it is a common practice to classify fish and other consumers by their diet breadth as specialists (narrow diets) and generalists (broad diet) (Dearing, 1996), an equivalent ecological concept has not been developed from the prey perspective. For example, a measure of “predation breadth,” a degree of the range of predation experienced by different prey groups, would be useful in informing their importance as sources of nourishment to sustain the diversity of predators.

A thorough understanding of trophic relationships among species and guilds is becoming more important as the human population grows and climate change advances (Bestion et al., 2019; Pecl et al., 2017). Long-term increases in temperature and marine heatwaves in temperate marine regions are causing the redistribution of tropical species towards higher latitudes (Burrows et al., 2019). Among these, tropical fishes are some of the most prominent groups experiencing successful poleward range shifts in all the oceans of the world (Poloczanska et al., 2013). However, primary producers and invertebrate species are also shifting distribution, and some temperate species are suffering declines (Edgar et al., 2023). Changes in the diversity of fish species and their prey will modify trophic processes and energy flux, including primary production, detritus creation, herbivory, and carnivory (Emmerson et al., 2004). This may cause predator-prey mismatches and lead to changes in biodiversity, structure, and functioning across the trophic network (Durant et al., 2019). As global warming, extreme events, and the human population continue to increase in the future, it is expected that some temperate marine regions will transition to novel ecosystems in the coming decades (Vergés et al., 2014). Hence, knowledge of current trophic interactions is required to understand and predict the potential changes that temperate marine ecosystems can experience in the future.

This study aimed to shed light on the trophic interdependency between reef fish species and their prey by characterizing the trophic guilds of temperate reef fish across two biogeographical regions of southwestern Australia (SWA). Specifically, the objectives were to (1) define and quantify the diversity of trophic guilds at high resolution, (2) quantify the relative importance of different prey groups as nourishment sources based on diet proportions and the number of predators that consume them at the metacommunity scale, (3) assess their trophic roles in the ecosystem through trophic network analysis, and (4) assess the spatial variability in network structure across the climatic gradient in the region: Jurien Bay (northern and warmer), Ngari Capes (central), and Esperance (southern and colder).

METHODS

Temperate reef fish metacommunity

The region of study encompasses all the temperate reefs of SWA. Extending along ~1600 km of coast, from Jurien Bay Marine Park ($30^{\circ}18.6\text{ S}$, $115^{\circ}0.1\text{ E}$) to the Recherche Archipelago Nature Research ($33^{\circ}53.7\text{ S}$, $123^{\circ}52.3\text{ E}$; Figure 1), the temperate reefs of SWA are distributed across the Leeuwin and Houtman biogeographical ecoregions (Spalding et al., 2007), conforming to approximately one-third of the total distribution of temperate Australia, known as the Great Southern Reef (Bennett et al., 2016). Typically, these reefs are subtidal, shallow, and dominated by the canopy-forming kelp *Ecklonia radiata* and fucoids such as *Sargassum* spp. or *Cystophora* spp., with understory macroalgae, filamentous turf, and some sessile invertebrates (Wernberg et al., 2003).

The species composition of the metacommunity of temperate reef fishes of the region was obtained from a total of 4589 underwater visual surveys conducted across 206 reefs in 12 locations by the Reef Life Survey (RLS) citizen science program and the Australian Temperate Reef Collaboration (ATRC, with support from the Department of Biodiversity, Conservation and Attractions; <https://www.atrc.au>) from 1997 to 2021. Each survey consisted of a 50-m-long transect, with surveyors registering the abundance and composition of all fishes sighted within 5 m on each side of the transect, as well as a subset of cryptic fishes when sighted within 1 m on each side of the transect (Edgar & Stuart-Smith, 2014). More details on the spatial and temporal design of the surveys can be found in the RLS methods manual available online (<https://www.reeflifesurvey.com/methods>).

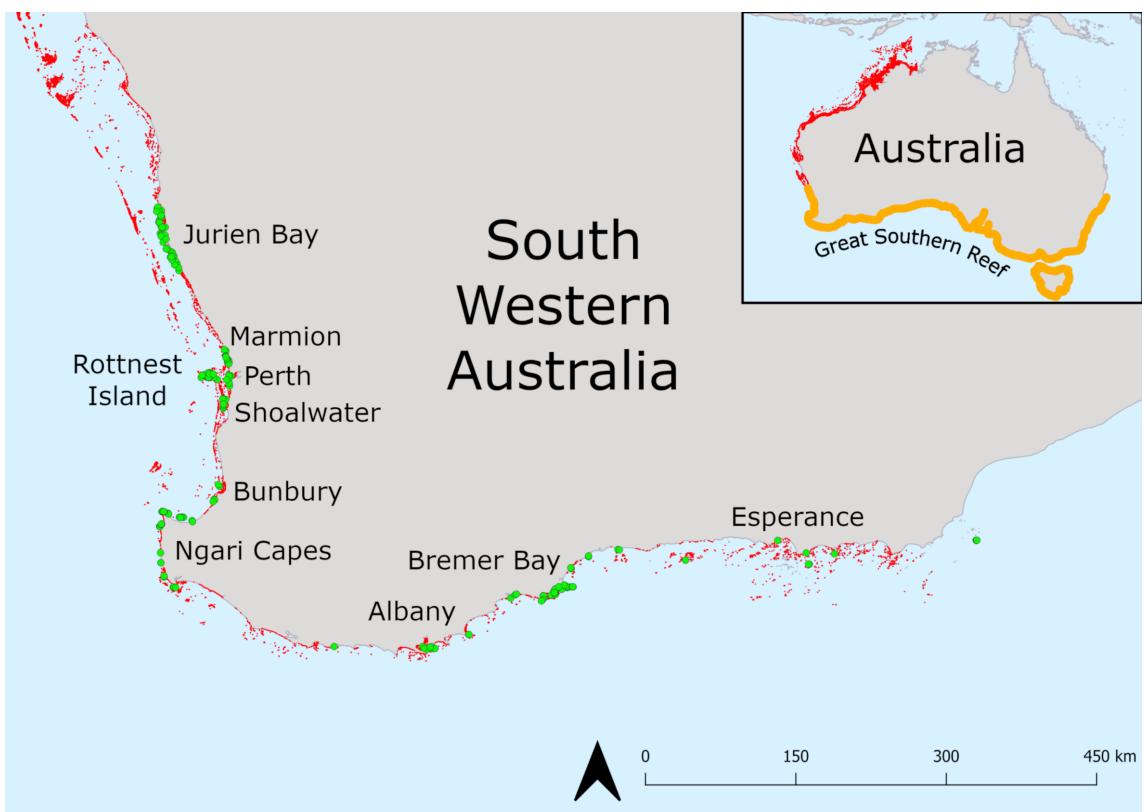


FIGURE 1 Sampling sites (green dots) in temperate reefs (in red) of south-western Australia by the Reef Life Survey and Australian Temperate Reef Collaboration (<https://www.atrc.au>). Reef distribution is sourced from <https://seamapaustralia.org>.

Collection of trophic information

All fish species listed in the RLS-ATRC database were classified in trophic guilds based on collected diet information from studies of gut content analyses in SWA or other Australian and international regions in the absence of local information. A total of 298 fish species composed the metacommunity. For every species, we obtained diet information from the scientific literature reported on Fishbase (Froese & Pauly, 2019) and through the search engine Scopus using the search terms: TS = (*name of species** OR **common name of species**) AND TS = (diet OR *stomach content* OR *gut content* OR consump* OR herbi* OR predat* OR feeding). Diet information consisted of the average proportions of food items represented as the number of items (%N), percent volume (%V), or biomass (%W) in a population of each species. Preference was given to diet studies conducted in the region of study and those presenting biomass proportions. Species that lacked diet information globally were assigned diet proportions based on phylogenetically related species with similar sizes and habitat preferences based on the Fish Tree of Life (Chang et al., 2019). The percentages of diet categorized as “unidentified” by stomach content studies were ignored since these data do not

contribute to the categorization of trophic guilds. Prey were recorded to the lowest taxonomic level possible depending on the available information for each group, usually family level (e.g., Acanthuridae); then, these were grouped into (1) broader taxonomic groups from class to order level (e.g., amphipoda and gastropoda) and subsequently into (2) major diet categories at functional group and phylum level (e.g., shelled mollusks and mollusks).

Trophic guild classification

To quantify the diversity of trophic guilds and identify important fish consumers of specific groups of prey, we classified the fish species into trophic guilds performing a multistep cluster analysis. Firstly, species were grouped into main trophic guilds using the mutually exclusive major categories of prey items. The diet proportions in these categories were used to create a dissimilarity matrix among species based on the Bray–Curtis linkage method using the function vegdist of the R package Vegan (Oksanen et al., 2022), which was used to run a sequential divisive hierarchical cluster analysis using the function diana (divisive analysis)

of the R package Cluster (Maechler et al., 2022). Subsequently, because there are mismatches in the resolution of diet identification between species belonging to different trophic levels (e.g., the diets of herbivorous fish tend to have higher resolution on macrophytes, while carnivorous species tend to have higher resolution on animal prey), species within each identified main trophic guild were subject to a cluster analysis with a higher definition of prey items to identify groups of species with diet specialization using sequential agglomerative hierarchical cluster analysis based on Ward's Method and Bray–Curtis or Euclidean dissimilarity matrix according to the highest value of the clustering coefficient of the function AGNES, which measures the clustering structure of the dataset (Maechler et al., 2022; Pineda-Munoz & Alroy, 2014).

The stomach content of most scarine species (parrotfish; Labridae: Scarinae) is very difficult to identify due to their pharyngeal mill, which grinds all food items to indiscernible particles. However, they are well identified as a special group that ingest detritus and algae by scraping the reef substrate with their specialized fused teeth. Thus, for the sake of differentiating their trophic guild, the proportions of diet for species of parrotfish were arbitrarily defined based on field observations as sediment and detritus (90%) and short filamentous algae (10%) (Bonaldo et al., 2014). Additionally, cleaner fish and false cleaners are a special group of fishes that are difficult to group by diet given that they feed on prey that could be identified as zooplankton or zoobenthos, while in fact true cleaners forage, at least in part, on parasitic invertebrates attached to bigger fish, in addition to fish skin and scales (Grutter, 1997); thus, given their particular trophic ecology, these labrid and blenniid species were arbitrarily grouped in the major trophic group “fish cleaners” for the subsequent specialized trophic group classifications.

All clustering results were visually analyzed and plotted with dendograms and heat maps created with the function fviz_dend of the R package factoextra (Kassambara, 2016). Visual analysis of the differences in multidimensional space between trophic guilds was done with nonmetric multidimensional scaling based on the dissimilarity matrix calculated for clustering using the function metaMDS of the R package vegan (reported in Appendix S1; Oksanen et al., 2022). Statistical significance in dietary differences among major and specialized trophic guilds (diet proportions ~ trophic guilds) was tested with permutational analysis of variance (PERMANOVA) using the function adonis2 of the R package vegan (Oksanen et al., 2022), followed by pairwise comparisons using the function pairwise.adonis2 of the R package pairwiseAdonis (Martinez, 2017).

Prey importance analyses

The diet information of all fish species was summed to consolidate a pool of trophic resources consumed by the metacommunity (i.e., metadiet) to quantify the relative importance of prey groups as sustenance for reef fish based on proportion and frequency of predation. For the latter, we calculated the frequency of appearance in the diet of all fish species and the sum and mean of their diet proportions (in percentage) of major and broad prey groups within the metadiet. We tested for statistical significance in differences of trophic importance among major and specialized prey groups using generalized linear models (GLM) with quasibinomial regression with a logit link function for proportions (diet proportions ~ prey groups), and binomial regression with a logit link function for frequency of occurrence (presence-absence across diets [i.e., eaten-not eaten] ~ prey groups), essentially modeling probabilities of predation, using the R package STATS (R Core Team, 2022). We checked dispersion metrics and inspected residual plots to ensure model assumptions were met; *p*-values were calculated with likelihood ratio tests with the function drop1 of the R package STATS and estimated marginal means for post hoc comparisons with the R package emmeans (Lenth, 2023).

Trophic network analyses

The direct and indirect trophic functions of trophic guilds and prey groups were assessed by building a trophic network. The trophic links between fishes and their invertebrate and macrophyte prey groups were identified by our trophic guild classification; however, the trophic role of piscivores is faced with what here we called a “trophic matryoshka paradox,” because to know their links with other guilds, we must first know the trophic links of their prey. Moreover, this is not straightforward because the highest taxonomic identification of piscivorous prey is usually limited to family level, which could belong to multiple trophic guilds. This paradox is usually not explicitly stated, and it is unclear how trophic links have been drawn in previous studies without performing detailed quantitative trophic classifications. Here, we estimated the trophic links between piscivorous guilds and the rest of the fish guilds by (1) assigning each fish family identified in the diets of piscivorous fishes into their respective specialized guilds based on our trophic classification, (2) pooling their diet proportions into each specialized trophic guild they could belong to, (3) standardizing values by the number of species in each piscivorous guild, and (4) dividing by the total sum of diet proportions to estimate their potential predation (0%–100%) on other trophic guilds in the trophic

network. Trophic links that had pooled diet proportions with values <5% were discarded for clarity of the network. This information was joined with the trophic information from non-piscivorous trophic guilds and formatted as a list of nodes (guilds and prey groups), and links between nodes (source-target) to create the trophic network of the entire temperate reef fish metacommunity. Links between invertebrate and macrophyte prey groups were drawn based on primary trophic interactions documented in the literature (Briones-Fourzán & Hendrickx, 2022; Gutow et al., 2020; Hansson et al., 2005; Poore et al., 2012); however, since the taxonomic identification of invertebrate groups is broad, and quantitative diet information is lacking, no weight was assigned to their links as consumers.

For the construction of the trophic networks of Jurien Bay, Ngari Capes, and Esperance, we followed the same process but limited it to their specific fish communities. Once the networks were constructed, we calculated the average weighted degree (AWD; the mean of weighted in-degree and out-degree values of all nodes in the network) as a measure of the overall interaction strength between the nodes in the network, and the weighted in-degrees (WIDs; sum of number of predator linkages weighted by their diet proportions) for each node as a measure of predation intensity per node (López et al., 2018). Additionally, we calculated the modularity of the network to identify subgroups of guilds that have stronger trophic interactions to identify different trophic flows across the network that could dictate stability in the food web (Eskuche-Keith et al., 2023). All network analyses were done using the computer program for network visualization and analysis Gephi v0.1 (Bastian et al., 2009).

RESULTS

Major trophic guilds

The 298 reef fish species belonging to 94 families were classified into five major trophic guilds (PERMANOVA; pseudo- $F_{4,325} = 81.3$, $p = 0.0001$; Figure 2; Appendix S1: Figure S1, Table S2). The first cluster of the divisive hierarchical dendrogram constituted the guild of herbivorous fishes, grouping 45 species of 13 families whose diets were dominated by macrophytes and detritus ($87.18\% \pm 2.16$ [mean \pm SE]) and complemented by zooplankton ($4.57\% \pm 1.4$) and zoobenthos ($80.01\% \pm 1.48$). The second cluster constituted the guild of cleaner fishes, comprising six species of three families that had diets dominated by fish scales and skin ($71.76\% \pm 11.98$), zooplankton ($15.45\% \pm 8.92$), and zoobenthos ($12.53\% \pm 5.06$). The third cluster constituted the guild of

zooplanktivorous fishes, grouping 20 species of fish belonging to 12 families that consumed high amounts of zooplankton ($89.81\% \pm 2.63$), followed by zoobenthos ($6.73\% \pm 2.21$). The fourth cluster formed the trophic guild of piscivorous fishes, grouping 36 species of 24 families, whose diet was mainly composed of fishes ($79.71\% \pm 2.92$), zoobenthos ($14.35\% \pm 0.63$), and cephalopods ($4.34\% \pm 1.68$). The last and biggest cluster comprised the guild of zoobenthivorous fishes, including 191 species belonging to 62 families, having diets dominated by zoobenthos ($87.92\% \pm 1.01$), complemented by fishes ($5.06\% \pm 0.72$), macrophytes ($3.87\% \pm 0.65$), and zooplankton ($2.2\% \pm 0.42$).

Specialized trophic guilds

Cluster analyses within each major trophic guild at a higher resolution of prey items showed more refined trophic classifications, revealing generalist and specialist species, branching into 26 trophic subgroups (Appendix S1: Table S1). Herbivorous species were classified into seven trophic guilds divided into three main branches separating consumers of leafy and fleshy macrophytes from consumers of small filamentous algae and detritus (PERMANOVA; pseudo- $F_{6,38} = 29.449$, $p = 0.001$; Figure 3A; Appendix S1: Table S3). The first main group comprised three specialized subgroups: *Seagrass browsers* (seven species) had diets dominated by seagrass; *canopy browsers* (four species) had diets with high proportions of canopy-forming brown macroalgae; *understory browsers* (11 species) mainly consumed understory macroalgae. The second main group also consisted of three specialized subgroups: *Turf grazers* (seven species) consumed mostly turf algae; *Mixed grazers* (five species) had diets mixed with turf and understory macroalgae; *zooplanktivorous grazers* (five species) fed mostly on turf and zooplankton. *Scrapers* (six species of parrotfishes) formed a unique branch of species ingesting high amounts of turf, detritus, and sediment by biting deep in the substratum with their specialized fused teeth (Appendix S1: Figure S2).

Zooplanktivorous fishes were grouped in three distinct subgroups (PERMANOVA; pseudo- $F_{2,17} = 11.931$, $p = 0.0001$; Figure 3B; Appendix S1: Table S4): *Planktonic crustaceavores* (nine species) fed almost exclusively on planktonic copepods; *planktonic mixed-feeders* (seven species) also consumed significant proportions of planktonic crustaceans (copepods, diplostracans, and euphausiids) but complemented this with a higher variety of larvae, zoobenthos, gelatinous zooplankton, and macroalgae; *planktonic crustacea-larvivores* (four species) fed mostly on planktonic crustaceans and larvae (bivalves, nauplii, and echinoderms; Appendix S1: Figure S3).

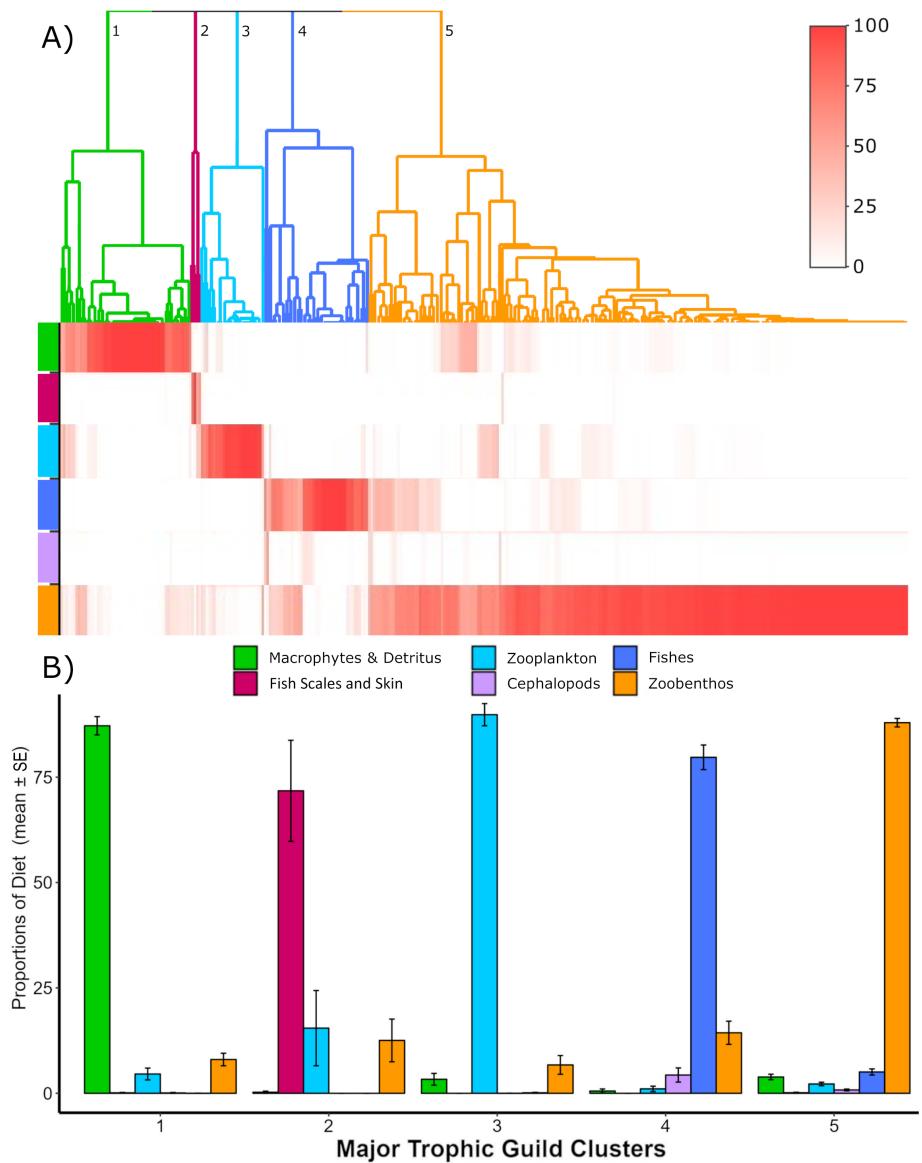


FIGURE 2 Classification of major trophic guilds of the temperate reef fishes of southwestern Australia. (A) Dendrogram of divisive cluster analysis with heatmap of the diet composition per species divided into major prey/food categories. (B) Barplot showing the mean proportions of the diet composition per cluster of major trophic guilds. 1, Herbivores; 2, Cleaners; 3, Zooplanktivores; 4, Piscivores; and 5, Zoobenthivores.

Cleaner fishes were divided into three clusters of two species each (Figure 3C). Statistical tests for diet differences between these specialized trophic groups were not possible to conduct due to low sample size per group ($n = 2$); however, their average diets were clearly distinguishable, reflected in the separation of their data points in the NMDS plot (Appendix S1: Figure S4). The trophic group *crustacivore cleaners* had diets with high proportions of benthic invertebrates (amphipods, isopods and copepods), followed by fish scales and skin; *piscivore cleaners* had diets comprising mostly fish scales and skin, followed by zoobenthos (copepods); *zooplanktivore cleaners*' diets contained fish scales and skin, zoobenthos

(benthic worms), and zooplankton (fish larvae and copepods).

Piscivore fishes were classified in four specialized trophic guilds (PERMANOVA; pseudo- $F_{3,32} = 20.9$, $p = 0.0001$; Figure 3D; Appendix S1: Table S5). *Piscizoobenthivores* (16 species) had diets dominated by fishes and zoobenthos (caridean shrimps and crabs). *Piscicephalovores* (seven species) had diets with high proportions of fishes and cephalopods (octopus, cuttlefish, and squids). *Piscivores* (12 species) fed almost exclusively on fishes and small portions of zoobenthos. The grey nurse shark *Carcharias taurus* was the only species classified as a *High-piscivore* since it was the only species that

complemented its diet of teleost fishes with a high proportion of Elasmobranchii (56.8%; Selachimorpha 17.6% and Batoidea: 39.2%; Appendix S1; Figure S5).

Zoobenthivorous fishes were differentiated into nine specialized trophic guilds separated in three main clusters (PERMANOVA; pseudo- $F_{8,182} = 60.247$, $p = 0.0001$;

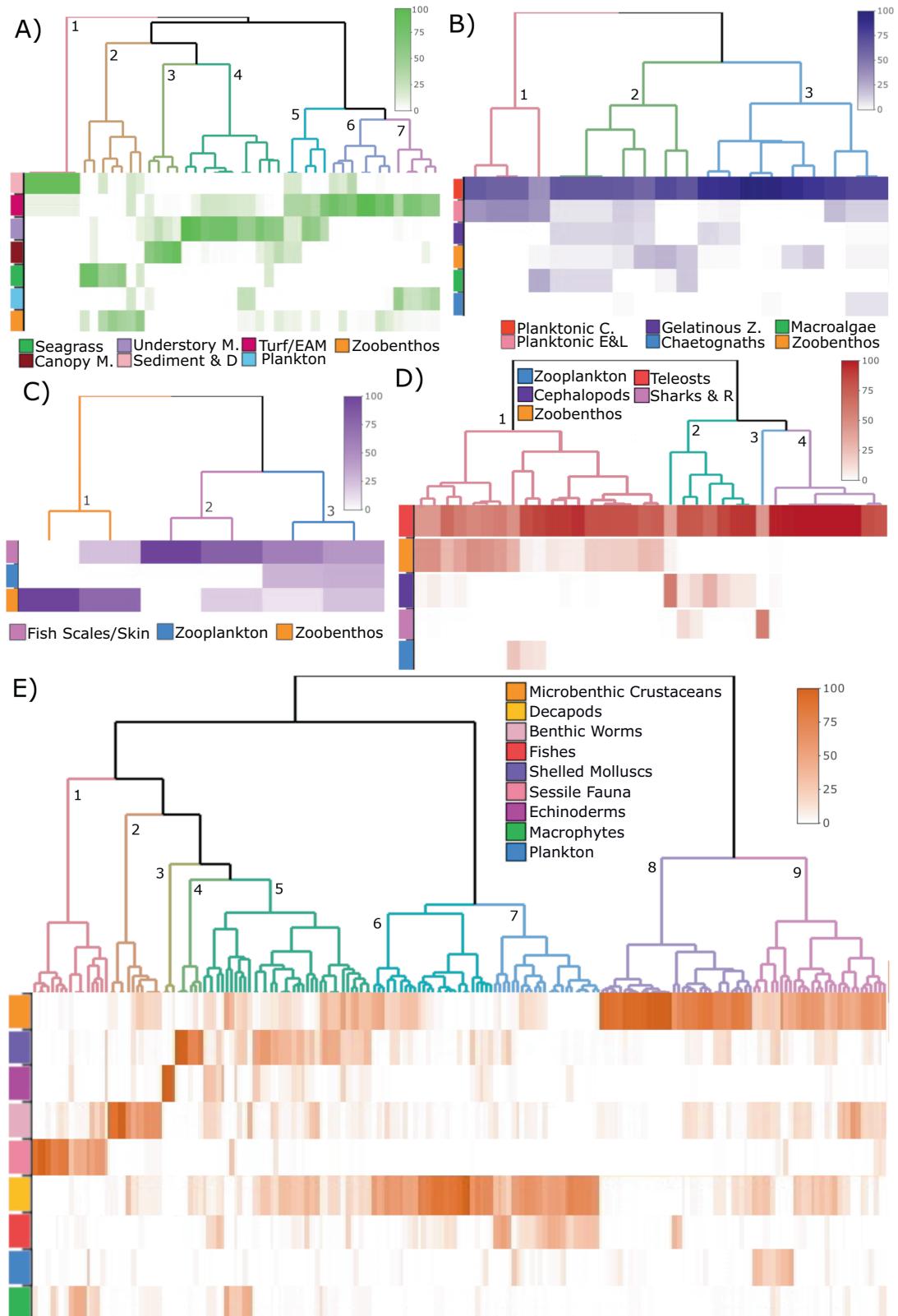


FIGURE 3 Legend on next page.

Figure 3E; Appendix S1: Table S6). The first cluster consisted of five guilds with important diet proportions of all benthic invertebrate groups: *Sessile invertivores* (17 species) fed mostly on sessile invertebrates (anthozoans, hydroids, and sponges); *benthic wormivores* (12 species) had diets with high proportions of polychaetae worms; *echinodermivores* (3 species) had high diet proportions of echinoderms; *molluscivores* (6 species) consumed mostly gastropods, bivalves, and chitons, complementing with decapods, while *mixed zoobenthivores* (38 species) fed on shelled mollusks, decapods, microcrustaceans, benthic worms, echinoderms, and fishes (Appendix S1: Figure S6). The second main branch included two guilds that had high proportions of decapods in their diet: *Decapod-piscivores* (24 species) fed mainly on decapods (caridean shrimps and crabs) but complemented with teleost fish, while *decapodovores* (27 species) fed almost exclusively on decapods (dendrobranch prawns, caridean shrimps, squat lobsters, and crabs; Appendix S1: Figure S6). The third main branch was subdivided into two guilds that fed predominantly on microcrustaceans (Figure 3E): *microcrustaceavores* (34 species) that fed mostly on amphipods, copepods, mysids, tanaids, isopods, cumaceans, and ostracods; *crustacea-wormivores* (30 species) mostly consumed microcrustaceans (amphipods, copepods, isopods, mysids, cumaceans, ostracods, and tanaids), decapods, and benthic worms (Figure 3E; Appendix S1: Figure S6).

Importance of prey groups

Considering the frequency of occurrence in fish diets, invertebrates were the most important prey groups, consumed by 268 species (90% of the fish species in the region) from 87 families (Figure 4). Invertebrates also dominated dietary proportions, accounting for ~63% of the meta-diet (GLM, LTR = 143, $p < 0.0001$; Figure 5; Appendix S1: Table S9, Figure S7). Invertebrates were particularly important to species of the family Labridae (13.2% of metadiet). At the species level, invertebrates dominated the diet of 178 species (75%–100% diet proportion), were very important for 38 species (50%–74%), important for 18 species (25%–49%), substantial for 19 species (10%–24%), and a minor component

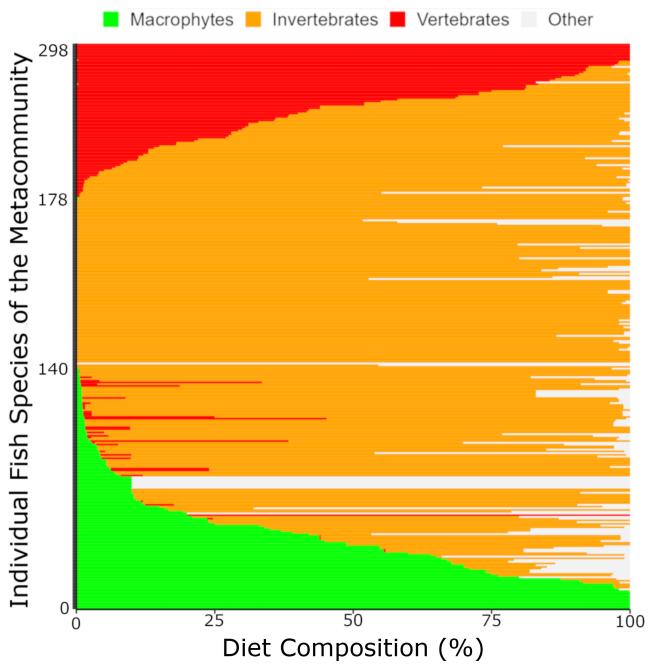


FIGURE 4 The importance of major prey groups regarding their proportion in the metadiet and their frequency of consumption by fish species. Stacked bar chart showing the pervasiveness of the major traditional groups of prey: plants, invertebrates, and vertebrates among all the individual temperate reef fish species in southwestern Australia.

for 15 species (<10%). Crustacean groups were the most important invertebrate prey considering frequencies and diet proportions. Decapods (e.g., lobsters, prawns, shrimps, and crabs) and benthic microcrustaceans (e.g., amphipods, copepods, isopods, and mysids) were consumed by 167 and 191 fish species and accounted for 15.2% and 17.5% of the meta-diet, respectively. More specifically, gammaridean and corophiid amphipods had high predator numbers (153 spp.) and meta-diet proportion ($8.9 \pm 1.0\%$; GLM, LTR = 26.289, $p = 0.0018$; Figure 6; Appendix S1: Table S10, Figure S8). Brachyuran crabs were consumed by 116 fish species and had the second highest average proportions ($7.3 \pm 0.9\%$) among all prey groups. Polychaetes were the most frequent prey group in the meta-diet, being consumed by 157 fish species (GLM, LTR = 530.6, $p = 0.0001$, Appendix S1: Table S11, Figure S9) while accounting for $5.8 \pm 0.8\%$ of the meta-diet. Planktonic copepods, gastropods, bivalves, sessile

FIGURE 3 Classification of the temperate reef fishes of south-western Australia in specialized trophic guilds. (A) Herbivores: 1, Scrapers; 2, Seagrass browsers; 3, canopy browsers; 4, understory browsers; 5, mixed grazers; 6, turf grazers; and 7, zooplanktivorous grazers. (B) Zooplanktivores: 1, Planktonic crustacea-larvivores; 2, planktonic mixed-feeders; and 3, planktonic crustaceavores. (C) Cleaners: 1, Zoobenthivorous cleaners; 2, pisci-cleaners; and 3, zooplanktivorous cleaners. (D) Piscivores: 1, Pisci-zoobenthivores; 2, pisci-cephalovores; 3, high-piscivore; and 4, piscivores. (E) Zoobenthivores: 1, Sessile invertivores; 2, benthic wormivores; 3, echinodermivores; 4, molluscivores; 5, mixed-zoobenthivores; 6, decapodovores; 7, decapod-piscivores; 8, microcrustaceavores; 9, and crustacea-wormivores. Canopy M.; Canopy macroalgae; Understory M.; Understory macroalgae; Sediment and D; Sediment and detritus; Planktonic C.; Planktonic crustaceans; Planktonic E&L; Planktonic eggs and larvae; Sharks and R, sharks and rays.

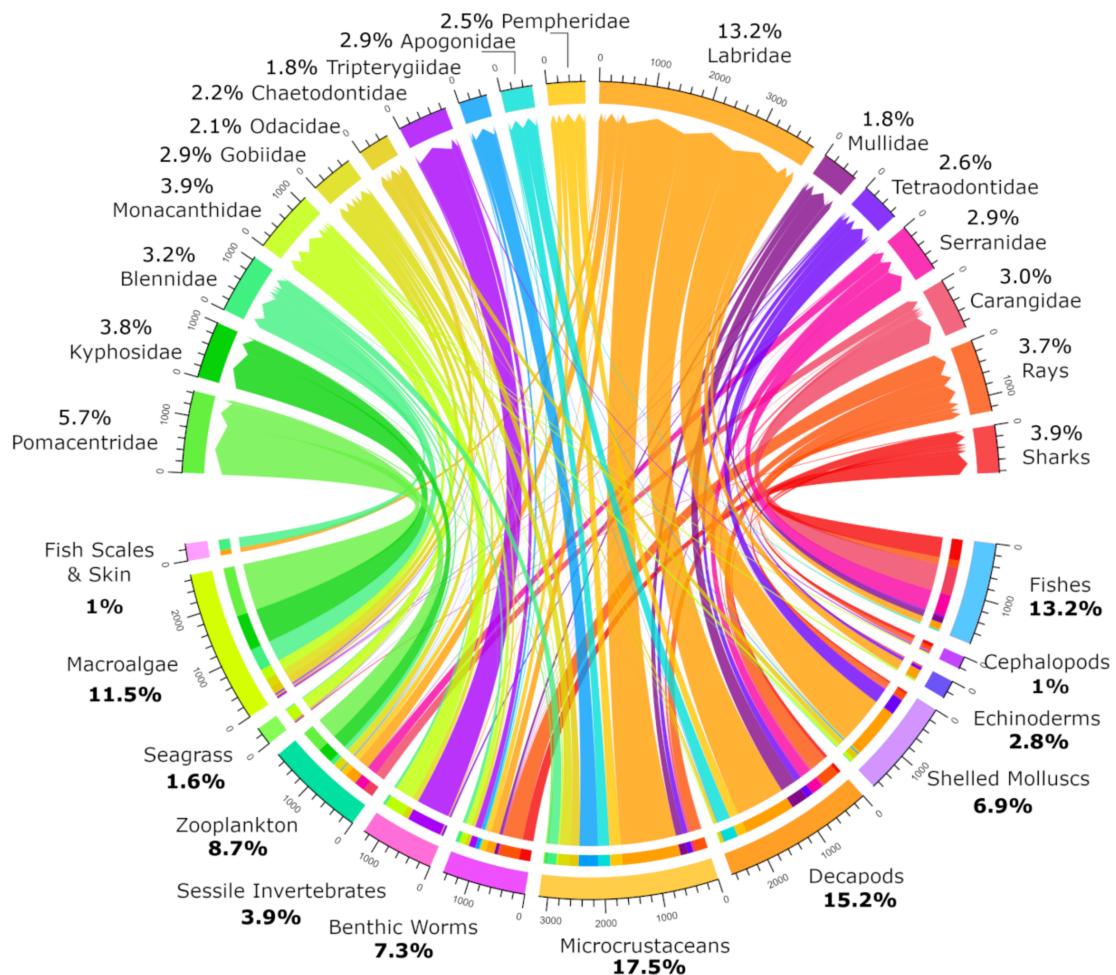


FIGURE 5 Circular flow plot showing the total proportions of the metadiet accounted for by the main prey groups (lower half) and their correspondence to the diets of the main families of temperate reef fishes of southwestern Australia (upper half).

invertebrates (i.e., sponges and anthozoans), and other microcrustaceans, decapods, mollusks, and echinoderms had an intermediate number of predators (~75–50 spp.) and proportions of the meta-diet (Figure 6).

Vertebrate prey were present in the diet of 39% of species ($n = 118$) and 54 families of the temperate reef fish community, accounting for 13.2% of the meta-diet, with bony fishes being the most important (Teleosts, 12.8%), followed by sharks and rays (Elasmobranchs, 0.27%; Figures 4 and 5). They provided important sustenance to sharks (7 species, 11.4% of vertebrate prey proportion in metadiet), rays (10 spp., 3.1%), and the teleost families Serranidae (9 spp., 13.2%) and Carangidae (8 spp., 12.8%). Fish prey dominated the diet of 25 species (75%–100% diet proportion), were very important for 7 species (50%–74%), important for 22 species (25%–49%), less important for 14 species (10%–24%), and were a minor component for 52 species (<10%). Among prey groups, Clupeiformes had the highest average proportion in the metadiet (1.1% \pm 0.5; Figure 6). Most groups of teleost fish had low

numbers of predators, except for the teleost orders Eupecaria (preyed by 42 predators) and Perciformes (22 spp.). At the family level, the most important prey were Engraulidae (7% of vertebrate proportions), with the rest having proportions below 4% (e.g., Carangidae, Sparidae or Labridae).

Macrophytes were present in the diet of all trophic guilds (except for cleaners), amounting to 47% of the fish community (140 species; Figure 4), particularly macroalgae (36% = 109 species). Proportionally, they accounted for 13.25% of the meta-diet, with macroalgae comprising most of this proportion ($11.4 \pm 1.4\%$), seconded by seagrass ($1.6 \pm 0.4\%$; Figure 5). Macrophytes provided important sustenance to species of the families Pomacentridae (13 species, 23.4%), Kyphosidae (11 spp., 17%), Monacanthidae (14 spp., 12.1%), and Blenniidae (8 spp., 11.8%). They dominated the diet of 21 species (75%–100% diet proportion), were very important for 16 species (50%–74%), important for 9 species (25%–49%), less important for 24 species (10%–24%), and were a minor component for 70 species (<10%). Turf

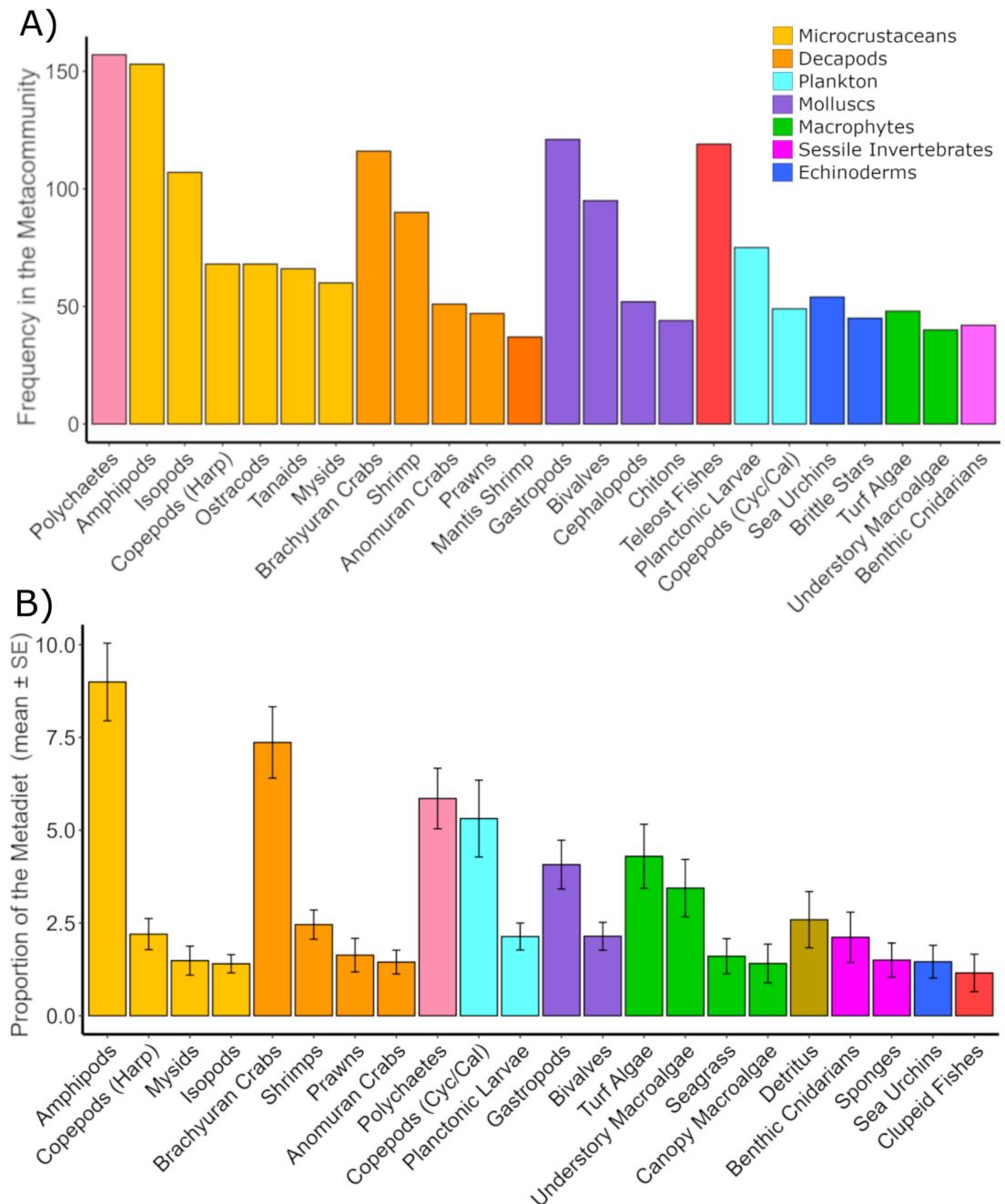


FIGURE 6 The importance of prey groups regarding their frequency of consumption by fish species. (A) Frequency of prey groups at higher resolution in the diets of all the 298 fish species of the metacommunity. (B) The average proportion of the metadiet accounted for by more specific prey groups. Amphipods represent the suborder Senticaudata: Gammaridea, Caprelloidea, and Corophiida. Copepods Harp: Harpacticoida; Cyc/Cal: Cyclopoida/Calanoida.

filamentous algae (which might include kelp epiphytes) were consumed by 48 species of fish and were the 5th most important prey group in the meta-diet ($4.3 \pm 0.8\%$; Figure 6), accounting for 40% of all the proportions of macrophytes, followed by fleshy understory macroalgae (40 consumers; $3.2 \pm 0.7\%$), seagrass (32 spp.; $1.6 \pm 0.5\%$), canopy-macroalgae (19 spp.; $1.4 \pm 0.5\%$), and calcareous understory (19 spp.; $0.5 \pm 0.2\%$).

Metacommunity and subregional trophic networks

The trophic network of the metacommunity was structured by 43 trophic nodes among specialized trophic guilds of fishes and prey groups (Figure 7). Dietary data showed that piscivorous fish guilds consumed 51 different fish families belonging to 33 orders from all five major

trophic guilds and 26 specialized trophic guilds (Appendix S1: Table S7). The likelihood of piscivory was higher on zoobenthivorous guilds occupying intermediate levels in the trophic network. The guilds of crustacea-wormivores, mixed-zoobenthivores, microcrustaceavores, planktonic crustaceavores, and decapodovores were preyed upon by many piscivore guilds; however, predation differences among piscivores were found (Appendix S1: Table S8). High-piscivores had a higher likelihood of preying on mixed-zoobenthivores (17%), pisci-cephalovores (16%), benthic wormivores (16%), and decapod-piscivores (16%) than the other piscivore guilds. Pisci-cephalovores potentially prey more on piscivores (12%), pisci-zoobenthivores (10%), planktonic-mixed feeders (10%), planktonic crustacea-larvivores (8%), and trophic conspecifics (intra-guild, 9%). Piscivores likely preyed more on decapodovores (8%), pisci-zoobenthivores (8%), planktonic crustaceavores (8%), zoobenthivore cleaners (6%), and molluscivores (6%). Pisci-zoobenthivores had stronger trophic links with crustacea-wormivores (22%), turf-grazers (11%), and zooplanktivore cleaners (8%). Finally, decapod-piscivores likely predated more on sessile invertivores (9%) and mixed-grazers (7%).

Overall, the trophic guilds of fish crustacea-wormivores (70.8), mixed-zoobenthivores (59.5), decapod-piscivores (41.1), and microcrustaceavores (32.5) had the highest WID values, while among invertebrate and macrophyte prey groups, microcrustaceans (292), planktonic crustaceans (246), turf algae (228), understory macroalgae (149), decapods (138), benthic worms (134), and shelled mollusks (127) had the highest values of WID. Modularity analysis identified five different clusters of nodes. Module 1 had the highest number of nodes (17), extending from microcrustaceans, benthic worms, and shelled mollusks to the top of the trophic network. In contrast, Modules 2 and 3 were the smallest and only included echinodermivores and sessile invertivores, respectively. Module 4 grouped zooplanktivores and cleaners, while Module 5 included herbivores and macrophytes (Figure 7).

The structure of trophic networks varied in some respects across different locations. The northernmost region, Jurien Bay, had the most complex trophic network and strength in trophic interactions, having a higher AWD value (364) than Ngari Capes (258) and Esperance (166). The network of Jurien Bay was

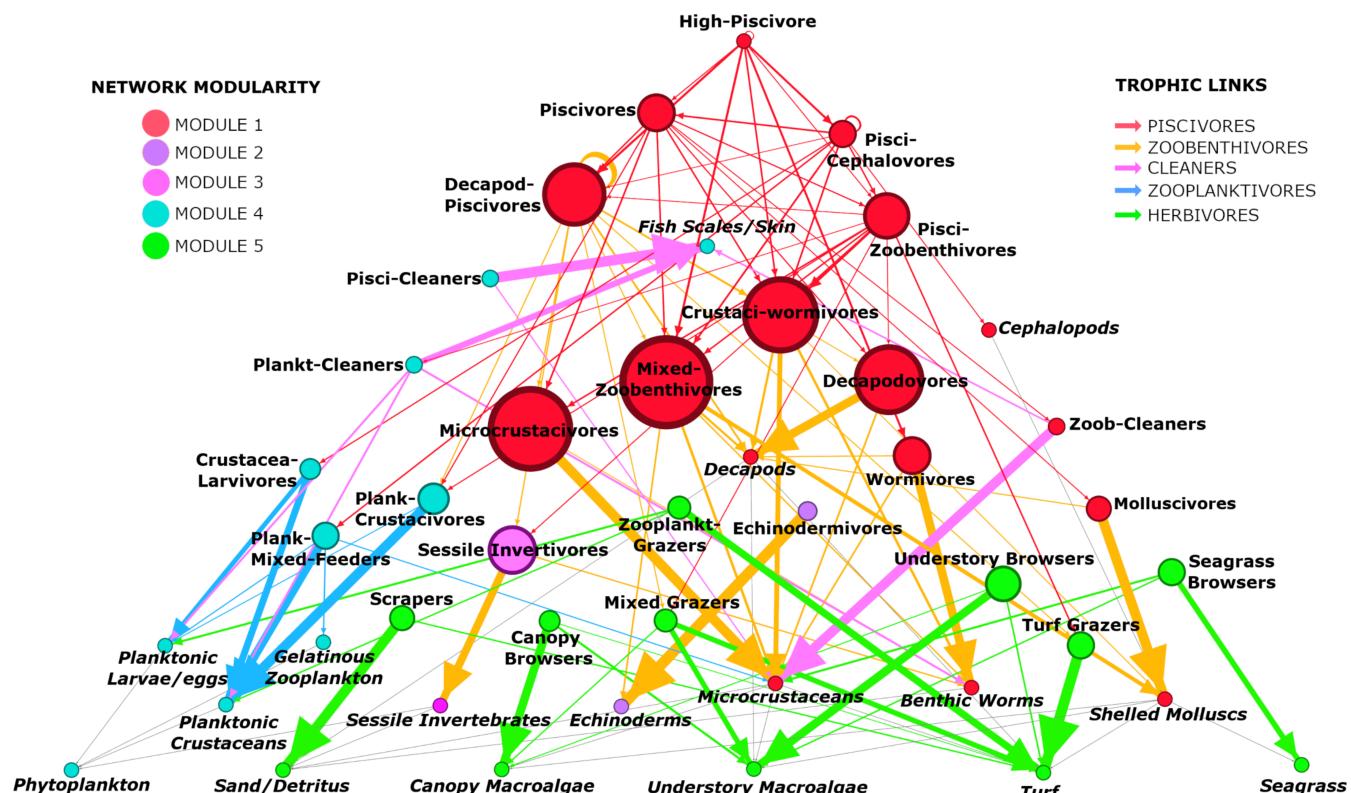


FIGURE 7 Trophic network of the metacommunity of temperate reef fish of southwestern Australia represented by specialized trophic guilds of piscivores, zoobenthivores, cleaners, zooplanktivores, herbivores, and their invertebrate and macrophyte prey (italics). Nodes are sized according to species richness and colored by module membership in the network. The width of trophic links is weighted by diet proportion and colored by the major trophic guilds of consumers.

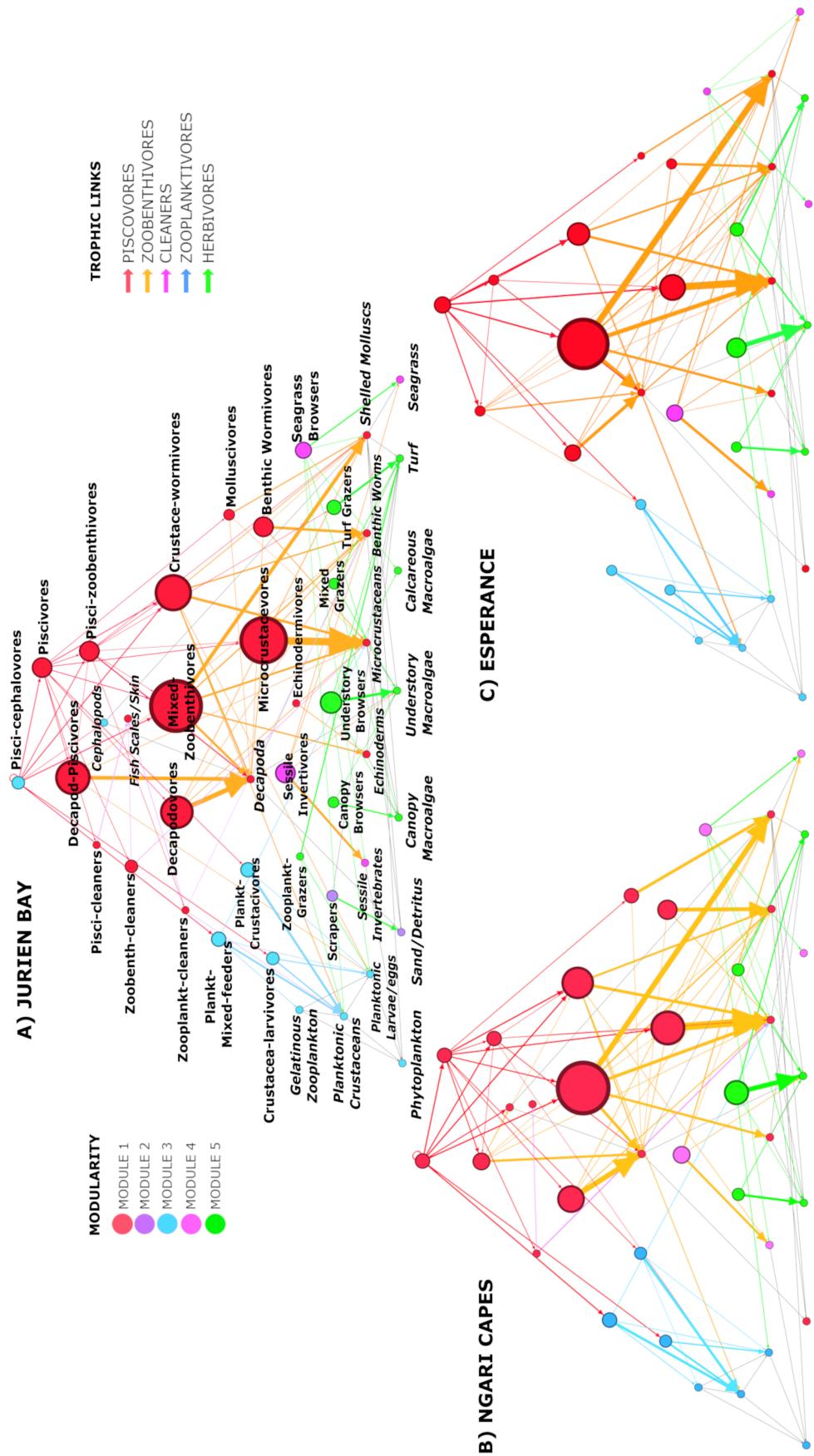


FIGURE 8 Regional trophic networks of temperate reef fish along the coast of south-western Australia represented by specialized trophic guilds of piscivores, zoobenthivores, cleaners, zooplanktivores, herbivores, and their invertebrate and macrophyte prey (italics): (A) Northern end: Jurien Bay (-30° S, 115° E); (B) central point: Ngari Capes (-34° S, 115° E), and (C) southern end: Esperance (-34° S, 122° E). The location and identity of nodes are the same in all networks. Node labels of Ngari Capes and Esperance are not shown for clarity in structure comparison. Nodes are sized according to species richness and colored by module membership in the network. Width of trophic links is weighted by diet proportion and colored by the major trophic guilds of consumers.

TABLE 1 Fish species richness of specialized trophic guilds in the locations of Jurien Bay, Ngari Capes, and Esperance in southwestern Australia.

Specialized trophic guild	Major trophic guild	Species richness		
		Jurien Bay	Ngari Capes	Esperance
Mixed-zoobenthivores	Zoobenthivores	26	20	15
Microcrustacevores	Zoobenthivores	23	12	7
Crustacea-wormivores	Zoobenthivores	17	11	6
Decapod-piscivores	Zoobenthivores	16	5	2
Decapodovores	Zoobenthivores	15	9	4
Understory browsers	Herbivores	9	8	5
Benthic wormivores	Zoobenthivores	8	6	2
Pisci-zoobenthivores	Piscivores	8	4	2
Piscivores	Piscivores	8	4	4
Sessile invertivores	Zoobenthivores	8	5	4
Seagrass browsers	Herbivores	6	3	1
Planktonic crustaceavores	Zooplanktivores	5	3	2
Planktonic mixed-feeders	Zooplanktivores	5	4	2
Turf grazers	Herbivores	5	0	0
Pisci-cephalovores	Piscivores	4	4	0
Planktonic crustacea-larvivores	Piscivores	4	3	2
Zooplanktivorous grazers	Herbivores	4	0	0
Canopy browsers	Herbivores	3	3	2
Mixed grazers	Herbivores	3	3	3
Molluscivores	Zoobenthivores	3	4	1
Scrapers	Herbivores	3	0	0
Echinodermivores	Zoobenthivores	1	0	0
Pisci-cleaners	Cleaners	1	0	0
Zoobenthivorous cleaners	Cleaners	1	1	0
Zooplanktivorous cleaners	Cleaners	1	0	0

composed of 187 fish species forming 25 nodes of specialized trophic guilds consuming 18 nodes of prey groups. In contrast, the network of Ngari Capes consisted of 113 fish species forming 19 nodes of specialized guilds and 17 nodes of prey groups, while the network of Esperance consisted of 64 fish species forming 17 nodes of specialized guilds and 16 prey groups (Figure 8). Despite these differences, mixed-zoobenthivores, microcrustaceavores, crustacea-wormivores, decapod-piscivores, decapodovores, and understory browsers had the highest species redundancy in the three locations (Table 1). Similarly, the network modularity was alike among locations. The network of Jurien Bay clustered in five modules, while Ngari Capes and Esperance had four modules. The main differences were a higher connectivity of Pisci-cephalovores to zooplanktivore trophic guilds and the absence of Scrapers (parrotfishes) in the southern regions, which was

separated from the rest as a unique module in Jurien Bay (Figure 8).

The values of predation intensity per node as indicated by WIDs were generally higher at Jurien Bay, but the identity of the most important prey groups was consistent among locations as evidenced by the number and width of trophic links in the networks (Figure 8). For Jurien Bay, microcrustaceans had the highest WID (3008), followed by decapods (2894), shelled mollusks (1305), benthic worms (1280), planctonic crustaceans (1164), and turf algae (819). Similarly, for Ngari Capes, the groups with the highest WID were microcrustaceans (1809), decapods (1374), shelled mollusks (1009), benthic worms (890), planctonic crustaceans (776), and fleshy understory macroalgae (735). Lastly, for Esperance, microcrustaceans (1056), decapods (755), shelled mollusks (643), fleshy understory macroalgae (512),

planctonic crustaceans (493), and benthic worms (451) were the most important prey groups.

DISCUSSION

Trophic diversity

We aimed to advance our understanding of the trophic complexity and interdependency between temperate reef fish species and their prey at a metacommunity scale by characterizing their trophic guilds at high resolution based on quantitative diet information. Our results indicated a higher diversity of trophic guilds than previously considered and concurrently showed that predation in the benthic and pelagic space is more complicated than previously reported. We found a total of 26 specialized trophic guilds nested in five major trophic groups, representing a ~200% increase in trophic diversity compared with previous reports that have classified hundreds of fish species in 12 or fewer trophic guilds (Bulman et al., 2001; Parravicini et al., 2020; Viviani et al., 2019). These results confirm our hypothesis that trophic diversity in fish communities must correlate with the ecological process of resource partitioning within the high diversity of prey available to them among primary producers, invertebrates, and vertebrates. Trophic diversity increased in all major trophic guilds which previously have been grouped into singular guilds. Most of the trophic diversity found in our study was accounted for by fishes which fed on invertebrate species, the most diverse group of prey in natural ecosystems (Ruppert et al., 2003). Trophic guilds of cleaners, zooplanktivores, and zoobenthivores accounted for 15 specialized trophic guilds, representing 64% of all the diversity. After herbivores, the trophic classification of zoobenthivore fishes has arguably been the most detailed, having been classified in guilds such as sessile invertivores, corallivores, crustacivores, macroinvertivores, and microinvertivores (Parravicini et al., 2020). However, our results illustrate that these categories remain very broad, as we found nine statistically significant specialized zoobenthivore trophic guilds, which alone are similar to all trophic guilds previously reported for coral or rocky reef fish communities (Honório et al., 2010; Yeager et al., 2017). Our study refines the trophic classification of this diverse group of predators with divergent hunting strategies and morphologies and better depicts the complexity of trophic links between zoobenthivorous fishes and the invertebrate community residing in temperate reefs, as was suggested by previous studies that have identified diet specializations at smaller taxonomic and spatial scales (Bellwood et al., 2006; Soe et al., 2021).

Top-down function and redundancy of trophic guilds

The identification of specialized groups of consumers allows a better depiction of trophic functions and species redundancy for direct and indirect top-down control. Despite the high trophic diversity among zoobenthivorous fishes, species redundancy was contrasting among specialized trophic guilds. Redundancy of species with the potential to exert top-down control on crustaceans and hard-shelled mollusks was high. In contrast, low redundancy was found for echinoderm consumption. Great numbers of herbivorous species of amphipods, isopods, gastropods, and sea urchins can have significant impacts in the ecosystem by consuming habitat-forming macroalgae (Gutow et al., 2020; Ling et al., 2015; Poore et al., 2012). The high species redundancy of crustaceavores and molluscivores indicates resilience in the system for the top-down control of these invertebrate consumers. However, our results suggest a low redundancy of echinodermivores, which could be a vulnerability for the top-down control of herbivorous sea urchins in the region. Although temperate western Australia has a relatively low density of sea urchins by global standards, and barrens have not yet been reported (Fowler-Walker & Connell, 2002), an increase in their diversity and abundance by climate change could lead to the creation of barrens due to a lack of predators (Ling et al., 2015).

The overall species richness in the herbivore guild was within the range expected for the entire temperate region, although this value is likely to decrease at smaller spatial scales (Steneck et al., 2017). Likewise, species redundancy of browsers of seagrass and canopy-forming macroalgae was low, which appears typical of temperate regions (Meekan & Choat, 1997). A low number of browsing species implies that canopy browsing is spatially patchy, particularly because most species form schools. This likely benefits temperate reef ecosystems, since the canopy of macroalgae is important for supporting high levels of biodiversity in these ecosystems (McHenry et al., 2021; Teagle et al., 2017). The tropicalization of temperate communities due to climate change, where tropical herbivorous species are poised to shift distributions to temperate regions, might increase trophic redundancy and primary consumption rates in certain locations in the future (Bennett et al., 2015; Zarco-Perello et al., 2017). However, given the current low redundancy of browsers, herbivory impacts at a regional scale might not cause overgrazing, particularly in places where novel species do not overlap with native browsers (Zarco-Perello et al., 2020).

Piscivorous guilds are considered important top-down regulators of other trophic guilds of fish. However, their specific impacts have been difficult to determine because

in situ evidence of their trophic interactions is limited, and the taxonomic identification of their prey in diet analyses is broad (Cortes, 1999). Previous studies have shown the potential functional roles of top predators through broad correlation of abundances, mostly on coral reefs (Dedman et al., 2024; Sandin et al., 2022). Thus, the ecological significance of top-predatory fish in temperate reefs is uncertain. Most evidence of trophic cascades involves top-down control by zoobenthivore species, particularly sea urchin predators (Pinnegar et al., 2000). However, a few studies have shown how piscivorous guilds (meso-piscivores) could control the impact of zoobenthivore fishes (Frid & Marliave, 2010). Our high-resolution trophic classification allowed a more precise inference on how piscivore groups could be exerting top-down control on different trophic pathways in the network. Results showed that two piscivorous guilds were at the top of the trophic network by likely predating on other piscivorous fishes, in addition to zoobenthivore guilds. The high-piscivore *Carcharias taurus* was identified as the top predator, being the only species with high diet proportions of sharks and rays. As such, the trophic links suggested by our results indicate that the functional role of top-piscivores could be important to control the predation of meso-piscivores, inflicting an indirect positive effect on invertivore and herbivore fish guilds, potentially cascading down to the benthic community.

The other two piscivore guilds (pisci-zoobenthivores and piscivores) showed stronger trophic links with fishes at lower trophic levels, especially with zoobenthivore guilds that consumed important proportions of crustaceans (crustaceavores, microcrustaceavores, microcrustacea-omnivores, and worm-crustaceavores), suggesting their potential function in modulating the consumption of crustacean groups, which in turn predate on other invertebrates (e.g., lobsters and crabs) (Pinnegar et al., 2000). These piscivore guilds also showed potentially strong trophic links with herbivorous fishes; however, consumption seemed to be important only for turf grazers. Unlike some studies on tropical reefs, these results suggest that fish herbivory in temperate reefs may not be subject to strong top-down control (Sandin et al., 2022). Moreover, it also suggests that herbivorous fishes might not play a significant role in the energy transfer between primary producers and fishes at higher trophic levels, as indicated by the network modularity, although they may do so indirectly by producing macrophyte-derived detritus and through the scavenging trophic pathway (Zarco-Perello et al., 2019). Indeed, in contrast to herbivorous sea urchins, top-down control on temperate herbivorous fish has not been reported previously (Shears & Babcock, 2002). At present, this predatory function is unlikely to be of importance because fish

herbivory in temperate reefs is not significant at large spatial scales (Jones & Andrew, 1990). However, a lack of control on fish herbivory in the future might represent a vulnerability for temperate reefs with the advent of tropical herbivorous fish, particularly if native predators may not recognize novel herbivorous species as prey (Hille Ris Lambers et al., 2013).

Bottom-up importance of prey groups

Prey importance analyses illustrated the significance of different prey groups as direct sources of nourishment to sustain temperate fish biodiversity in western Australia. The relative importance of prey groups aligned with the diversity of trophic guilds and their species redundancy. Hence, the dominance of invertebrates as the most consumed prey groups was reflected by the classification of 15 specialized trophic guilds of zoobenthivores, zooplanktivores, and cleaner fishes. These findings highlighted that not all groups of zoobenthos and zooplankton have the same trophic weight for the fish metacommunity, as can be indicated by simplistic trophic classifications. Benthic crustaceans had the greatest importance as shown by WIDs, their proportion, and frequency in fish diets. Similarly, the differences found between and within the rest of the invertebrate groups were significant. Noteworthy, polychaetes were a very prominent prey group, ranking third behind crustaceans considering diet proportions, and first considering frequency, even being consumed importantly by elasmobranch stingarees and carpetsharks. On the other hand, the lower proportional importance in the metadiet by fishes (12.7%) is generally expected, given the lower species richness of piscivores we found (41 species), and the thermodynamic laws for energy transfer in trophic networks, where consumption diminishes in higher trophic levels (Saint-Béat et al., 2015).

Consumer-prey interactions reflected in the trophic network also revealed the indirect importance of prey groups for all fish species. Macrophytes accounted for 13% of the metadiet, directly benefiting species of herbivores and omnivores and multiple other species with lower proportions of consumption. However, their greatest importance to the fish community likely resides indirectly by fueling energy flows through the trophic pathway of herbivorous and detritivorous invertebrates (Kramer et al., 2013). Herbivores include species of gastropods, microcrustaceans, and sea urchins, while polychaetes, decapods, sea cucumbers, bivalves, and sessile invertebrates also consume macrophyte-derived detritus (Yorke et al., 2019). The indirect importance of macrophytes then expands to the top of the trophic network, as

the energy of these invertebrates passes to zoobenthivore fishes and piscivore guilds through the predation links found in our study. Indeed, modularity analyses of the trophic network highlighted the ecological importance of these benthic invertebrates, showing that module 1 acted as the central pillar of the trophic network, connecting crustaceans, benthic worms, and shelled mollusks all the way up to high piscivores. This points out that the biodiversity of temperate reef fishes relies heavily on these invertebrates as links of primary production and higher trophic levels, a similar trophic function suggested for coral reefs (Kramer et al., 2013). According to trophic links, the disappearance of crustaceans alone could directly affect 150 fish species that had at least 30% of crustaceans in their diet, representing 50% of the species in the metacommunity. Changes in the abundance of these species could ripple across the entire network and change community structure. Given the diet plasticity demonstrated by fishes, it is likely that many species could survive by switching consumption to other prey; however, populations might be affected in the long term if their nutrition and fitness decrease (Hamilton et al., 2011).

Spatial variation in network structure

The meta-trophic network of the study sums up trophic relationships at a biogeographical scale; however, the network structure and relative importance of prey groups for fish communities can vary across space depending on the local community (Stål et al., 2007; Truong et al., 2017). Climate differences can be determinant for these variations, since warmer ecosystems at lower latitudes generally have higher species richness and functional groups (Cowman et al., 2017; Stuart-Smith et al., 2013) and some analyses have shown that warmer regions have more complex trophic networks than the colder regions (López-López et al., 2022). Our comparison of trophic networks from warmer to colder locations agreed with this, since the trophic network of Jurien Bay had 24% and 32% more trophic diversity than Ngari Capes and Esperance, respectively, as well as higher species richness per node and strength in trophic interactions as indicated by AWD values. Yet, the networks showed consistent structural properties across locations. The highest species redundancy in the three locations was found in guilds of crustaceavores and other zoobenthivores, while the prey groups of crustaceans, shelled mollusks, polychaetes, and understory macroalgae had the highest concentration of predation links. This resulted in equivalent modularity, which means that perturbations on different nodes would

propagate similarly through the networks (Eskuche-Keith et al., 2023).

As in the meta-network, Module 1 constituted the main axis of energy flow, from prey groups of microinvertebrate grazers to top predatory fishes in the three locations of study. Thus, disturbances affecting these nodes can result in the highest perturbations in these ecosystems. While these results indicate a relatively homogeneous functioning of the temperate reef ecosystems in the region, the lower functional redundancy in colder locations may translate into increased vulnerability to disturbances in these subregions, since this property has been positively related to the stability and resilience of ecosystems (Biggs et al., 2020). Nevertheless, because the Leeuwin Current maintains strong connectivity dynamics in the entire region of western Australia (Maxwell & Cresswell, 1981), functional redundancy in colder locations can increase if climate change progresses and facilitates the arrival of species from higher latitudes that have similar trophic habits to the native species (Zarco-Perello et al., 2021).

Future research directions

Trophic ecology plays a central role in understanding ecosystem function; however, the indirect effects of species interactions make it an extensive and complex subject of study. Even though we found increased trophic diversity and complexity than previously reported, our results may still not capture the real-world trophodynamics given the uncertainties in prey identification, availability of diet information in space and time, and likely ubiquitous ontogenetic shifts in diet. This is particularly critical for piscivorous fishes, whose diets have high percentages of unidentified prey fishes, totaling 54% of vertebrate prey proportions. Moreover, diet studies tend to focus on species with fishing importance in pelagic systems, and substantial knowledge gaps exist for reef fishes of ecological and conservation relevance. In our study, a total of 122 species were endemic to temperate Australia but lacked regional diet information, which introduces uncertainty in the analyses of trophic guilds and prey importance. A study assessing the effect of location and taxonomy for the prediction of fish diet in temperate Australia found little effect (1–3%) in the overall accuracy of diet predictions (73%), after accounting for fish size, suggesting that by sourcing diet information from other locations and congeneric species our estimations should be within an acceptable range (Soler et al., 2016). Several other studies have shown that many species tend to change their diet according to ontogenetic stages and locations due to shifts in microhabitats, gape

size, feeding modes, or locations that result in different prey availabilities (Behrens & Lafferty, 2012). Unfortunately, most species lack assessment of diet plasticity, and further work in this direction is needed across the world to improve spatial analyses of trophic interactions. Moreover, it must be considered that our trophic analysis provides inferences for the importance of prey groups for the diversity of species only and it is possible that their importance can change considering other aspects, such as its nutritional value, their abundance in the ecosystem, and its contribution to the secondary productivity of different fish groups, calling for more research to be done in these alternative trophic dimensions (Truong et al., 2017).

Interdisciplinary collaborations and the application of new emerging technologies are needed to reduce regional knowledge gaps on the diet of fish species and further increase the resolution of our understanding of trophic interactions. Many biological disciplines beyond trophic ecology involve the collection of hundreds of individual fish for life-history studies, genomic analyses, and even parasitology studies, which could well be used for trophic analyses but are regularly discarded. Increasing the use of DNA analysis for trophic ecology in reef ecosystems, in combination with other methods, such as fatty acid and stable isotope analyses, can revolutionize the identification of prey groups to the species level, the accurate definition of trophic niches, redundancy of energy flows, and resilience of the ecosystem (Carreon-Martinez & Heath, 2010; Sturbois et al., 2022).

In addition to achieving accurate trophic linkages, trophic networks should include all species of significant trophic relevance in the ecosystem. The methodology used to survey the fish community could influence results, since some techniques differ significantly in species detection. For instance, underwater visual censuses tend to capture fewer predatory species and more herbivorous and small species in comparison with stationary video methods (i.e., Baited Remote Underwater Video (BRUV)) (Jessop et al., 2022; Zarco-Perello & Enríquez, 2019). In this case, it is unlikely that this factor affected our results significantly, given that the species composition used for our analyses was derived from a very large sampling effort across space and time (i.e., 4589 surveys), and the vast majority of resident top-predatory fish of the shallow temperate reefs of western Australia are likely represented in our study. Nonetheless, the inclusion of other groups of vertebrates, such as seabirds and marine mammals, should be included in further studies if possible to have a full spectrum of top-down forces in the ecosystems (Fromant et al., 2020).

CONCLUSIONS

We carried out a broad empirical evaluation of the trophic interdependency between temperate reef fish species and their prey groups across a biogeographical scale, synthesizing trophic linkages considering high levels of biodiversity. Our higher resolution analyses showed that the trophic diversity of temperate reef fish was two times higher compared with previous characterizations, including tropical reefs which host a higher diversity of fish species. The higher trophic diversity in temperate reefs suggests that our understanding of functional diversity is likely more incomplete across biogeographical scales. A finer scale trophic analysis allows a better understanding of specific ecological interactions and functions for top-down control and bottom-up effects. Here, we show direct evidence of the potential trophic links of top predators with other specialized guilds of fishes in the trophic network, allowing us to assess their functional role on specific trophic pathways. The energy flow from primary producers to top predators seems to be strongly modulated by invertebrates across locations in the region, as we found little evidence of piscivory on herbivorous fish. Among all invertebrate groups, crustaceans seemed to have a keystone role in consolidating the trophic network, suggesting that special attention should be given to understanding their ecology and assuring its conservation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Zarco-Perello, 2023) are available from Zenodo: <https://zenodo.org/records/10073476>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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