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

Zarco-Perello S.[1, 2, *] , Bennett, S. [3], Jordan, G. [4, 5], Holmes, T. [4, 6], Stuart-Smith, R. [3], White E. R.[2]

[1] Harry Butler Institute, Murdoch University, Perth, Australia.
[2] College of Life Sciences and Agriculture, University of New Hampshire, Durham, USA.
[3] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia.
[4] Department of Biodiversity Conservation and Attractions of Western Australia, Perth, Australia.
[5] School of Molecular and Life Sciences, Curtin University, Perth, Australia.
[6] The UWA Oceans Institute, The University of Western Australia, Perth, Australia.

*Corresponding author: Salvador Salvador.zarco.perello@gmail.com

Abstract

Marine fish communities are highly diverse, including all trophic levels of consumers and contributing to many ecosystem processes. Understanding the specific functional roles of many fish species and the importance of different prey groups for sustaining fish communities has, however, been limited by the historical classification of fishes into a few coarse trophic guilds. Using detailed diet information to perform a high-resolution trophic classification of 298 temperate reef fish species distributed across south-western Australia, we built a metacommunity trophic network to evaluate the most important trophic relationships and energy pathways. We identified 26 specialized trophic guilds within the broader groups of herbivores, zoobenthivores, zooplanktivores, piscivores and cleaners. Zoobenthivorous fishes had the highest species richness and trophic diversity with 191 species in 9 guilds. Micro-crustaceavores, decapodovores, mixed-crustaceavores, and crustacea-wormivores showed greater species richness and therefore 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 consuming other piscivorous fishes, and others at lower trophic levels, particularly crustaceavores. Evidence of potential predation on herbivorous guilds was only found for turf grazers, suggesting that fish herbivory might not function as a significant energy-transfer 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 much more highly consumed by fishes than macrophytes themselves. These higher resolution predator-prey interactions represent important steps in increasing 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 crucial for ecological forecasting and the prioritization of conservation and resource management regulations in our current fast-changing world.

Keywords: Trophic guild; ecological network; ecosystem function; functional groups; feeding ecology; diet; predation; herbivory; top-predator; kelp forest; rocky reefs; Great Southern Reef.

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 get 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 specific 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 of sea urchin populations and helping maintain high abundances of kelp forests in temperate reefs (Hamilton and 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 and results of correlative studies of prey-predator abundances is 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 and Floeter 2008, Mouillot et al. 2014, Parravicini et al. 2020). However, other studies with narrower taxonomic and geographical scope 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 in 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 in at least five trophic groups when feeding differences are considered in more detail: scrapers/excavators, grazers, macroalgae browsers, seagrass browsers and detritivores (Halpern and 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 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 to 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 and 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 measure 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 human population grows and climate change advances (Pecl et al. 2017, Bestion et al. 2019). 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 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 south-western Australia. Specifically, the objectives were to (i) define and quantify the diversity of trophic guilds at high resolution, (ii) assess their trophic roles in the ecosystem through trophic network analysis, and (iii) quantify the relative importance of different prey groups as nourishment sources based on diet proportions and number of predators that consume them at the metacommunity scale.

Methods

Temperate Reef Fish Metacommunity

The region of study encompasses all the temperate reefs of south-western Australia (SWA). Extending along ~1600 km of coast, from Jurien Bay Marine Park (30° 18.6 S, 115° 0.1 E) to the Recherche Archipelago Nature Research (33° 53.7 S, 123° 52.3 E; supplementary Fig. S1), the temperate reefs of SWA are distributed across the Leeuwin and Houtman biogeographical ecoregions (Spalding et al. 2007), conforming approximately ⅓ 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 large fishes within 5 m at each side from the transect and cryptic fishes within 1 m at each side from the transect (Edgar and 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).

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 and 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 size 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 this data does 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 (i) broader taxonomic groups from class to order level (*e.g.* amphipoda, and gastropoda), and subsequently into (ii) major diet categories at functional group and phylum level (*e.g.* shelled molluscs and molluscs).

Trophic guilds 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 multi-step 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 higher definition of prey items to identify groups of species with diet specializations using sequential agglomerative hierarchical cluster analysis based on Ward's Method and Bray-Curtis or Euclidean dissimilarity matrix (Pineda-Munoz and Alroy 2014).

The stomach content of most scarid 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 was 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 blenny 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 dendrograms 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 Non-metric Multidimensional Scaling based on the dissimilarity matrix calculated for clustering using the function *metaMDS* of the R package vegan (reported in supplementary materials; (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).

Metacommunity Trophic Network

The direct and indirect trophic function of trophic guilds and prey groups was 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 "matrioshka 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 fish guilds by (i) assigning each fish family identified in the diets of piscivorous fishes into their respective specialized guilds based in our trophic classification, (ii) pooling their diet proportions into each specialized trophic guilds they could belong to, (iii) standardizing values by number of species in each piscivorous guild, and (iv) 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 (Hansson et al. 2005, Poore et al. 2012, Gutow et al. 2020, Briones-Fourzán and Hendrickx 2022); 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. Once the network was constructed, we calculated the weighted in-degrees (WID; 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 analyzes Gephi v0.1 (Bastian et al. 2009).

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 (%) 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 logit link function for proportions (diet proportions ~ prey groups), and binomial regression with 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).

Results

Major Trophic Guilds

The 298 reef fish species belonging to 94 families were classified in five major trophic guilds (PERMANOVA; pseudo-$F_{4,325}$ = 81.3, P= 0.0001; Table S2, Fig. S2, Fig. 1). 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 (mean ± standard error: 87.18% ± 2.16) and complemented with zooplankton (4.57% ± 1.4) and zoobenthos (80.01% ± 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% ± 11.98), zooplankton (15.45% ± 8.92) and zoobenthos (12.53% ± 5.06). The third cluster constituted the guild of zooplanktivorous fishes, grouping 20 species of fish belonging to 12 families which consumed high amounts of zooplankton (89.81% ± 2.63), followed by zoobenthos (6.73% ± 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% ± 2.92), zoobenthos (14.35% ± 0.63) and cephalopods (4.34% ± 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% ± 1.01), complemented with fishes (5.06% ± 0.72), macrophytes (3.87% ± 0.65) and zooplankton (2.2% ± 0.42).

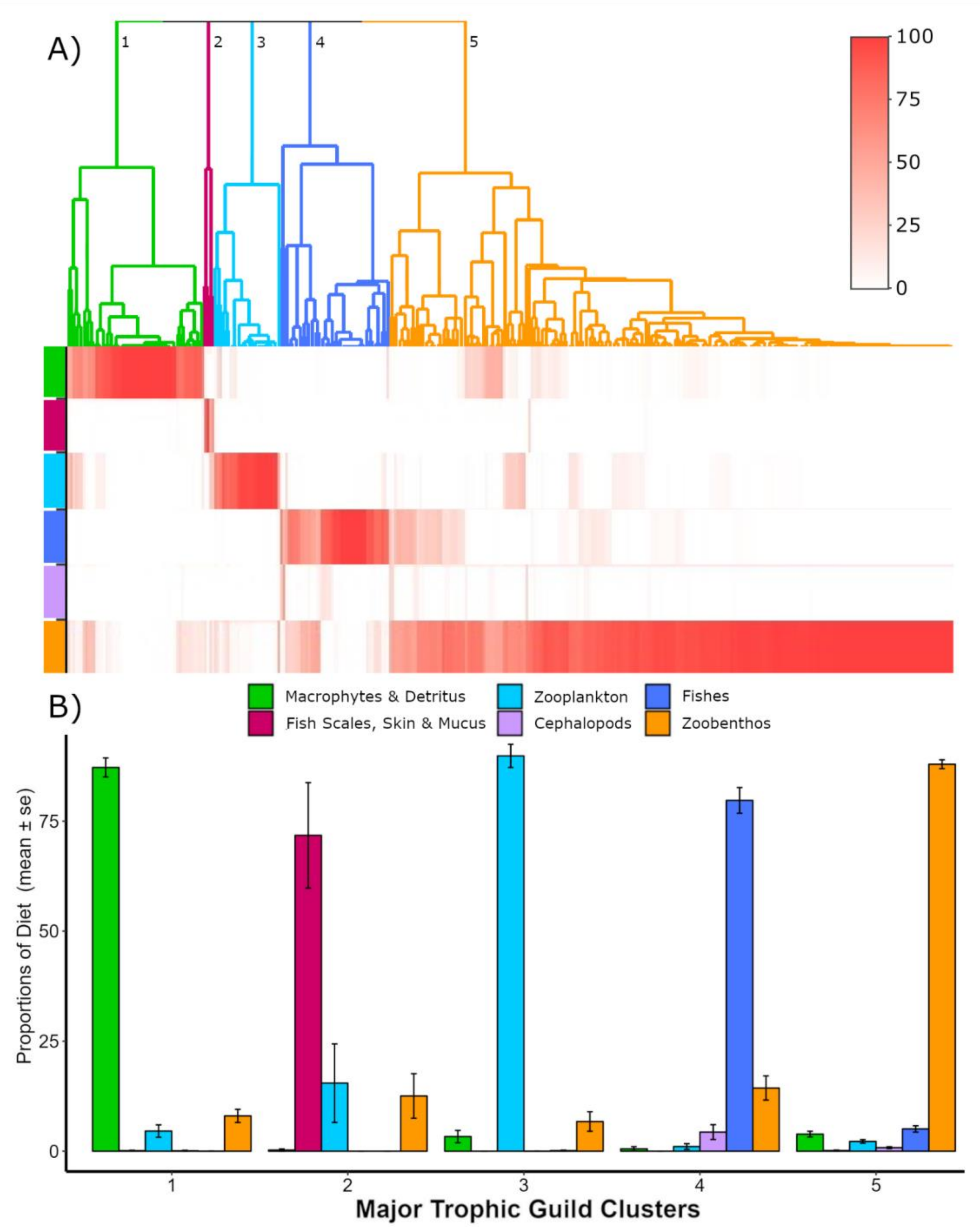


Figure 1. Classification of major trophic guilds of the temperate reef fishes of south-western Australia. (A) Dendrogram of divisive cluster analysis with heatmap of the diet composition per species divided in major prey/food categories. (B) Barplot showing the mean proportions of the diet composition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

Specialized Trophic Guilds

Cluster analyses within each major trophic guild at higher resolution of prey items showed more refined trophic classifications, revealing generalists and specialist species, branching into 26 trophic subgroups (Table S1). Herbivorous species were classified into seven trophic guilds divided in 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; Table S3, Fig. 2a). 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 (Fig. S3).

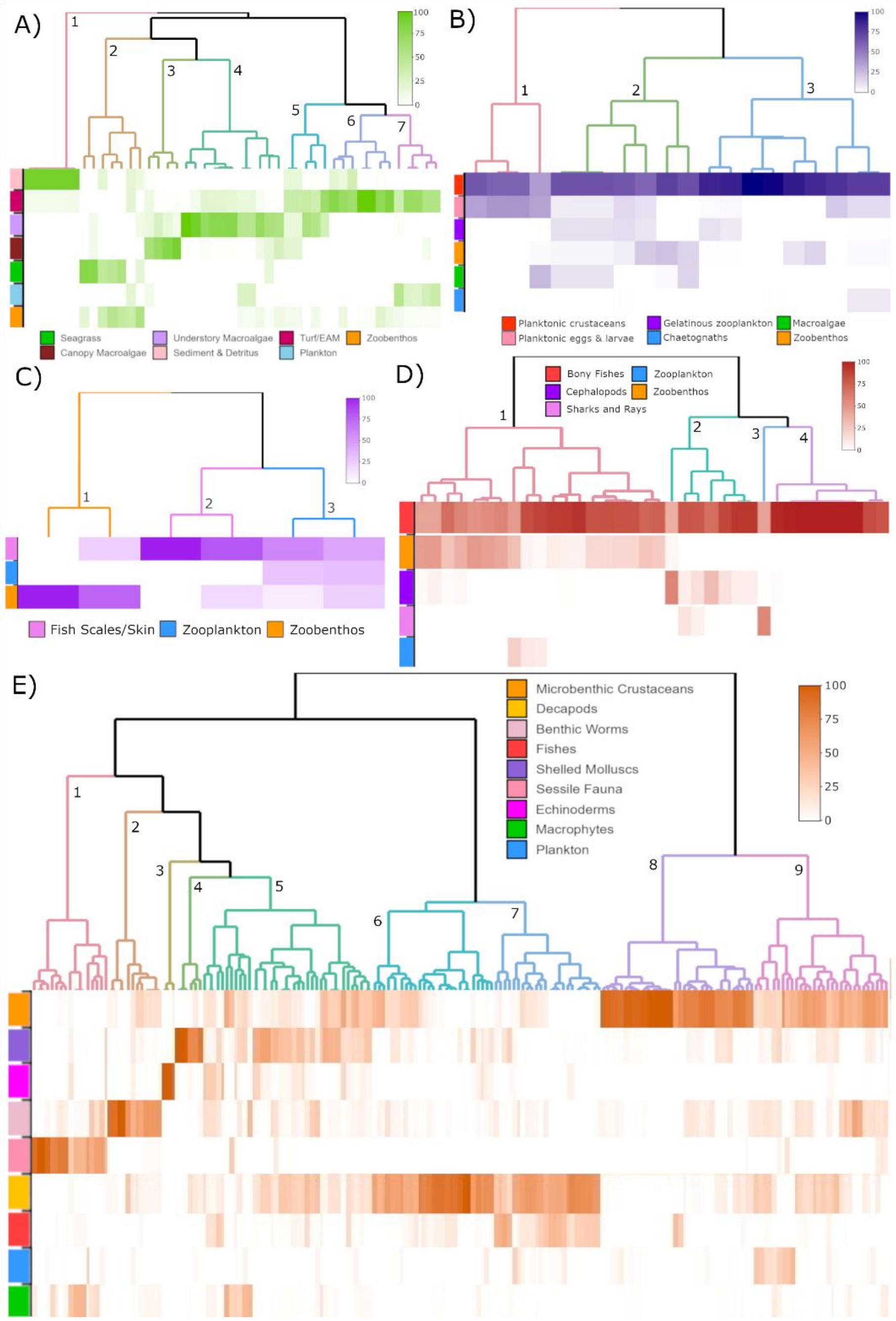
Zooplanktivorous fishes were grouped in three distinct subgroups (PERMANOVA; pseudo-$F_{2,17}$ =11.931, P= 0.0001; Table S4, Fig. 2b): *Planktonic crustaceavores* (nine species) fed almost exclusively on planktonic copepods; *planktonic mixed-feeders* (seven species) also consumed significant proportions of planktonic crustaceans (copepods, diplostracans and euphausiids), but complemented 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; Fig. S4).

Cleaner fishes were divided in three clusters of two species each (Figure 2c). 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 (Fig. S5). 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, seconded by zoobenthos (copepods); *zooplanktivore cleaners* diet contained fish scales and skin, and zoobenthos (benthic worms) but also zooplankton (fish larvae and copepods).

Piscivore fishes were classified in four specialized trophic guilds (PERMANOVA; pseudo-$F_{3,32}$ = 20.9, P= 0.0001; Table S5, Fig. 2d). *Pisci-zoobenthivores* (16 species) had diets dominated by fishes and zoobenthos (caridean shrimps and crabs). *Pisci-cephalovores* (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 greynurse shark *Carcharias taurus* was the only species classified as *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%; Fig. S6).

Zoobenthivorous fishes were differentiated into nine specialized trophic guilds separated in three main clusters (PERMANOVA; pseudo-$F_{8,182}$ =60.247, P= 0.0001; Table S6; Fig. 2e). 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* (six species) consumed mostly gastropods, bivalves and chitons, complementing with decapods; while *mixed zoobenthivores* (38 species) fed on shelled molluscs, decapods, microcrustaceans, benthic worms, echinoderms and fishes (Fig. S7). 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 complementing with teleost fish, while *decapodovores* (27 species) fed almost exclusively on decapods (dendrobranch prawns, caridean shrimps, squat lobsters, and crabs; Fig. S7). The third main branch was subdivided in two guilds that fed predominantly on microcrustaceans (Fig. 2e): *microcrustaceavores* (34 species) who 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 (Fig. 2e; Fig. S7).

Figure 2.



Classification of the temperate reef fishes of south-western Australia in specialized trophic guilds. (A) *Herbivores*: (i) Scrapers, (ii) Seagrass browsers, (iii) canopy browsers, (iv) understory browsers, (v) mixed grazers, (vi) turf grazers, and (vii) zooplanktivorous grazers. (B) *Zooplanktivores*: (i) Planktonic crustacea-larvivores, (ii) planktonic mixed-feeders and (iii) planktonic crustaceavores. (C) *Cleaners*: (i) Zoobenthivorous cleaners, (ii) pisci-cleaners and (iii) zooplanktivorous cleaners. (D) *Piscivores*: (i) Pisci-zoobenthivores, (ii) pisci-cephalovores, (iii) high-piscivore and (iv) piscivores. (E) *Zoobenthivores*: (i) Sessile invertivores, (ii) benthic wormivores, (iii) echinodermivores, (iv) molluscivores, (v) mixed-zoobenthivores, (vi) decapodovores, (vii) decapod-piscivores, (viii) microcrustaceavores, (ix) crustacea-wormivores.

Metacommunity Trophic Network

The trophic network of the metacommunity was structured by 43 trophic nodes amog specialized trophic guilds of fish and prey groups (Fig. 3). 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 (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 by many piscivore guilds; however, predation differences among piscivores were found (Table S8). High-piscivores had 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 weighted in-degree (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 molluscs (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 molluscs 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 (Fig. 3).

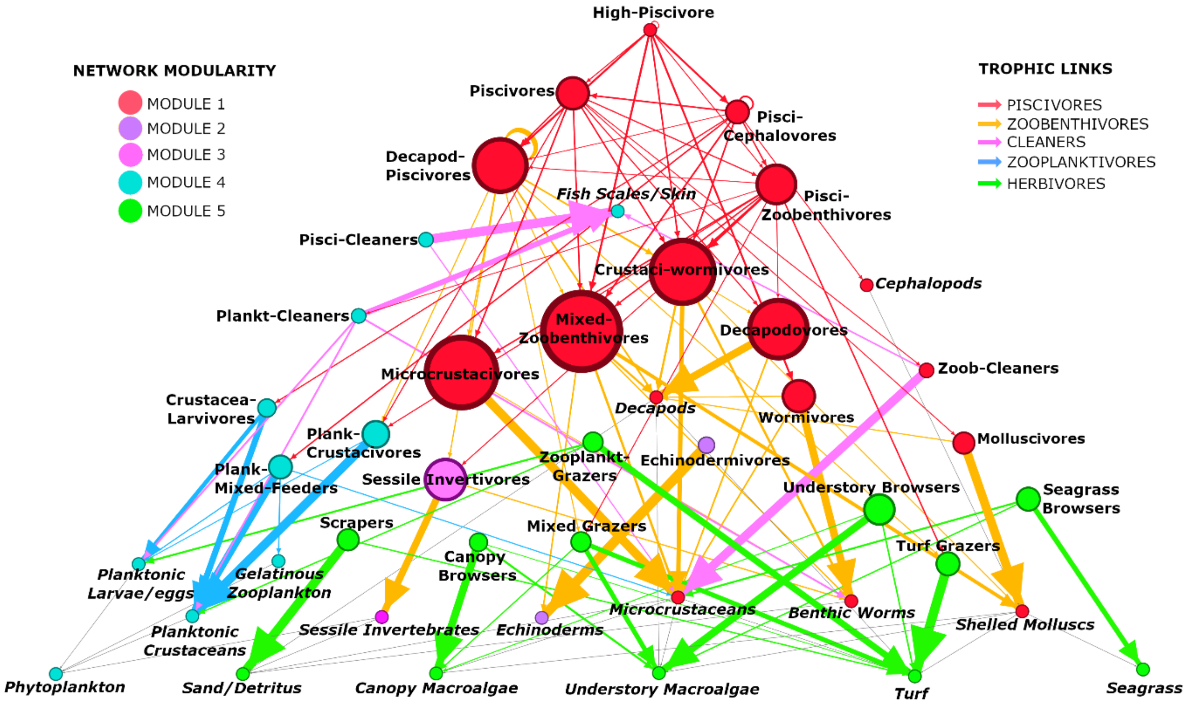


Figure 3. Trophic network of the metacommunity of temperate reef fish of southwestern Australia represented by specialized trophic guilds of piscivores, zoobenthivores, cleaners, zooplanktivores, herbivores and their invertebrate and macrophyte prey (italics). Nodes are sized according to species richness and colored by module membership in the network. Width of trophic links is weighted by diet proportion and colored by the major trophic guilds of consumers.

Importance of Prey Groups

Considering 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 (Fig. 4a). Invertebrates also dominated dietary proportions, accounting for ~63% of the meta-diet (GLM, LTR=143, $p<0.0001$, Table S9, Fig. S8; Fig. 4b). Invertebrates were particularly important to species of the family Labridae (13.2% of metadiet). At 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 for 15 species (<10%). Crustaceans 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 metadiet, respectively. More specifically, gammaridean and corophiid amphipods had high predator numbers (153 spp) and metadiet proportion (8.9 ± 1.0%; GLM, LTR=26.289, p=0.0018, Table S10, Fig. S9; Fig. 4c,d). Brachyuran crabs were preyed by 116 fish species and had the second highest average proportions (7.3 ± 0.9%) among all prey groups. Polychaetes were the most frequent prey group in the metadiet, being consumed by 157 fish species (GLM, LTR=530.6, p=0.0001, Table S11, Fig. S10) while accounting for 5.8 ± 0.8% of the metadiet. Planktonic copepods, gastropods, bivalves, sessile invertebrates (*i.e.* sponges and anthozoans) and other microcrustaceans, decapods, molluscs, and echinoderms had an intermediate number of predators (~75-50 spp) and proportions of the metadiet (Fig. 4c,d).

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%; Fig. 4a,b). 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% ± 0.5; Fig. 4c). 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 family level, the most important prey were Engraulidae (7% of vertebrate proportions), with the rest having proportions <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; Fig. 4a), particularly macroalgae (36% =109 species). Proportionally, they accounted for 13.25% of the meta-diet, with macroalgae comprising most of this proportion (11.4 ± 1.4%), seconded by seagrass (1.6 ± 0.4%; Fig. 4b). 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 filamentous algae was consumed by 48 species of fish and was the 5th most important prey group in the metadiet (4.3 ± 0.8%; Fig. 4c,d), accounting for 40% of all the proportions of macrophytes, followed by fleshy understory macroalgae (40 consumers; 3.2 ± 0.7%), seagrass (32 spp; 1.6 ± 0.5%), canopy-macroalgae (19 spp; 1.4 ± 0.5%), and calcareous understory (19 spp; 0.5 ± 0.2%).

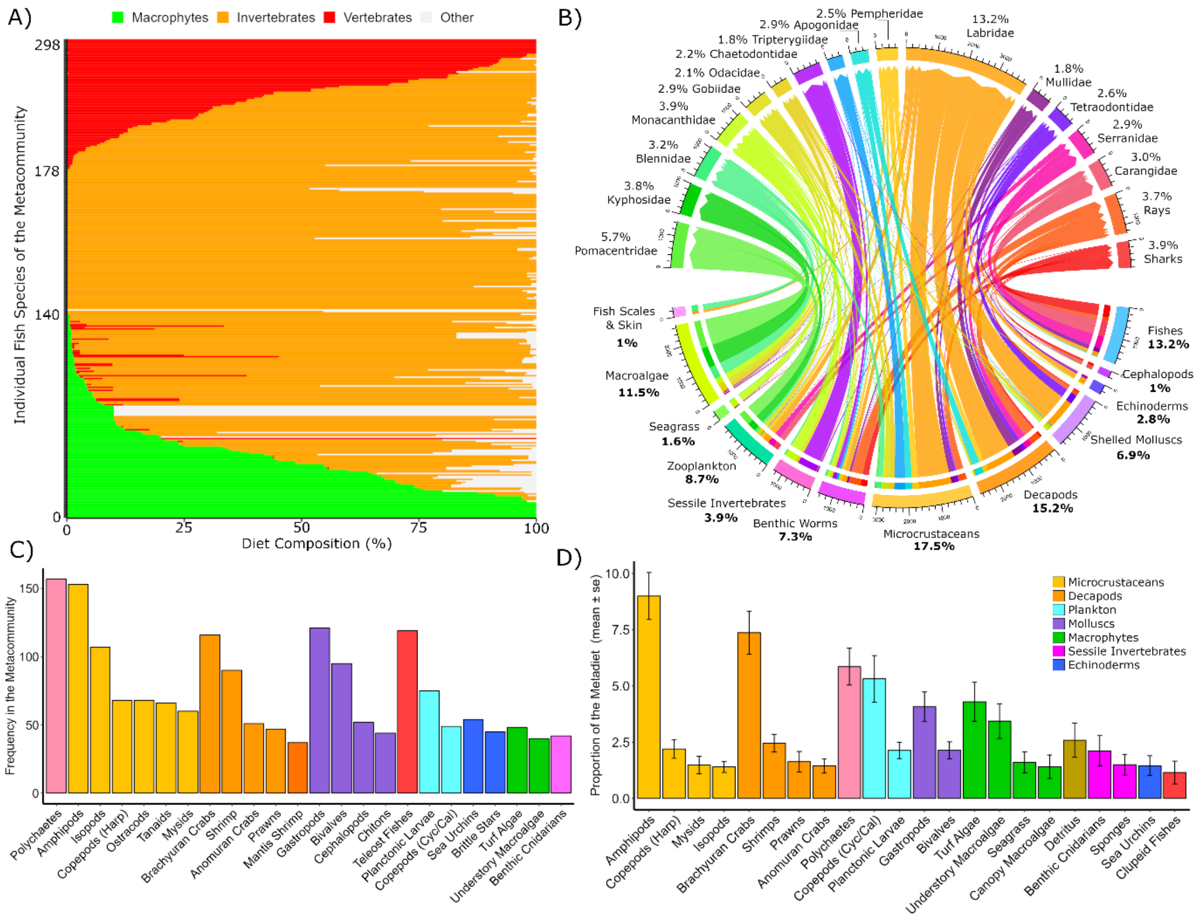


Figure 4. The importance of prey groups regarding their proportion in the metadiet and their frequency of predation among fish species. A: Stacked bar chart showing the pervasiveness of the major traditional groups of prey: plants, invertebrates and vertebrates. B: Circular flow plot showing the total 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 fish of southwestern Australia (upper half). C: Frequency of prey groups at higher resolution in the diets of all the 298 fish species of the metacommunity. D: 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.

Discussion

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 to previous reports that have classified hundreds of fish species in twelve or less trophic guilds (Bulman et al. 2001, Viviani et al. 2019, Parravicini et al. 2020). 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 9 statistically significant specialized zoobenthivore trophic guilds, which alone is 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).

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 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 (Poore et al. 2012, Ling et al. 2015, Gutow et al. 2020). The high species redundancy of crustaceavores and molluscivores indicates resilience in the system for the top-down control on these invertebrate consumers. However, our results suggest a low redundancy of echinodermivores, which could be a vulnerability for the top-down control on herbivorous sea-urchins in the region. Although temperate western Australia has relatively low density of sea urchins by global standards, and barrens have not yet been reported (Fowler-Walker and 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 and 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 (Teagle et al. 2017, McHenry et al. 2021). The tropicalization of temperate communities due to climate change, where tropical herbivorous species are posed 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 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 to be 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 (Sandin et al. 2022). Thus, the ecological significance of top-predatory fish in temperate reefs is uncertain. Most evidence of trophic cascades involve 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 and 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 and 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 and 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 because native predators may not recognize novel herbivorous species as prey (HilleRisLambers et al. 2013).

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, zooplanktovivores, 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 weighted in-degrees, their proportion and frequency in fish diets. Similarly, the differences found between and within the rest of the invertebrate groups were significant. Noteworthy, polychaetes was 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 would 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 one acted as the central pillar of the trophic network, connecting crustaceans, benthic worms, and shelled molluscs 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's 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 decreases (Hamilton et al. 2011).

The present study sums-up trophic relationships at a biogeographical scale, covering an extensive length of coast (~1600 km) and a substantial number of fish species. However, the relative importance of prey groups for fish communities will vary across different spatial scales depending on the local community composition (Behrens and Lafferty 2012). A study focused on fish communities of temperate reefs along ~10km in Sweden also found that invertebrate prey groups are important regarding frequency in the diets of 15 fish species, but gastropods were found to have the highest frequency (37%), followed by amphipods (27%), copepods (21%), decapods (12.5%), bivalves (7%), fish (7%), and polychaetes (7%; (Stål et al. 2007). Likewise, a local study in southeastern Australia along ~16 km of coast found that zooplankton constituted most of the diet proportions (16.8%) of 66 species of fishes, with macroalgae and decapods accounting for 14.9% and 9.5% respectively (calculations based on supplementary material; (Truong et al. 2017). Moreover, our trophic analysis provides inferences for the importance of prey groups for the diversity of species only, and is likely that their importance would change considering other variables, 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).

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, our results may still not capture the real world trophodynamics given the uncertainties in prey identification and availability of diet information in space and time. 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 important 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.

However, 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%), suggesting that by sourcing diet information from other locations and congeneric species our estimations should be within an acceptable range (Soler et al. 2016). The methodology used to survey the fish community also could influence our results, since underwater visual censuses tend to capture less predatory species in comparison with stationary video methods (*i.e.* BRUVs and RUVs (Zarco-Perello and Enríquez 2019, Jessop et al. 2022). 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 high amount of sampling effort across space and time (*i.e* 4589 surveys), and all resident top-predators of the shallow temperate reefs of western Australia are very likely represented in our study. Nonetheless, interdisciplinary collaborations and applying new emerging technologies are further 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 fish individuals for life-history studies, genomic analyses and even parasitology studies (Cribb et al. 2021), which could well be used for trophic analyses but are regularly discarded. Moreover, increasing the use of DNA analysis for trophic ecology in reef ecosystems can revolutionize the identification of prey groups to species level, allowing accurate assessments of ecological functions (Carreon-Martinez and Heath 2010).

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 to previous characterizations, including tropical reefs which host a higher diversity of fish species. This higher trophic diversity in temperate reefs also means that our knowledge of functional diversity is likely also missing more pieces of the story than we have 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. Particularly, 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 seem to be strongly modulated by invertebrates, 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 understand their ecology and assure its conservation.

Acknowledgements

Special thanks to Paul Day, Neville Barrett, Graham Edgar, and anonymous volunteers for organizing and conducting the RLS-ATRC surveys in western Australia. Data from RLS and ATRC used to generate the species list for this study were sourced from Australia's Integrated

Marine Observing System (IMOS) – IMOS is enabled by the National Collaborative Research Infrastructure Strategy (NCRIS*).* Salvador Zarco-Perello gratefully acknowledges financial support for this research via the Fulbright Foreign Scholar Program, U.S. Department of State, Australian-American Fulbright Commission and the Kinghorn Foundation. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of the aforementioned sponsors.

Bibliography

Bastian, M., S. Heymann, and M. Jacomy. 2009. Gephi: an open source software for exploring and manipulating networks. Proceedings of the International AAAI Conference on Web and Social Media 3:361–362.

Behrens, M. D., and K. D. Lafferty. 2012. Geographic variation in the diet of opaleye (Girella nigricans) with respect to temperature and habitat. Plos One 7:e45901.

Bellwood, D. R., P. C. Wainwright, C. J. Fulton, and A. S. Hoey. 2006. Functional versatility supports coral reef biodiversity. Proceedings. Biological Sciences / the Royal Society 273:101–107.

Bennett, S., T. Wernberg, S. D. Connell, A. J. Hobday, C. R. Johnson, and E. S. Poloczanska. 2016. The “Great Southern Reef”: social, ecological and economic value of Australia’s neglected kelp forests. Marine and Freshwater Research 67:47.

Bennett, S., T. Wernberg, E. S. Harvey, J. Santana-Garcon, and B. J. Saunders. 2015. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. Ecology Letters 18:714–723.

Bestion, E., A. Soriano-Redondo, J. Cucherousset, S. Jacob, J. White, L. Zinger, L. Fourtune, L. Di Gesu, A. Teyssier, and J. Cote. 2019. Altered trophic interactions in warming climates: consequences for predator diet breadth and fitness. Proceedings. Biological Sciences / the Royal Society 286:20192227.

Bonaldo, R. M., A. S. Hoey, and D. R. Bellwood. 2014. The ecosystem roles of parrotfishes on tropical reefs. Pages 81–132 *in* R. N. Hughes, D. J. Hughes, and I. P. Smith, editors. Oceanography and marine biology: an annual review, volume 52. CRC Press.

Briones-Fourzán, P., and M. E. Hendrickx. 2022. Ecology and diversity of marine decapod crustaceans. Diversity 14:614.

Bulman, C., F. Althaus, X. He, N. J. Bax, and A. Williams. 2001. Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. Marine and Freshwater Research 52:537.

Burns, T. P. 1989. Lindeman’s contradiction and the trophic structure of ecosystems. Ecology 70:1355–1362.

Burrows, M. T., A. E. Bates, M. J. Costello, M. Edwards, G. J. Edgar, C. J. Fox, B. S. Halpern, J. G. Hiddink, M. L. Pinsky, R. D. Batt, J. García Molinos, B. L. Payne, D. S. Schoeman, R. D. Stuart-Smith, and E. S. Poloczanska. 2019. Ocean community warming responses explained by thermal affinities and temperature gradients. Nature Climate Change.

Carreon-Martinez, L., and D. D. Heath. 2010. Revolution in food web analysis and trophic ecology: diet analysis by DNA and stable isotope analysis. Molecular Ecology 19:25–27.

Chang, J., D. L. Rabosky, S. A. Smith, and M. E. Alfaro. 2019. An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. Methods in Ecology and Evolution.

Cortes, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science 56:707–717.

Cribb, T. H., S. B. Martin, P. E. Diaz, R. A. Bray, and S. C. Cutmore. 2021. Eight species of Lintonium Stunkard & Nigrelli, 1930 (Digenea: Fellodistomidae) in Australian tetraodontiform fishes. Systematic Parasitology 98:595–624.

Dearing, M. D. 1996. Disparate determinants of summer and winter diet selection of a generalist herbivore, Ochotona princeps. Oecologia 108:467–478.

Durant, J. M., J.-C. Molinero, G. Ottersen, G. Reygondeau, L. C. Stige, and Ø. Langangen. 2019. Contrasting effects of rising temperatures on trophic interactions in marine ecosystems. Scientific Reports 9:15213.

Edgar, G. J., R. D. Stuart-Smith, F. J. Heather, N. S. Barrett, E. Turak, H. Sweatman, M. J. Emslie, D. J. Brock, J. Hicks, B. French, S. C. Baker, S. A. Howe, A. Jordan, N. A. Knott, P. Mooney, A. T. Cooper, E. S. Oh, G. A. Soler, C. Mellin, S. D. Ling, J. C. Dunic, J. W. Turnbull, P. B. Day, M. F. Larkin, Y. Seroussi, J. Stuart-Smith, E. Clausius, T. R. Davis, J. Shields, D. Shields, O. J. Johnson, Y. H. Fuchs, L. Denis-Roy, T. Jones, and A. E. Bates. 2023. Continent-wide declines in shallow reef life over a decade of ocean warming. Nature 615:858–865.

Edgar, G. J., and R. D. Stuart-Smith. 2014. Systematic global assessment of reef fish communities by the Reef Life Survey program. Scientific data 1:140007.

Emmerson, M., T. Martijn Bezemer, MarkD. Hunter, T. Hefin Jones, GregoryJ. Masters, and N. M. Van Dam. 2004. How does global change affect the strength of trophic interactions? Basic and Applied Ecology 5:505–514.

Eskuche-Keith, P., S. L. Hill, P. Hollyman, M. L. Taylor, and E. J. O’Gorman. 2023. Trophic structuring of modularity alters energy flow through marine food webs. Frontiers in Marine Science 9.

Fowler-Walker, M. J., and S. D. Connell. 2002. Opposing states of subtidal habitat across temperate Australia: consistency and predictability in kelp canopy-benthic associations. Marine Ecology Progress Series 240:49–56.

Frid, A., and J. Marliave. 2010. Predatory fishes affect trophic cascades and apparent competition in temperate reefs. Biology Letters 6:533–536.

Froese, R., and D. Pauly. 2019. FishBase. http://www.fishbase.org.

Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2003. Effect of complexity on marine ecosystem models. Marine Ecology Progress Series 253:1–16.

Geary, W. L., M. Bode, T. S. Doherty, E. A. Fulton, D. G. Nimmo, A. I. T. Tulloch, V. J. D. Tulloch, and E. G. Ritchie. 2020. A guide to ecosystem models and their environmental applications. Nature Ecology & Evolution 4:1459–1471.

Grutter, A. S. 1997. Spatiotemporal Variation and Feeding Selectivity in the Diet of the Cleaner Fish Labroides dimidiatus. Copeia 1997:346.

Gutow, L., A. G. B. Poore, M. A. Díaz Poblete, V. Villalobos, and M. Thiel. 2020. Small burrowing amphipods cause major damage in a large kelp. Proceedings. Biological Sciences / the Royal Society 287:20200330.

Halpern, B. S., and S. R. Floeter. 2008. Functional diversity responses to changing species richness in reef fish communities. Marine Ecology Progress Series 364:147–156.

Hamilton, S. L., J. E. Caselle, C. A. Lantz, T. L. Egloff, E. Kondo, S. D. Newsome, K. Loke-Smith, D. J. Pondella, K. A. Young, and C. G. Lowe. 2011. Extensive geographic and ontogenetic variation characterizes the trophic ecology of a temperate reef fish on southern California (USA) rocky reefs. Marine ecology progress series 429:227–244.

Hamilton, S. L., and J. E. Caselle. 2015. Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. Proceedings. Biological Sciences / the Royal Society 282:20141817.

Hansson, L. J., O. Moeslund, T. Kiørboe, and H. U. Riisgård. 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). Marine Ecology Progress Series 304:117–131.

Heupel, M. R., Y. P. Papastamatiou, M. Espinoza, M. E. Green, and C. A. Simpfendorfer. 2019. Reef shark science – key questions and future directions. Frontiers in Marine Science 6.

HilleRisLambers, J., M. A. Harsch, A. K. Ettinger, K. R. Ford, and E. J. Theobald. 2013. How will biotic interactions influence climate change-induced range shifts? Annals of the New York Academy of Sciences 1297:112–125.

Honório, P. P. F., R. T. C. Ramos, and B. M. Feitoza. 2010. Composition and structure of reef fish communities in Paraíba State, north-eastern Brazil. Journal of Fish Biology 77:907–926.

Jessop, S. A., B. J. Saunders, J. S. Goetze, and E. S. Harvey. 2022. A comparison of underwater visual census, baited, diver operated and remotely operated stereo-video for sampling shallow water reef fishes. Estuarine, coastal and shelf science 276:108017.

Jones, G. P., and N. L. Andrew. 1990. Herbivory and patch dynamics on rocky reefs in temperate Australasia: The roles of fish and sea urchins. Austral ecology 15:505–520.

Kassambara, A. 2016. Factoextra: extract and visualize the results of multivariate data analyses. R package version.

Kramer, M. J., O. Bellwood, and D. R. Bellwood. 2013. The trophic importance of algal turfs for coral reef fishes: the crustacean link. Coral reefs (Online) 32:575–583.

Lenth, R. 2023. emmeans: Estimated Marginal Means, aka Least-Squares Means. Computer software, R.

Ling, S. D., R. E. Scheibling, A. Rassweiler, C. R. Johnson, N. Shears, S. D. Connell, A. K. Salomon, K. M. Norderhaug, A. Pérez-Matus, J. C. Hernández, S. Clemente, L. K. Blamey, B.

Hereu, E. Ballesteros, E. Sala, J. Garrabou, E. Cebrian, M. Zabala, D. Fujita, and L. E. Johnson. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 370:20130269.

López, D. N., P. A. Camus, N. Valdivia, and S. A. Estay. 2018. Food webs over time: evaluating structural differences and variability of degree distributions in food webs. Ecosphere 9:e02539.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2022. Cluster: Cluster Analysis Basics and Extensions. Computer software, R.

Martinez, A. P. 2017. _pairwiseAdonis: Pairwise Multilevel Comparison using Adonis_. Computer software, R.

McHenry, J., A. Rassweiler, G. Hernan, C. K. Uejio, S. Pau, A. K. Dubel, and S. E. Lester. 2021. Modelling the biodiversity enhancement value of seagrass beds. Diversity & Distributions.

Meekan, M. G., and J. H. Choat. 1997. Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. Marine Biology 128:373–383.

Mouillot, D., S. Villéger, V. Parravicini, M. Kulbicki, J. E. Arias-González, M. Bender, P. Chabanet, S. R. Floeter, A. Friedlander, L. Vigliola, and D. R. Bellwood. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proceedings of the National Academy of Sciences of the United States of America 111:13757–13762.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2022. Vegan: Community Ecology Package. Computer software, R.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Parravicini, V., J. M. Casey, N. M. D. Schiettekatte, S. J. Brandl, C. Pozas-Schacre, J. Carlot, G. J. Edgar, N. A. J. Graham, M. Harmelin-Vivien, M. Kulbicki, G. Strona, and R. D. Stuart-Smith. 2020. Delineating reef fish trophic guilds with global gut content data synthesis and phylogeny. PLoS Biology 18:e3000702.

Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I.-C. Chen, T. D. Clark, R. K. Colwell, F. Danielsen, B. Evengård, L. Falconi, S. Ferrier, S. Frusher, R. A. Garcia, R. B. Griffis, A. J. Hobday, C. Janion-Scheepers, M. A. Jarzyna, S. Jennings, J. Lenoir, H. I. Linnetved, V. Y. Martin, P. C. McCormack, J. McDonald, N. J. Mitchell, T. Mustonen, J. M. Pandolfi, N. Pettorelli, E. Popova, S. A. Robinson, B. R. Scheffers, J. D. Shaw, C. J. B. Sorte, J. M. Strugnell, J. M. Sunday, M.-N. Tuanmu, A. Vergés, C. Villanueva, T. Wernberg, E. Wapstra, and S. E. Williams. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 355.

Pineda-Munoz, S., and J. Alroy. 2014. Dietary characterization of terrestrial mammals. Proceedings. Biological Sciences / the Royal Society 281:20141173.

Pinnegar, J. K., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M. L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, G. D’Anna, and C. Pipitone. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental conservation 27:179–200.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson, and A. J. Richardson. 2013. Global imprint of climate change on marine life. Nature climate change 3:919–925.

Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E. E. Sotka, J. J. Stachowicz, R. B. Taylor, M. A. Vanderklift, and J. E. Duffy. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecology Letters 15:912–922.

Raymundo, L. J., A. R. Halford, A. P. Maypa, and A. M. Kerr. 2009. Functionally diverse reef-fish communities ameliorate coral disease. Proceedings of the National Academy of Sciences of the United States of America 106:17067–17070.

Ruppert, E. E., R. S. Fox, and R. D. Barnes. 2003. Invertebrate Zoology: A Functional Evolutionary Approach. Page 1008. Seventh edition. Cengage Learning, Belmont, CA.

R Core Team. 2022. R: A language and environment for statistical computing. Computer software, R Foundation for Statistical Computing, Vienna, Austria.

Saint-Béat, B., D. Baird, H. Asmus, R. Asmus, C. Bacher, S. R. Pacella, G. A. Johnson, V. David, A. F. Vézina, and N. Niquil. 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. Ecological Indicators 52:458–471.

Sanders, D., E. Thébault, R. Kehoe, and F. J. Frank van Veen. 2018. Trophic redundancy reduces vulnerability to extinction cascades. Proceedings of the National Academy of Sciences of the United States of America 115:2419–2424.

Sandin, S. A., B. J. French, and B. J. Zgliczynski. 2022. Emerging insights on effects of sharks and other top predators on coral reefs. Emerging topics in life sciences 6:57–65.

Shears, N., and R. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132:131–142.

Smith, J. E., C. L. Hunter, and C. M. Smith. 2010. The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507.

Soe, K. K., S. Pradit, and S. Hajisamae. 2021. Feeding habits and seasonal trophic guilds structuring fish community in the bay mouth region of a tropical estuarine habitat. Journal of Fish Biology 99:1430–1445.

Soler, G. A., G. J. Edgar, R. D. Stuart-Smith, A. D. M. Smith, and R. J. Thomson. 2016. Predicting the diet of coastal fishes at a continental scale based on taxonomy and body size. Journal of Experimental Marine Biology and Ecology 480:1–7.

Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. A. X. Finlayson, B. S. Halpern, M. A. Jorge, A. L. Lombana, S. A. Lourie, K. D. Martin, E. Mcmanus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. Bioscience 57:573.

Stål, J., L. Pihl, and H. Wennhage. 2007. Food utilisation by coastal fish assemblages in rocky and soft bottoms on the Swedish west coast: Inference for identification of essential fish habitats. Estuarine, coastal and shelf science 71:593–607.

Steneck, R. S., D. R. Bellwood, and M. E. Hay. 2017. Herbivory in the marine realm. Current Biology 27:R484–R489.

Teagle, H., S. J. Hawkins, P. J. Moore, and D. A. Smale. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. Journal of Experimental Marine Biology and Ecology 492:81–98.

Truong, L., I. M. Suthers, D. O. Cruz, and J. A. Smith. 2017. Plankton supports the majority of fish biomass on temperate rocky reefs. Marine Biology 164:73.

Vergés, A., P. D. Steinberg, M. E. Hay, A. G. B. Poore, A. H. Campbell, E. Ballesteros, K. L. Heck, D. J. Booth, M. A. Coleman, D. A. Feary, W. Figueira, T. Langlois, E. M. Marzinelli, T. Mizerek, P. J. Mumby, Y. Nakamura, M. Roughan, E. van Sebille, A. S. Gupta, D. A. Smale, F. Tomas, T. Wernberg, and S. K. Wilson. 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proceedings. Biological Sciences / the Royal Society 281:20140846.

Viviani, J., C. Moritz, V. Parravicini, D. Lecchini, G. Siu, R. Galzin, and L. Viriot. 2019. Synchrony patterns reveal different degrees of trophic guild vulnerability after disturbances in a coral reef fish community. Diversity & Distributions.

Wernberg, T., G. A. Kendrick, and J. C. Phillips. 2003. Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. Diversity and Distributions 9:427–441.

Yeager, L. A., M. C. M. Deith, J. M. McPherson, I. D. Williams, and J. K. Baum. 2017. Scale dependence of environmental controls on the functional diversity of coral reef fish communities. Global Ecology and Biogeography 26:1177–1189.

Yorke, C. E., H. M. Page, and R. J. Miller. 2019. Sea urchins mediate the availability of kelp detritus to benthic consumers. Proceedings. Biological Sciences / the Royal Society 286:20190846.

Zarco-Perello, S., and S. Enríquez. 2019. Remote underwater video reveals higher fish diversity and abundance in seagrass meadows, and habitat differences in trophic interactions. Scientific Reports 9:6596.

Zarco-Perello, S., T. J. Langlois, T. Holmes, M. A. Vanderklift, and T. Wernberg. 2019. Overwintering tropical herbivores accelerate detritus production on temperate reefs. Proceedings. Biological Sciences / the Royal Society 286:20192046.

Zarco-Perello, S., T. Wernberg, T. J. Langlois, and M. A. Vanderklift. 2017. Tropicalization strengthens consumer pressure on habitat-forming seaweeds. Scientific Reports 7:820.

Zarco-Perello, S., G. Carroll, M. Vanderklift, T. Holmes, T. J. Langlois, and T. Wernberg. 2020. Range-extending tropical herbivores increase diversity, intensity and extent of herbivory functions in temperate marine ecosystems. Functional Ecology.