Trophodynamics in Coral Reefs: Current Knowledge and Research Perspectives

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Abstract

Coral reef trophodynamics is extremely complex and still poorly understood, while investigated for decades. Recent advances on organic matter sources, fluxes, trophic niches of species, and spatiotemporal variations of food webs are first summarized. Then, tools used in trophodynamics research are briefly documented, from traditional pioneer methods of stomach content analysis to more recent biochemical methods (stable isotopes, fatty acids, biochemical composition, metabolomics, DNA metabarcoding, etc.) and modeling approaches. Eventually, future challenges and perspectives are presented addressing the diverse scenarios of coral reef trophic functioning response in front of the ongoing changes in global and local stressors.

Keywords

Trophic relationships · Biochemical tracers · Stable isotopes · DNA metabarcoding · Modeling

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1.1 Context of Trophic Ecology in Coral Reefs

Coral reefs are characterized by poorly resolved innumerable and nonrandom linkages across an intricate network of ecological interactions (Jordano 2016). Accounting for such complexity is critical to define energetic pathways and, ultimately, ecosystem functioning, productivity, and mechanisms behind the maintenance of biodiversity (Tilman et al. 2014). Indeed, a food web perspective may emerge as the most appropriate for verifying and assessing the integrated effects of multiple pressures on natural ecosystems, as internal food web mechanisms can buffer or even reverse the effects exerted at the population or species scale (Gray et al. 2014). Many aspects of the trophodynamic processes have already been investigated in coral reefs over the last decennies and are summarized below (Fig. 1.1).

1.1.1 Main Questionings in the Trophic Studies

1.1.1.1 Major Organic Matter Resources and Fluxes

Understanding the mechanisms that maintain ecosystem productivity requires a definition of the major sources of nutrients and energy that fuel the entire coral reef ecosystem (Letourneur et al. 2013; Robinson et al. 2024). The characterization of these energy flows is still complicated due to a high diversity of organic matter (OM) sources available to primary consumers in these systems. Coral reef food webs rely both on an allochthonous oceanic production supported by phytoplankton and on autochthonous benthic primary producers, that is, coral symbionts, macroalgae, algal turf, microphytobenthos, crustose coralline algae, and seagrasses (Dromard et al. 2013; Briand et al. 2015, 2016; Fey et al. 2020). Moreover, both benthic and pelagic potential food sources, plus the inputs from the terrestrial realm, may be important indirect contributors to the OM pools, that is,

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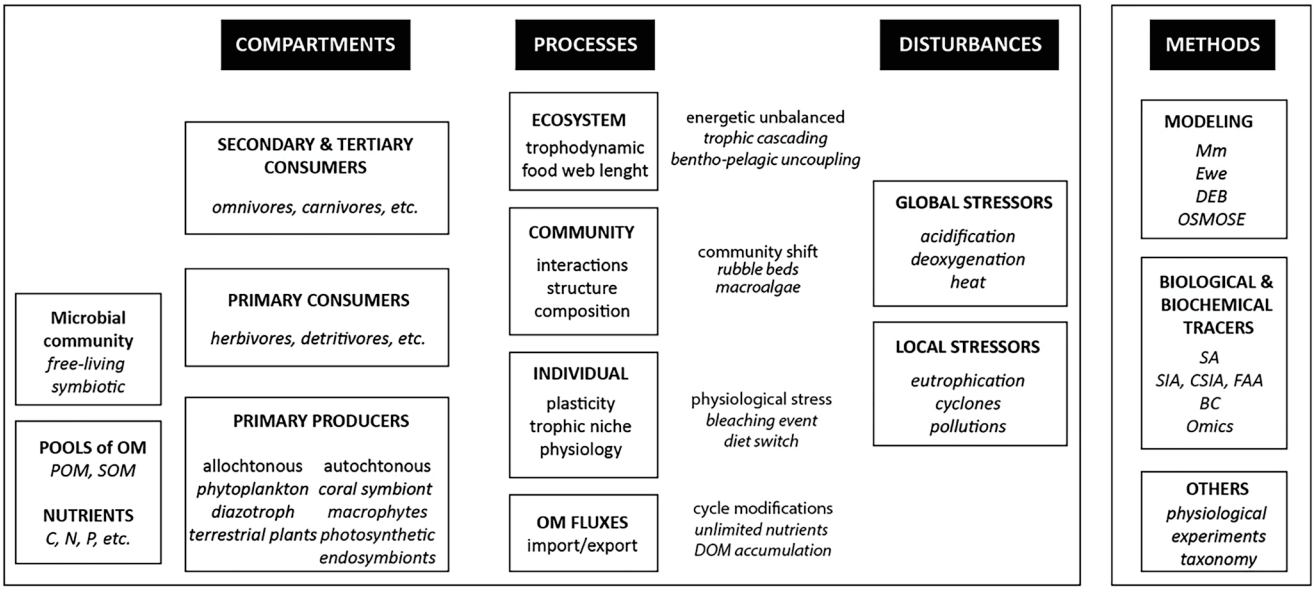

Fig. 1.1 Summary scheme of the main compartments, processes, disturbances, and methods (abbreviations in the text) involved in trophodynamics research for the last decades and in the future

detritus, particulate, and sedimentary OM (Crossman et al. 2001; Wyatt et al. 2013).

The rapid recycling of OM is a characteristic of coral reef functioning, sustaining high productivity in relatively oligotrophic environments. The roles of different organisms and pathways having a key influence on nutrient biogeochemistry and fluxes were thus pointed out. For example, sponges are both filter feeders and hosts to abundant symbiont communities, and have a major role in the transfer of dissolved organic matter (DOM) to higher trophic levels in the benthos, for example, sponge-associated and free-living detritivores (Rix et al. 2017). Several species recycle carbon by directly assimilating dissolved organic carbon (DOC) into biomass (McMurray et al. 2016) or converting DOC exudates released by corals and algae into bioavailable particulate organic carbon (POC) and cellular detritus through the sponge loop pathway (De Goeij et al. 2013). In addition, sponges are important sink and/or sources of dissolved inorganic nitrogen, phosphate, and silicate through their metabolism and the inextricable activity of their associated microbial communities (Pawlik and McMurray 2020). Indeed, microorganisms also efficiently recycle the dissolved organic matter (DOM) released by sponges and other primary producers through the microbial loop (Haas et al. 2013; Silveira et al. 2017). Recent studies even highlighted the significant impact of DOM components like metabolites (e.g., tryptophan, phenylalanine, caffeine) produced by sponges on the success of microbial communities and organisms associated with microbial symbionts (Fiore et al. 2017). Finally, planktonic diazotrophs fix and reduce atmospheric N_2 and release part of this nitrogen into bioavailable ammonium (NH_4^+) in seawater. Abundant in coral lagoon waters, these prokaryotes are providing sufficient nitrogen stocks for the development of the planktonic food web in oligotrophic waters (Bonnet et al. 2016).

By consuming these sources, primary consumers are initiating tranfers of OM into the food webs. Their food preferences are therefore decisive and can be explained by several factors; for instance, mature forms of macroalgae are more or less consumed by herbivores according to their palatability, that being a function of the algal morphology (e.g., soft or calcareous), physiological strategies (e.g., synthesis of repellent molecules), and nutritional quality (Dromard et al. 2017 and included references). All other trophic network interactions also lead to important fluxes of energy, and many studies reinforce the evidence of a tight bentho-pelagic coupling that might become an increasingly important characteristic in future coral reefs (Fey et al. 2020; Skinner et al. 2021).

1.1.1.2 Trophic Niche and Plasticity of Species

It remains difficult to clearly capture dynamic energetic processes on coral reefs (Harmelin-Vivien 2002; Briand et al. 2016), and understanding species' roles and interactions requires an accurate assessment of their trophic status and niche. Thus, the trophic position is an important concept typically used to calculate food chain length, degree of omnivory or compound bioaccumulation into food webs (Post 2002). The trophic niche, issued from the ecological niche theory applied to feeding processes, is also largely employed; its size and specialization result from complex interactions between biological traits and local constraints,

generating difficulties to disentangle the respective effects of each characteristic (Futuyma and Moreno 1988). This balance between different traits and characteristics may lead to different responses and thus influence feeding plasticity in response to changes of resource availability (Letourneur et al. 2017). Therefore, it is critical and urgent to better assess how and through what mechanisms species or functional groups can adapt and cope with changing environmental conditions.

Identifying interspecific diet and niches specializations is critical (Cybulski et al. 2022 and included references). For instance, the diverse range of feeding behaviors and adaptive morphologies employed by invertivores on coral reefs is a clear indication of the widely underestimated role of cryptofauna in the reef trophodynamics (Glynn et al. 2011). However, it has been challenging to delineate such complex behaviors and interactions, and a paucity of empirical information often leads to inconsistent definitions of trophic guilds based on expert opinions (Parravicini et al. 2020). Dietary variation of individuals within species is also widespread (Wyatt et al. 2019), so characterizing intraspecializations within a larger population is essential for delineating a species' trophic niche. Besides, reef organisms may change their resource use with ontogeny (Cummings et al. 2010), and alter their resource use according to what is available by plasticity process (Fey et al. 2021a).

1.1.1.3 Spatial and Temporal Variations of Food Webs

Due to changes in environmental conditions and in the structure of benthic and pelagic primary producers, OM resources fluctuate within and between reefs (Johnson et al. 1995). In one hand, variations along spatial scales have shown influence of numerous environmental factors, such as the distance from the coast and the terrestrial or oceanic exposure, or the connectivity between adjacent habitats (Briand et al. 2015). On the other hand, short- as long-term temporal changes have been less investigated, and, for example, few data were recorded about the effects of nycthemeral variations on reef communities (de Lira et al. 2014). As a result, relevancy of isotopic spatiotemporal comparisons is limited unless isotopic baselines are standardized between sampling periods or locations (Tamelander et al. 2009), and therefore understanding such variations associated with trophic structure is often complicated.

1.1.2 Tools Used in Trophodynamic Research

1.1.2.1 Traditional Methods

From the 1950s, in parallel to direct observation of foraging, stomach analysis (SA) is one of the first and the most applied methods for qualitative and quantitative evaluation of consumers' diet (Hyslop 1980). It concerns the analysis of food items in all portions of the digestive tract (mostly the stomach), through (1) a sampling step using nonlethal (i.e., regurgitation) or, most often, lethal methods (i.e., extraction of the digestive tract), and (2) an identification step requiring visual and/or DNA-based techniques (Da Silveira et al. 2020 and included references). SA provides punctual information on ingested food (not assimilated one), at individual to community levels, revealing intra- and interspecific relationships strong enough to schemed coherent trophic functioning (Harmelin-Vivien 1981). However, SA also goes with high sampling costs and laborious laboratory work, which is reliant on potential degradation and/or fragmentation of samples, implying a possible nonidentification of the food item, and does not allow the determination of the origins of consumed inorganic matter.

1.1.2.2 Biochemical Tracers

From the 1980s, biochemical tracers were used to reveal detailed and integrated diet information, with accuracy and high resolution (Nielsen et al. 2018). The synthesis of body tissues is related to the chemical elements present in consumed foods, so both should be isotopically related. Stable isotope analysis (SIA) of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) has then emerged as a powerful method for revealing "time-integrated assimilated food" information and for giving insight into their trophic ecology. Specifically, there is a historically accepted change in bulk isotopic ratio values at each trophic level (i.e., ~1‰ for $\delta^{13}C$ and ~ 3‰ for $\delta^{15}N$; Post 2002, McCutchan Jr et al. 2003), widely used to estimate the basal sources of carbon and nitrogen in a particular food chain, prey composition, and trophic position (Michener and Kaufman 2007). Such assumptions may have led to biased results in the past, as since values of trophic fractionation factors have been largely reevaluated (Letourneur et al. 2024); they are generally higher between primary producers and herbivores than between consumers of medium to high levels, and vary substantially among species (Wyatt et al. 2010). Thanks to improvements in analytical techniques, plus given the much larger range of variation in resource sulfur signatures and the low consumer-diet shift (McCutchan Jr et al. 2003), the $\delta^{34}S$ ratio is increasingly being used as a third tracer to disentangle sources and trophic level identification in food webs (Skinner et al. 2022). Despite many assets, the SIA tool needs to rely on isotopically distinct food sources for accurate interpretations, a condition that is often not observed in the field (Da Silveira et al. 2020).

After that, a refinement of the SIA method called compound-specific isotope analysis (CSIA) has been successfully applied in trophic research. While SIA evaluates the "bulk" isotopic concentration of a given biological sample, CSIA evaluates isotopic signatures of specific individual

macronutrients such as amino acids and lipids (e.g., $\delta^{15}N$ of glutamic acid or phenylalanine, $\delta^{13}C$ of fatty acids; Twining et al. 2020). The conservative and predictable assimilation patterns obtained in consumers allow for a more accurate identification of the food source (McMahon et al. 2016), and provide specific information on both the assimilated baseline and the length of food chains (Fey et al. 2021a).

Fatty acids analysis (FAA) is also a conservative method providing integrated qualitative information regarding the diet of consumers in short- and long-term approaches (Iverson et al. 2004; Iverson 2009). FAs are carbon-rich compounds that are ubiquitous and greatly diversified in most organisms (25–70 unique molecules). Although some are biosynthesized de novo by specific organisms at the base of the food chain (e.g., bacteria, diatoms, macroalgae, vascular plants), most FAs are acquired through diet and are poorly metabolized by the consumers (Dalsgaard et al. 2003). Owing to their predictable assimilation patterns and their multivariate profiles, these lipid biomarkers are useful tool to distinguish potential dietary items at a low identification level (Iverson et al. 2004). Data on the presence, amount, and ratios of different FAs can also be used to infer food consumption and energetic mobilizations along the consumers' life cycles (Dalsgaard et al. 2003; Fey et al. 2021a). As CSIA, the FAA is an expensive and time-consuming method, and profiles can change dramatically due to environmental conditions (e.g., temperature, light, nutrients; Da Silveira et al. 2020).

At last, the analysis of the biochemical composition (BC) of the OM as the sum of lipids, proteins, and soluble carbohydrates concentrations has been used to provide information on the energetic value of food material potentially available to consumers (Krogdahl et al. 2005).

The rise of omics approaches in recent years provides molecular-level insights into food relationships and biogeochemical cycling. High-resolution *metabolomics* techniques were used to probe the composition of OM (e.g., DOM) including metabolites relevant to the growth of many organisms (Fiore et al. 2017; Wegley Kelly et al. 2022). Untargeted or discovery-based analysis allows for a semiquantitative profile-view of low-molecular-weight molecules within a sample, while the targeted analysis provides a quantitative comparison of a small subset of metabolites (Patti et al. 2012; Kido Soule et al. 2015). DNA metabarcoding (DNAm) methods can capture individual-level dietary variations, improving trophodynamic assessments, but they are limited to the gut contents of the animal at the time of sampling (Casey et al. 2019).

Each method has its own objectives, sampling and analysis procedures, data resolution, spatial and temporal coverage, results interpretation, and limitations. The combination of these approaches, including stomach content analysis, surpasses most of these limitations and is therefore greatly recommended (Da Silveira et al. 2020; Robinson et al. 2024). A joint perspective that can be applied to different ecological levels (population, community, and ecosystem), providing valuable diet information on intra- (e.g., ontogenetic, reproductive, migration) and interspecific relationships, clarifying the origin of food resources explored, spatial-temporal patterns, and trophic-web structuration (Matley et al. 2018).

1.1.2.3 Modeling Approaches

Biochemical methods are not able to estimate the amounts of consumed foods without modeling (Iverson et al. 2004). Consequently, in the last 20 years, several analytical methods called "Bayesian models" have been proposed to convert stable isotope data into robust derived metrics. Mixing models (MM) allow (i) the estimation of the relative contribution of isotopically different OM sources in a mixture and the reconstruction of animal diets from isotopic ratios and/or multiple chemical tracers (e.g., *"SIAR"*, then "SIMMR" and "MIXSIAR" models in R; Stock et al. 2018), (ii) the calculation of consumer trophic position at the population level (*"tRophicPosition"* in R; Quezada-Romegialli et al. 2018), (iii) the measurements of the isotopic niche space of populations and communities ["SIBER" model in R; Jackson et al. 2011, or also MCPs (minimum convex polygon); Fey et al. 2021b], and (iv) the evaluation of entire food webs ("IsoWeb" model; Kayoda et al. 2012). Needless to say, that outputs must be carefully interpreted, in the light of strengths and weaknesses of each model, and that current stomach-content analysis and in situ direct observations should guide model inputs (Twining et al. 2020).

Trophic ecology also provides basic information for structuring complex ecotrophic models. *ECOPATH* has been developed to estimate mean annual biomass, production, and consumption for components of an ecosystem (Polovina 1984). The software and techniques have been improved to include methods of comparing ecosystems using Ecological Network Analysis (Christensen and Pauly 1992), to model dynamic changes using *ECOSIM* (Walters et al. 1997), to model spatial changes using *ECOSPACE* (Walters et al. 1999), and to model dynamics using the spatial-temporal framework and the habitat foraging capacity model (Christensen et al. 2014). Is born out a combined *Ecopath with Ecosim (EwE)* software package, widely applied for modeling marine ecosystems and able to address many of the questions asked by managers on marine policy issues (Christensen and Walters 2004). For example, *ECOTRACER* included in EwE simulate and analyze the transport of contaminants through coral reefs (e.g., methylmercury or radiocesium, Walters and Christensen 2018). However, still to date, easy access with limited quality control contributes to the low utilization of EwE models for management applications.

Other models less used in coral environment are nevertheless of interest. Models of energetics called dynamic energy budget or "DEB" claims to provide a comprehensive description of the metabolic organization and rates underlying the physiological functions of an organism throughout its life cycle in a fluctuating environment (Kooijman 2010). The predator-prey model *OSMOSE* is a two-dimensional, individual-based, and multispecies model explicitly representing major processes in the life cycle of high trophic level (HTL) groups of fish and invertebrate species (Grüss et al. 2015). Such models have already been useful to predict the effects of global change, and better understand trophic dynamics, environmental stressors effects, species geographical patterns, bio-production optimization, or management of exploited resources (Lesser 2013).

1.2 Future Challenges and Prospectives

Pristine areas are no more (Pandolfi et al. 2003), and even under best-case emissions trajectories, coral reefs will likely continue to be transformed by the global anthropogenic climate change (Hoey et al. 2016) and face escalating local human threats which cause severe destruction (i.e., coastal development, overfishing, pollution, and eutrophication; Zaneveld et al. 2016). Due to the complexity of coral reef ecology plus local and regional differences, understanding and identifying effective research and management practices to address corals' present and future fate is therefore challenging (Wilkins et al. 2021). In particular, among the coral regions studied by the French research community, the Caribbean and the French Polynesia should be prioritized for inclusion in international conservation programs (Guan et al. 2020). Therefore, multiple scientific challenges, economic progress, as well as a surge in technological innovations will be of importance for the future of coral reefs. We have chosen to focus on several critical scenarios here, for which trophic research might provide answers and solutions (Fig. 1.1).

1.2.1 Scientific Key Lever for Future Researches

1.2.1.1 Changes in OM Fluxes

The pool of nutrients can be altered by several drivers of natural and anthropogenic origin (D'Angelo and Wiedenmann 2014), and changes in OM fluxes are a crucial problematic, not only to assess food web functioning and the resilience of coral reefs, but also to anticipate unexpected cascading effects and undesirable ecological surprises. In the context of climate change, marine heat waves are becoming more intense and frequent (Hughes et al. 2018), and water acidification is increasing energy requirements of calcifying organisms, in particular scleractinian corals. As well, anthropogenic nutrient enrichment in reef waters, mostly of nitrogen and phosphorus compounds, induces direct and indirect negative effects on coral physiological performances and ecosystem functioning (D'Angelo and Wiedenmann 2014). Because of the combined effect of heat, CO_2, and nutrient stress, coral reefs are experiencing increasingly frequent and devastating bleaching events (Hughes et al. 2017).

The global warming disrupts the key symbiosis interaction between corals and their endosymbiotic dinoflagellates and therefore decreases coral nitrogen acquisition capacity (Godinot et al. 2011). Thus, the ability of coral reefs to cope with future ocean conditions will depend on their capacity to fulfil their metabolic requirements (Meunier et al. 2021). More physiological studies on coral nutrition are therefore crucial to understand the feeding strategies of these polytrophic and opportunistic feeders faced with future life conditions, that is, via capture of plankton and organic particles by polyps and/or via translocation of photosynthetic products from their endosymbiotic algae (Duprey et al. 2016). An interesting track to resist and recover from stressing episodes is the store of energy reserves and/or the switch from an autotrophic to a heterotrophic diet. Selective feeding on picoplankton-sized unicellular cyanobacteria (*Synechococcus* spp.) and prochlorophytes (*Prochlorococcus* sp.) is a significant rich food N-input, and benefit from increasing feeding rates on zooplankton has been less studied (Meunier et al. 2021). Besides, both the activity and geographical distribution of diazotrophs, for example, *Trischodesmium* spp., will likely increase with future rising sea surface temperature (Ani et al. 2023). They could be an increasingly external alternative nutrient source for bleached corals (Meunier et al. 2019), reducing calcification sensitivity to heat stress and high pCO_2 conditions by a surplus of bioavailable N (Meunier et al. 2022). Such increasing atmospheric N_2 inputs into planktonic trophic webs may have positive consequences on the functioning of coral reefs. Thus, reef systems characterized by high planktonic diazotroph dynamic fluctuations in terms of abundance, community composition, and activity could be more resistant to climate change, as already observed in different regions, i.e. New Caledonia, Papua New Guinea, the Australian Great Barrier Reef, Hawaii, the Caribbean Sea, and the Red Sea (Luo et al. 2012; Bonnet et al. 2017). With corals decline, OM fluxes could also be disturbed by other organisms implicated into nutrient cycles. For instance, certain sponges may increase in abundance and in some cases, become functionally dominant on coral reefs (Bell et al. 2018). However, sponges are also negatively affected under future climate change scenarios with impacts on their symbionts and higher mortality rates (Fan et al. 2013). A thermal stress coupled with extreme acidification and deoxygenation may cause metabolic shifts and disturb nutrient cycling, by

inducing a reduction or a break in the loop pathway and therefore in the particulate and detritus production, and by reducing photosynthetic functioning of associated photosymbionts (Maggioni et al. 2023).

Ongoing climate changes may also have an important effect by modifying the exchanges of OM at the interface between ocean and land (Liénart et al. 2018). For instance, higher rainfalls due to more recurrent and intense cyclonic events (Kossin 2018) might generate an increase of terrigenous river runoffs and sediment resuspension (Devlin et al. 2001). Even considerably distant from reefs, increase in dissolved nutrient level might have secondary direct combined effects that need to be furthered. Indeed, in conditions of sporadic events, nutrients are rapidly used by primary producers to fuel planktonic and benthic food webs (Delesalle et al. 1993). But in case of too recurrent events and nutrient excess, induced phytoplankton blooms and subsequent post-bloom changes produce increases of decomposing OM, bacterial load, and altered oxygen levels (D'Angelo and Wiedenmann 2014), which could ripple through the entire food web. The escalating risk of common mechanisms resulting from such an unbalanced ecosystem and subsequent consequences is then likely the overgrowth by successive, conspicuous blooms of benthic macroalgae (Harmelin-Vivien 1994), the prevalence and severity of coral diseases (Voss and Richardson 2006), but also the outbreaks of coral eaters and bioeroders. Top-down control processes can reduce the impact of negative indirect effects of elevated nutrient levels for example, but involve abundant and diversified assemblages of reef consumers, as grazers of benthic algae, detritivores, or predators of corallivores (Hoey and Bellwood 2009).

In other words, several scientific levers are still largely unknown under future scenarios and are of high priority for next trophic investigations. Among them, consequences of quantitative and qualitative changes of the planktonic communities on the entire reef system, impacts of modifications in organism physiology and community ecology on the quality and quantity of OM fluxes within reefs, results on the pelagic-benthic coupling or food web dynamics across both fine and broad spatial and temporal scales. Besides, trophic ecology might help in knowledge-based optimization of management of multiple combined stress that becomes crucial for coral reef conservation (Brodie et al. 2012). As eutrophication driven by nitrogen (and other nutrients) is a major management challenge in many coastal settings (Bonsdorff 2021), quantifying the nitrogen contributed by diazotroph such as *Trichodesmium* spp. is a fundamental knowledge gap to fulfill. A supply of planktonic diazotrophs on the reefs could be included among innovative management approaches to improve the resilience of coral reefs with high conservation potential, during and after bleaching episodes (Hoey et al. 2016). Management strategies should aim for sustaining top-down control processes as well as reducing the nutrient influx in seawater, and future assessment will also strongly involve the optimal utilization of water quality bioindicators (Fabricius et al. 2012).

1.2.1.2 Becoming of Reef Communities

Trophic interactions underpin many of the processes that drive coral reef community structure and the key ecological services these ecosystems provide (Brandl et al. 2019). Many marine food webs are shaped by a small number of strong species interactions that have large effects on a community, that is, involving keystone and foundation species, plus species nested among many weaker interactions (Paine 1992). Consequently, trophic cascades tend to be particularly strong in marine systems (Shurin et al. 2002). When these impactful species interactions are altered by environmental conditions, they may act as ecological leverage points in the community that can magnify the effects of environmental change, for example, shifts in competitive dominance, intensification of predation/herbivory, increases in the frequency and severity of disease/parasite outbreaks, and disruption of facilitation/mutualism (Kroeker and Sanford 2022). Thus, ongoing fluctuations in ocean temperature, dissolved oxygen, and pH can impact community members differently, leading to shifts in the strength and outcome of species interactions and community dynamics. Indeed, environmental changes are translated into community changes via multiple organismal physiologies, that is, different physiological optima and environmental tolerances of species (Somero et al. 2017). In order to improve our ability to predict the emergent effects of ocean change, and allow marine scientists and managers to anticipate which ecosystems are especially vulnerable, trophic ecology can help a further exploration of leverage points in marine communities by way of a continued integration of physiology and ecology (Kroeker and Sanford 2022).

To cope with increased energetic demands imposed by ocean warming, deoxygenation, and ocean acidification, heterotrophs may, for instance, reallocate energy and/or increase rates of consumption; both responses can have substantial consequences for species interactions, including altering growth rates and competitive outcomes, and changing the intensity of herbivory or predation (Kroeker and Sanford 2022). Future research should therefore explore the presence of potential sublethal effects of habitat degradation on higher-order consumers, such as lower nutritional condition (Hempson et al. 2018). A given resource-consumer interaction might also vary with environmental changes (Gaylord et al. 2019). Thus, understanding how a species' dietary niche width relates to its functional role within an ecosystem is critical, given that increasing complexity of species interactions may serve to mitigate the effect of biodiversity loss on ecosystem function in future scenarios (Bregman et al.

2015). Indeed, omnivores play an important role in dampening potential trophic cascades (Bruno and O'Connor 2005) and would be expected to have a greater potential of short-term adaptive response to changes in habitat degradation, whereas specialist species would be more vulnerable (Letourneur et al. 2017). However, species-level analyses may, therefore, mask individual differences in dietary variation and limit the ability to identify more complex energy flows and trophodynamics within a specific study area or differences in species' ecological roles. So, determining the degree of trophic plasticity within species will help understand how they may cope with environmental change (Cybulski et al. 2022). The more deeply the trophic structure of the communities will be identified, the best the consequences of reef modifications on food chain characteristics, stability, and resilience will be understood.

Local and global pressures are leading to substantial benthic alterations in coral reefs (De'ath et al. 2012). For example, the primary impacts of ocean acidification include reductions in structural complexity, skeleton density and coral recruitment, as well as increases in bioeroders (Fabricius et al. 2017). Current habitat degradation and extensive coral mortality suggest that shifts to algal- and/or rubble-dominated states may be more prevalent in a future coral reefs system (Wolff et al. 2018). Habitat degradation is thought to be a major driver of trophic structure of ecosystems (Álvarez-Filip et al. 2013), and, for example, the generation of rubble beds can have lasting effects on structural habitat complexity, species interactions, food webs, and reef communities (Wolfe et al. 2021 and references therein). Though considered as seemingly barren, featureless habitats, rubble beds actually form complex microhabitats that can host a great density and diversity of predominantly cryptic life (Enochs and Manzello 2012); a suite of taxa from microbes and biofilms, sessile and encrusting organisms, motile cryptofauna, and cryptobenthic or juvenile fishes. Despite their rising prevalence in the coral reef benthos, less is known about the biology and ecology of rubble beds, and empirical data on direct transfers of biomass and energy from the cryptobenthos to higher-order fishes are scarce (Wolfe et al. 2020). Yet, these data are required to more holistically parameterize and predict how bottom-up processes may enhance the system productivity as reefs degrade. Besides, rubble generation sustaining or even enhancing a cryptic biodiversity initially depends on framework production by corals (Wolfe et al. 2021). Thus, the potential benefits of reef erosion on rubble-dwelling taxa and ecological functioning may be impaired over time, as the production of corals—and by extension potential for rubble generation—declines (Enochs and Manzello 2012). All these key ecological points require greater attention with the integration of more uniform and standardized trophic approaches to define and characterize degraded habitats and their associated community to improve the ability to monitor, predict, and manage these ecosystems into the future (Wolfe et al. 2021).

1.2.2 Next Steps in Means and Actions

1.2.2.1 Method Enhancements and Innovative Techniques

In the field of biochemical tracer (SIA, CSIA, FA, etc.), generating more data across a wider range of sources to get suitable baselines is a future priority. Also, lowering costs and increasing laboratory availability are necessary to combine approaches and answer macroevolutionary questions (Twining et al. 2020 and included references). By default, marine food web studies should employ a tri-isotope approach at least, this way additional examples of three-dimensional SIBER that explore cross-guild relationships should come out (Cybulski et al. 2022). However, more research into the effect of tissue lipid levels on $S^{34}S$ is sorely needed. Also, 70% of coral reef food web SIA studies focus solely on a single tissue type, mostly muscles (Skinner et al. 2022); although measuring stable isotope ratios across multiple consumer tissues can provide important information about the temporal dynamics of resource use, other tissues like liver or gonads are still less often utilized. Also, studies are beginning to perform SIA on fish eye lenses allowing reconstruction of an individual's trophic and habitat histories (Bell-Tilcock et al. 2021). Finally, hydrogen isotope (^2H) values have demonstrated a typically larger isotopic separation between diet sources and consumers than the more traditional C and N isotopes (e.g., 40‰ vs. 2‰ between aquatic and terrestrial plants), because of the greater relative mass differences associated with such a light isotope (Macko et al. 1983). Ecological research on stable hydrogen isotope ratios (δ^2H or δD) of fatty acids is still in its infancy, so future studies need to address basic questions (Twining et al. 2020), including the spatiotemporal variability of different sources, the trophic discrimination from one trophic level to the next, and the analytical limitations. Also, must be taken into account changes in hydrogen isotopes of environmental waters that can consequently affect δ^2H values in consumers, including the compound-specific level.

Robust application of the different biomarkers faces the same difficulties, with a lack of information concerning trophic discrimination and most studies limited to qualitative applications. For example, with the FA, researchers have only superficial acknowledgment of the uncertainty associated with the trophic transfer and storage in consumers of these bioactive molecules with diverse structures and functions (Iverson 2009), and these biotracers are rarely used to determine predator–prey interactions which form the basis of ecosystem models (Galloway and Budge 2020 and

included references). Yet, when genetic analyses are paired with empirical feeding studies, it is possible to link demonstrated synthesis of particular molecules, including fatty acids, with upregulation of specific genes (Kabeya et al. 2018). So, accounting for lipid trophic modification in consumers through project-specific feeding trials or by measurement and estimation of general dietary "calibration coefficients' is critical for fatty acid biomarker applications, especially quantitative ones (Jardine et al. 2020). Besides, despite a dazzling contribution in recent years, even omics methods cannot fully resolve the complex nature of some sources, for example, DOM, particularly the labile fraction within the low-molecular-weight component (i.e., metabolites; Wegley Kelly et al. 2022). It is likely due to both the limited representation of marine metabolites in current libraries and data quality that is compromised by sample complexity. Furthermore, measuring ecologically relevant changes in the concentrations of specific compounds often exceeds instrument precision (Fiore et al. 2017). Therefore, progress in both hardware advances of high-resolution tandem mass spectrometers and computational tools are still needed to semiquantitatively detect and characterize rare and diverse compounds (e.g., Petras et al. 2017; Ernst et al. 2019; Nothias et al. 2020).

As well, several cutting-edge methods are not yet widely used in ecological studies, but hold the potential to address some of the limitations of current isotopic techniques. Then, intramolecular isotope pattern studies are emerging as another promising tool to contribute to the development of new techniques using CSIA to study trophic ecology. Within a molecule's isotopic "fine structure," isotopomers are similar in isotopic composition but differ in the position of isotopes within the molecule and are preferentially used to investigate consumers' metabolic pathways by revealing enzyme activities and the nature of reordering reactions (Wiechert et al. 2013). Isotopologues, as molecules that differ in their isotope composition and profiles, offer more information on carbon fluxes and dietary routing of metabolites (Postle and Hunt 2009). However, although they offer finer-scale resolutions than CSIA for either $\delta^{13}C$ or $\delta^{2}H$, isotopomer and isotopologue labeling studies have yet to be applied in studies of marine trophic ecology (Twining et al. 2020).

1.2.2.2 Beyond the Prism of Trophic Ecology

The use of biochemical tracers requires bridging three distinct fields, that is, ecology, physiology, and chemistry. One fundamental limitation in the field at this point is that the experts may not understand the nuances of the other disciplines, therefore the path forward will involve interdisciplinary collaboration (Galloway and Budge 2020; Robinson et al. 2024). Indeed, there is the need to break traditional barriers across disciplines (e.g., biochemistry, microbiology, and ecology) and subdisciplines (e.g., limnology, ornithology, and soil ecology) in order to better understand trophic interactions and metabolism at the scale of whole food webs. Also, the need to cross new methodological frontiers, such as routinely combining empirical ecophysiological studies with food web analyses, to achieve deeper insight in how dietary tracers move through consumers, within food webs and across complex ecosystems (Twining et al. 2020). Thus, determining many physiological process and drivers of consumer trophic ecology represents an area ripe for further investigation (e.g., ingestion vs. excretion, thermal regulation, metabolic rates). Besides, despite a decline in interest in this discipline, taxonomy is still essential, and will be even more in future, to acknowledge and characterize ongoing massive changing in community composition. New feeding experimental works on the uptake and transfer in individual organisms are also required for the development and refinement of biomarker models that can accurately estimate animal diets, and to advance the field and make meaningful use of these tools at the scale of populations or ecosystems (Galloway and Budge 2020). Developments in modeling will definitely require acquisition of more and recent data, the use of multimodel approaches, and could rapidly evolve shortly thanks to progress in the mathematics of algorithms and the contributions of artificial intelligence (Xu et al. 2021).

Trophic ecology can offer improvements and solutions to problems that hamper coral restoration, and empirically testing methods of incorporating trophic interactions in restoration designs to assess their costs, effectiveness, and utility under different scenarios is an important priority (Ladd and Shantz 2020). Yet, despite rapidly growing interest, only 15% of restoration publications considered trophic interactions, highlighting a clear mismatch between the fundamental role of trophic ecology on coral reefs and its consideration in restoration efforts. So, the dire future of the planet's coral reefs will require the best working scientific collaborations to resolve the problems mentioned above.

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