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Heterotrophy in marine animal forests in an era of climate change

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ABSTRACT

Marine animal forests (MAFs) are benthic ecosystems characterised by biogenic three-dimensional structures formed by suspension feeders such as corals, gorgonians, sponges and bivalves. They comprise highly diversified communities among the most productive in the world's oceans. However, MAFs are in decline due to global and local stressors that threaten the survival and growth of their foundational species and associated biodiversity. Innovative and scalable interventions are needed to address the degradation of MAFs and increase their resilience under global change. Surprisingly, few studies have considered trophic interactions and heterotrophic feeding of MAF suspension feeders as an integral component of MAF conservation. Yet, trophic interactions are important for nutrient cycling, energy flow within the food web, biodiversity, carbon sequestration, and MAF stability. This comprehensive review describes trophic interactions at all levels of ecological organisation in tropical, temperate, and cold-water MAFs. It examines the strengths and weaknesses of available tools for estimating the heterotrophic capacities of the foundational species in MAFs. It then discusses the threats that climate

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change poses to heterotrophic processes. Finally, it presents strategies for improving trophic interactions and heterotrophy, which can help to maintain the health and resilience of MAFs.

Key words: benthic suspension feeders, filter-feeders, trophic interactions, ecosystem interactions, ocean warming, Anthropocene, restoration, conservation.

CONTENTS

I. INTRODUCTION

Heterotrophy refers to the process of obtaining energy and nutrients from organic material produced by other organisms. It contrasts with autotrophy, which is the primary production of organic material from inorganic nutrients, using light energy (photosynthesis) or chemical energy (chemosynthesis) (Sigman & Hain, 2012). Mixotrophic organisms are capable of using both sources of nutrients because the animal harbours photosynthetic/chemosynthetic microorganisms (Selosse, Charpin & Not, 2017). They can be primarily autotrophic, supplementing their diet with phagotrophy or uptake of dissolved organic matter (DOM); but they can also be primarily heterotrophic, capturing prey and particulate organic matter (POM).

The biomasses of autotrophic and heterotrophic organisms are differentially distributed in terrestrial and marine environments (Bar-On, Phillips & Milo, 2018). While primary producers are a major contributor to living biomass in terrestrial ecosystems, they make up only a small fraction of the living marine biomass (less than 1 GT of 6 GT), which is largely composed of heterotrophic species (Bar-On *et al*., 2018). This is due to the exponential decline in the availability of light in the deep oceans. Heterotrophic species are critical to maintaining the health and productivity of marine ecosystems and play a crucial role in the transfer of energy and nutrients through food webs (Ladd & Shantz, 2020). Benthic suspension and filter feeders, such as sponges, anthozoans, and bivalves (e.g. clams and oysters), are particularly efficient heterotrophs. These organisms take up DOM and capture particles by filtering water through their bodies or using specialised structures, such as tentacles and mucus nets. Particle capture by suspension feeders has been described as a low-energy-cost and highly efficient feeding mechanism (Gili & Coma, 1998).

In benthic communities where suspension feeders dominate and form three-dimensional structures, they provide refuges, food sources, as well as reproductive and nursery habitats for many other organisms. Such communities are referred to as marine animal forests (MAFs) (Orejas *et al*., 2022). MAFs are widespread ecosystems on Earth, occurring from the tropics to the poles and from the shallows to the deep sea. They include diverse communities, such as mussel beds, tropical and cold-water coral reefs, black coral and gorgonian gardens, and sponge grounds (Rossi *et al*., 2017). These underwater ecosystems, sometimes older than terrestrial forests, provide valuable ecosystem services and are essential to millions of people worldwide (Costanza *et al*., 2014; Rossi & Rizzo, 2020).

As macroalgal forests, MAFs are now facing an unprecedented loss of biodiversity and structure due to global and local stressors that threaten their foundational species (Souter *et al*., 2021; OSPAR, 2023; Verdura *et al*., 2023). In addition to affecting the health of MAF builders directly, ongoing climate change is rapidly reducing the availability of nutrient sources for these organisms (Rossi *et al*., 2017) and is acting synergistically with other anthropogenic stressors to alter MAF distribution, diversity, and functional capacity. Innovative and scalable interventions are needed to address the degradation of MAFs and increase their resilience under global change. Surprisingly, few studies have considered trophic interactions and the heterotrophic capacity of MAF builders as an integral component for MAF conservation. Yet trophic interactions are important for nutrient cycling, energy flow within the food web, increased biodiversity, carbon sequestration, and MAF stability. Therefore, it is important to understand the direct and indirect pathways in which heterotrophy is relevant for MAF conservation and restoration.

In this review, we discuss advances in our understanding of the importance of trophic and specifically heterotrophic processes for the growth and health of MAF builders. We provide an overview of the growing array of techniques used to assess heterotrophy across levels of ecological organisation, as well as their respective strengths and limitations. We highlight key research areas that require immediate attention from the scientific community, as well as knowledge gaps that urgently need to be addressed. In addition, we emphasise the need to incorporate trophic interactions and heterotrophy into the conservation framework for MAFs and highlight the potential of this approach alongside other existing solutions and the mitigation of climate change.

II. NUTRITIONAL STRATEGIES OF MAF BUILDERS

Food availability is a critical parameter affecting the distribution, composition, and productivity of MAFs (Portilho-Ramos *et al*., 2022). To cope with nutrient-poor oligotrophic environments, MAF builders have evolved a variety of nutritional strategies, ranging from heterotrophy to almost complete autotrophy, depending on the contribution of symbiotic partners in mixotrophic organisms (Rossi *et al*., 2019; Radice *et al*., 2022). Mixotrophy, common in shallow warm-water MAFs, is a particularly successful strategy because it expands the metabolic portfolio of animals (O'Malley, 2015). Coral reefs that thrive in tropical and subtropical well-lit environments are among the best-known MAFs built by mixotrophic organisms. Symbiotic corals, the main reef builders, form a holobiont (i.e. a metaorganism composed of the animal host, and prokaryotic and eukaryotic microorganisms, such as photosynthetic dinoflagellates from the family Symbiodiniaceae) (Voolstra *et al*., 2021). Symbiodiniaceae use sunlight to convert inorganic carbon and other dissolved inorganic nutrients into organic matter through photosynthesis and transfer most of the photosynthates to their host for its nutritional needs (Muscatine, 1980). In addition, the coral host captures particulate food with its tentacles and mucus web (Houlbrèque & Ferrier-Pagès, 2009), while other symbiotic microbes, such as diazotrophic bacteria, supplement the energy resources of the holobiont by fixing dinitrogen (Bednarz *et al*., 2021).

Under non-stressful conditions, shallow tropical scleractinian corals are typically considered to be more autotrophic than heterotrophic, whereas the opposite is assumed for deeper (mesophotic) corals (Frankowiak *et al*., 2016). However, several studies show high rates of heterotrophy in shallow waters, highlighting the heterotrophic nature of many corals (Grottoli, Rodrigues & Palardy, 2006; Martinez *et al*., 2020; Price *et al*., 2021). Other coral groups, such as mixotrophic tropical gorgonians, may have a higher proportion of heterotrophic inputs (Ribes, Coma & Gili, 1998) and outcompete scleractinians in certain reefs (Schubert, Brown & Rossi, 2017). In addition, heterotrophy can be an important means of acquiring food for symbiotic corals that experience bleaching (loss of symbiotic algae) as a result of stress (Grottoli *et al*., 2006; Levas *et al*., 2016) or for facultative symbiotic corals, which can alter the balance between auto- and heterotrophy to meet the variable demands of a changing environment (Trumbauer, Grace & Rodrigues, 2021). Other shallow MAF builders, such as bivalves (e.g. giant clams), are also symbiotic mixotrophs and follow similar feeding strategies as symbiotic corals (Mills *et al*., 2023). Finally, sponges dominate reef diversity and biomass in some areas, and are increasingly recognised as key MAF engineers that efficiently capture, retain, and transfer energy and nutrients within the reef (Richter *et al*., 2001; de Goeij *et al*., 2008). The sponge microbiome (photosynthetic cyanobacteria, and chemosynthetic and other bacteria) is involved in autotrophic and/or heterotrophic nutrient acquisition, sulphur cycling, and essential vitamin biosynthesis (Engelberts *et al*., 2020). Mixotrophy is a common strategy for sponges, but the contribution of autotrophy and heterotrophy to their carbon input has rarely been quantified (Hudspith *et al*., 2022). Nonetheless, most sponges are primarily net heterotrophs, as DOM has been documented to account for up to 97% of sponge diet in various MAFs from shallow to deep water (Morganti *et al*., 2017; Bart *et al*., 2021).

Heterotrophy is also the predominant trophic mode in temperate, mesophotic and cold-water MAFs (Fig. 1). The total area covered by these MAFs remains vague, but may equal or exceed that of tropical shallow reefs (Freiwald *et al*., 2004). Chemosynthetic bacteria expand the diet of sponges, deep-sea corals, and unique extremophile heterotrophs that thrive primarily in the deep sea near hydrocarbon seeps or hydrothermal vents (Cavanaugh, 1994). Typically, these MAFs are locally abundant when the food supply is sufficiently high and stable over long periods of time to support continuous production. A recent meta-analysis,

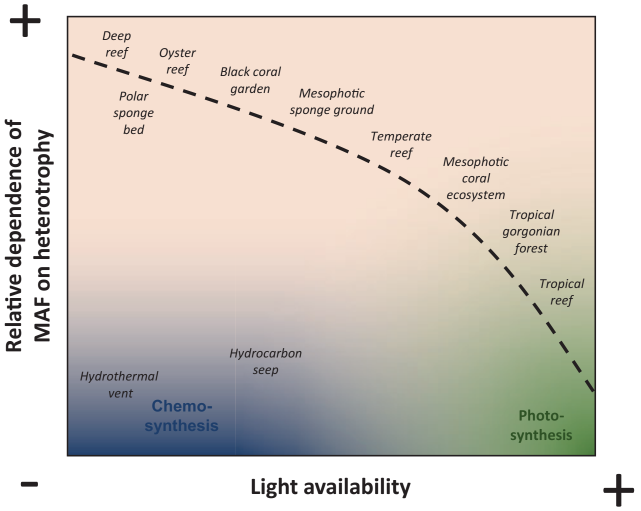


Fig. 1. Schematic representation of the relative dependence of examples of marine animal forest (MAF) communities on heterotrophy in response to light availability. Light (i.e. photosynthetically active radiation) varies along bathymetric and latitudinal gradients, as well as with sedimentation rate. The contribution of photosynthesis to MAF organisms (green shading) is higher only in environments with abundant light. Chemosynthesis (blue shading) is ubiquitous in deep-sea MAFs thriving around hydrothermal vents and hydrocarbon seeps.

involving six case studies of cold-water coral reefs in the North Atlantic and the Mediterranean Sea, found that food supply exerted the strongest influence on coral growth over the past 20,000 years (Portilho-Ramos *et al*., 2022). Processes that provide food or stimulate food production for deep-sea MAFs include high primary productivity in shallow waters, vertical migration of zooplankton, vertical and horizontal (down-slope) transport of particles by currents, vertical mixing through internal waves, and recycling of nutrients (Maier *et al*., 2023).

Overall, heterotrophy plays a critical role in the functioning of MAFs at all levels of ecological organisation. However, our knowledge of MAF heterotrophy is incomplete, ranging from observations at the level of individuals and populations, to theoretical models that encompass entire communities and ecosystems. Furthermore, the lack of information on the quality and quantity of available food makes it difficult to assess MAF responses to anthropogenic impacts at both local and global scales (Rossi *et al*., 2019). MAF builders, which are ectothermic animals, have a greater need for heterotrophic food at high temperatures to support their increased metabolic rates (Hoegh-Guldberg *et al*., 2014). Additionally, mixotrophic organisms affected by bleaching may require a heterotrophic diet to compensate for dysfunctional symbioses (Grottoli *et al*., 2006; Hughes & Grottoli, 2013; Tremblay *et al*., 2016). At the same time, all trophic processes in MAFs, including heterotrophy, will be affected by climate change. Recent models have estimated that by the year 2100, there will be global declines in marine primary production (Kwiatkowski *et al*., 2017), trophic transfer efficiency (Du Pontavice *et al*., 2020), zooplankton abundance (Wang *et al*., 2018), and downward particle flux, the latter affecting deep MAFs (Sweetman *et al*., 2017; Bindoff *et al*., 2019). Therefore, to assess how climate change may alter MAFs, it is necessary to evaluate not only the direct effects on the physiology of heterotrophic individuals, but also the indirect effects on species due to changes in primary and secondary producers, and their trophic interactions. Here, we focus on how heterotrophic processes affect the health and growth of MAFs and how promoting trophic interactions and heterotrophy could contribute to the conservation and restoration of MAFs.

III. HETEROTROPHY IN MAFs AMONG DIFFERENT ENVIRONMENTAL CONDITIONS AND LEVELS OF ECOLOGICAL ORGANISATION

Heterotrophic processes are closely linked to the diversity of MAFs and contribute to their resilience to environmental perturbations at all levels of ecological organisation (Fig. 2).

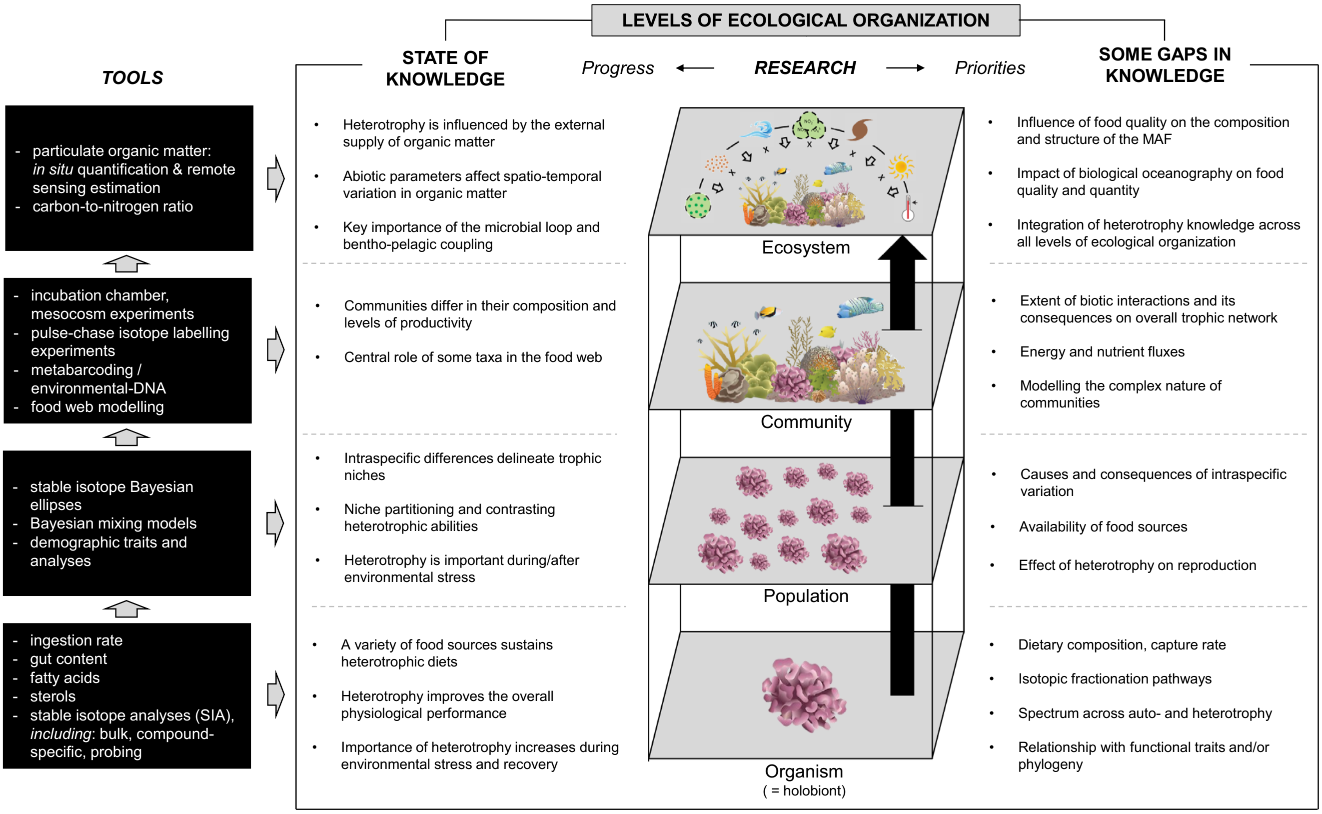


Fig. 2. State of knowledge and some gaps in knowledge on heterotrophy at different levels of ecological organisation. Knowledge gaps highlight research priorities. The tools used to achieve our current state of knowledge at the different levels of the organisation are provided on the left. MAF, marine animal forest.

At the organism level (i.e. individuals), knowledge of heterotrophic processes includes studies at the molecular, cellular, and whole organism scales (e.g. Levy *et al*., 2016; Maier *et al*., 2020; Rossi & Rizzo, 2021). Variation in the capture of size-selected particles among taxa allows for the emergence of a wide variety of feeding strategies among actively predatory and suspension-feeding (including filter-feeding) organisms (Gili & Coma, 1998). In addition, uptake of DOM has been shown to be a common strategy among MAF holobionts (Levas *et al*., 2016; Ribes *et al*., 2023). Insights into the role of heterotrophy in maintaining metabolic rates under non-stressful and stressful conditions have been gained mainly through laboratory experiments, with the exception of a few *in situ* studies (e.g. Grottoli *et al*., 2006; Mies *et al*., 2018; Rix *et al*., 2020). In most deep-water MAF builders, starvation depletes energy reserves and leads to the collapse of all physiological functions within a few weeks (Naumann *et al*., 2011; Larsson, Lundälv & van Oevelen, 2013). In mixotrophic organisms, numerous studies have shown that heterotrophy is an important source of nitrogen and phosphorus (Ribes *et al*., 1998, 2003), and improves the physiological performance of these organisms under different environmental conditions (e.g. Klumpp, Bayne & Hawkins, 1992; Rodrigues & Grottoli, 2006; Towle, Enochs & Langdon, 2015; Bedgood, Mastroni & Bracken, 2020), especially when symbiotic associations are facultative (Aichelman *et al*., 2016). In particular, sustained reliance on heterotrophic diets may represent an adaptive strategy to climatic stressors (Hughes & Grottoli, 2013; Meunier *et al*., 2022), alongside other strategies such as farming and feeding on their autotrophic symbionts (Wiedenmann *et al*., 2023). However, although the former strategy appears to benefit a variety of mixotrophic taxa, it may not be sufficient for all species under stressful conditions (Grottoli *et al*., 2006; Massaro *et al*., 2012). Finally, heterotrophy may also be important for larval survival and early development in some species, with the quality and quantity of food consumed by parental colonies influencing larval viability and, consequently, overall reproductive success (Viladrich, Linares & Padilla-Gamiño, 2022*b*).

At the population level (i.e. group of individuals of the same species, living in a given area), mesophotic and cold-water MAFs have limited nutritional plasticity, relying mainly on heterotrophy and/or chemotrophy (Wienberg & Titschack, 2017). By contrast, shallow populations of mixotrophic species display a wide range of feeding strategies, positioned along a gradient from heterotrophy to autotrophy, with significant differences even among individuals in the same environment (Fox *et al*., 2019). Thus, dependence on heterotrophy varies greatly among and within species (Hoogenboom *et al*., 2015; Fox *et al*., 2019; Price *et al*., 2021), and trophic flexibility becomes an important feature in the evolution of populations, especially during and after stressful situations (Rodrigues, Grottoli & Pease, 2008). For instance, the growth of octocorals tends to be favoured in seston-rich environments (Schubert *et al*., 2017) because they generally have a greater ability to shift towards an almost exclusively heterotrophic diet compared to scleractinian corals (Pupier *et al*., 2021). Elsewhere, sponges that feed on DOM and small particles are very efficient competitors compared to other MAF organisms with narrower trophic niches (Bell *et al*., 2018*a*).

At the community level (i.e. populations of different species living and interacting in a given area), a complex network of interactions among species includes several pathways promoting heterotrophy through direct and indirect transfer of nutrients. Sponges are one of the critical trophic links in MAF communities as they capture allochthonous picoplankton and convert them in their waste products to inorganic nutrients, which fuels reef production (Richter *et al*., 2001). They also take up large amounts of DOM and convert it into sponge biomass and particulate detritus, which are available to higher trophic level organisms through the sponge loop (de Goeij *et al*., 2013). The remaining DOM is remineralised into inorganic nutrients and incorporated into the food web *via* the microbial loop (Azam *et al*., 1983). In addition, sponges contain microbial symbionts in their tissue that are important for nutrient recycling, and trophic niche separation can occur between sponge species with different microbial abundances (Morganti *et al*., 2017). Thus, sponges not only represent local nutrient hotspots, but also mediate a complex array of nutrient transformations that ultimately benefit the entire community. Planktivorous fishes further increase benthic productivity and heterotrophy by excreting or egesting nutrients (Meyer, Schultz & Helfman, 1983). Finally, the effects of horizontal and vertical animal migration (e.g. sea turtles, fish, zooplankton), or seabird excretion on the overall food web could be locally significant in shallow or even mesophotic waters depending on the topography, but are still largely overlooked (Yahel, Yahel & Genin, 2005; Becker, Brainard & Van Houtan, 2019; Thibault *et al*., 2022).

At the ecosystem level, which is an interacting system between the biological community in a given area and its abiotic environment, allochthonous nutrient inputs (river and submarine groundwater discharges, lateral nutrient fluxes, deposition of aerial desert dust, etc.) and oceanographic conditions (downward or upward currents, eddies, internal waves, etc.) can also influence MAF heterotrophy (e.g. Soetaert *et al*., 2016; Silbiger, Donahue & Lubarsky, 2020; Lønborg *et al*., 2021) and add another layer of complexity (e.g. Wyatt *et al*., 2013; Lønborg *et al*., 2021). For example, coral reefs, mangroves, and seagrasses coexist in the tropics and all three habitats participate in biogeochemical and trophic exchanges, and recycle POM (Carlson *et al*., 2021; Maier *et al*., 2021). A mature MAF (i.e. with a high density of benthic suspension feeders and high structural complexity) can alter flow rates to retain particles and support heterotrophy in the MAF (Rossi *et al*., 2017). By contrast, an immature MAF (i.e. low density of suspension feeders and low structural complexity) provides a smaller surface area for nutrient-supplying flows and tends to retain far fewer particles (Nelson & Bramanti, 2020). Particle retention is especially important for MAFs that depend on pulses of allochthonous nutrients transferred from pelagic to benthic habitats (Campanyà-Llovet, Snelgrove & Parrish, 2017; Rossi & Rizzo, 2021). Finally, nutrient cycling within the ecosystem depends on abiotic factors such as light and temperature, and varies depending on the geographic location and depth of the MAF. For example, rates of nutrient recycling by microbes and phytoplankton growth are both faster in tropical MAFs than in cold-water MAFs (Morán *et al.*, 2020) and tropical MAFs are characteried by smaller plankton cells and lower biomasses (Morán *et al.*, 2020). Altogether, energy flow in MAF ecosystems is far more complex and variable than formerly thought.

Anthropogenic disturbances, such as water pollution, eutrophication, wastewater discharge, fishing, and climate change, can rapidly disrupt the trophic interactions in communities and ecosystems (Harris, 2020). For example, coral bleaching alters the production and composition of coral mucus, which in turn has cascading effects on the nutrient cycles driven by microbes and sponges (Vanwonterghem & Webster, 2020). Macroalgal or turf algae overgrowth of corals induces biogeochemical changes through large amounts of DOC release and enhancement of the heterotrophic microbial processes (Manikandan *et al.*, 2021). An increase in sponges at the expense of coral abundance due to seawater warming (Bell *et al.*, 2018*b*) results in a shift in the benthic community from primarily photoautotrophic to heterotrophic organisms, with unknown impacts at higher trophic levels (Bell *et al.*, 2018*b*). Changes in trophic interactions following anthropogenic disturbance in cold-water MAF communities have not been as well studied as in tropical shallow MAFs. However, cold-water reefs rely on nutrient recycling mediated by sponges and bivalves, which could be directly affected by global-change stressors (Maier *et al.*, 2020). In addition, as local currents, water column stratification, nutrient cycling, and primary production will be affected under global change, concentrations of allochthonous nutrients delivered to MAF communities are expected to decrease (Sweetman *et al.*, 2017; Bindoff *et al.*, 2019). This will significantly alter the structural and functional characteristics of MAF communities, ultimately affecting large-scale ecosystem processes such as nutrient cycling and carbon storage (Lesser & Slattery, 2020; Bax *et al.*, 2022). Thus, greater consideration of trophic interactions at all levels of MAF ecological organisation is important to assess the full extent of anthropogenic disturbances to these ecosystems.

IV. TOOLS TO ASSESS HETEROTROPHY IN MAFs

At the organism and population level, specific sterols and fatty acids are acquired through the diet and can be reliable indicators of heterotrophy in MAF species such as scleractinian corals, bivalves, and sponges (Mies *et al.*, 2018; Radice *et al.*, 2019; Carreón-Palau *et al.*, 2021; Pupier *et al.*, 2021). Some fatty acids [such as iso- and anteiso-fatty acids (BrFAs)], synthesised exclusively by bacteria, are a useful tool to understand the ecological function of symbiotic bacteria (Fey *et al.*, 2021). Analysis of sterols may allow different food regimes to be distinguished because zooplankton contains large quantities of cholesterol, while algae mainly contain phytosterols (Treignier *et al.*, 2008). Food sources can also be identified by direct observation of the stomach contents of corals, clams or bivalves (Ribes *et al.*, 1998; Dame & Kenneth, 2011; Goldberg, 2018), by monitoring the uptake of specific food particles or DOM in incubation chambers (Ribes, Coma & Gili, 1999; Ribes *et al.*, 2003; Dame & Kenneth, 2011; Levas *et al.*, 2016; Godefroy *et al.*, 2019), or by comparing the composition of organic matter in inhaled *versus* exhaled water (InEx method) in sponges, bivalves and tunicates (Morganti *et al.*, 2016). Taxonomic molecular barcoding (DNA markers) provides another tool for identifying the prey species ingested by predators (Leal *et al.*, 2013). However, for deep-sea MAF builders, the above techniques can often only be applied after they have been brought to the surface, which can bias the results.

Stable isotopes can be used as indicators of heterotrophy at both the organism and population levels. Although not very extensively used, stable sulphur isotope ratio (δ^{34}S) values are good indicators of the contribution of food derived from terrigenous organic matter, which has low δ^{34}S (~0‰) values (Yamanaka *et al.*, 2013). Measurements of stable carbon and nitrogen isotope ratios (δ^{13}C, δ^{15}N) in 'bulk' animal tissue (the consumer) and in potential food sources help to assess diet, trophic position, and also food origin (Duineveld *et al.*, 2012; Gori *et al.*, 2012). The carbon isotope ratio (δ^{13}C) can be used to identify the carbon source of the consumer as values show limited variation after trophic transfer, while the nitrogen isotope ratio (δ^{15}N) identifies the trophic position of the consumer as enrichment is progressive across trophic levels (Kolasinski *et al.*, 2016). In mixotrophic organisms, such as tropical corals, the percentage of heterotrophic contribution to the diet can also be qualitatively assessed by calculating the difference in carbon or nitrogen isotope values of the host and endosymbionts (e.g. Muscatine & Kaplan, 1994; Price *et al.*, 2021). However, interpretation of bulk tissue isotope values can sometimes be compromised by overlapping values between predators and potential food items and/or by the difficulty of sampling all possible food items. To address this issue, compound-specific isotope analyses (CSIA) of fatty acids and amino acids have been successfully used in deep and shallow MAFs to investigate their food sources and to reveal variations in the heterotrophic contribution among conspecific organisms (Gori *et al.*, 2018; Fox *et al.*, 2019; Martinez *et al.*, 2022). The basic principle of CSIA is that some fatty acids and/or amino acids (AAs) are routed directly from the diet into the animal tissue, hence they remain unchanged, while others are biochemically transformed during assimilation. For instance, the CSIA-AA technique has been used to study heterotrophy in sponges, revealing that the abundance and type of microbes can influence the sponge's ability to feed on specific food sources (Hanz *et al.*, 2022). This has been observed in other foundational species, where heterotrophy is linked to the

Symbiodiniaceae genotype (Leal *et al.*, 2015). CSIA has also proved to be a powerful and promising tool for understanding trophic plasticity in mixotrophic organisms (Wall *et al.*, 2021), but a good knowledge of the fractionation pathways in holobionts and food sources under contrasting environmental conditions is still required (Ferrier-Pagès *et al.*, 2021). To improve our knowledge of fractionation pathways, feeding experiments may be run in laboratory conditions with a controlled food source and isotopic measurements performed before and after feeding trials (Rangel *et al.*, 2019). Finally, the stable isotope pulse–chase technique, using a diet enriched in the heavier, naturally rare stable isotope, can be used to track the fate of the food within an organism or the exchange of heterotrophic nutrients between the host and its partners and within MAF communities (Hughes *et al.*, 2010; Rix *et al.*, 2020; Maier *et al.*, 2021). Combining this technique with nanoscale secondary ion mass spectrometry (NanoSIMS) allows imaging of the heavier isotopes in the tissues (Krueger *et al.*, 2018).

In mixotrophic animals, the stable isotope values of the host and symbionts can be further analysed by applying Bayesian frameworks, such as the stable isotope Bayesian ellipses in R (SIBER; Jackson *et al.*, 2011), to identify the dominant trophic strategies of a given population or niche variability among sympatric species and among and within populations (Conti-Jerpe *et al.*, 2020; Price *et al.*, 2021; Sturaro *et al.*, 2021; Thibault, Lorrain & Houlbrèque, 2021). In addition to SIBER, nicheROVER (Lysy, Stasko & Swanson, 2021) provides a suite of metrics to characterise niche ranges and overlap among MAF residents (Swanson *et al.*, 2015). δ^{13}C and δ^{15}N values (both in bulk and compound-specific) of food sources and predators can be also combined in hierarchical Bayesian modelling mixing models (such as MixSIAR; Stock *et al.*, 2018) to determine the proportional contribution of each heterotrophic food source into the animal's tissues (e.g. Price *et al.*, 2021). At the community level, several approaches are used to understand trophic structure and heterotrophy. Environmental metabarcoding and/or other DNA approaches are increasingly recognised as effective tools to complement species richness surveys, to identify prey availability, and to uncover unknown trophic interactions (Casey *et al.*, 2019). Flume experiments show that high structural complexity increases bottom friction with increasing water velocity, and intensifies plankton uptake (Ribes & Atkinson, 2007) and growth (Corbera *et al.*, 2022) of MAF communities. Field channels are employed to monitor community metabolism and characterise heterotrophic zones (Rogers, 1979). Incubation chambers and mesocosms are used, in conjunction with isotope pulse–chase experiments, to characterise carbon flow in ecosystems (Hughes *et al.*, 2010; Maier *et al.*, 2021). More recently, a multi-tracer assessment of organic matter pathways, combining fatty acids, bulk and compound-specific stable isotope analysis, and stable isotope mixing models, was used to delineate ecosystem functioning in tropical MAFs (Fey *et al.*, 2021). Finally, heterotrophy can be explored by identifying relevant variables and building integrative models to estimate total carbon and nitrogen fluxes (Ehrnsten *et al.*, 2020).

V. KNOWLEDGE GAPS

Although heterotrophy is recognised as an important process, much remains unknown at the different levels of ecological organisation. When studying heterotrophy at the organism level, researchers often encounter difficulties in accessing samples or ensuring that field conditions are accurately represented in experiments (Wang *et al.*, 2022). In addition, feeding in MAF organisms has only been studied in a limited number of species and locations, suggesting that the effects of environmental conditions and organism genotype on food acquisition still need to be studied in more detail. In symbiotic associations, we still know relatively little about which partner benefits from the heterotrophic diet or which diet is best for that partner (Tremblay *et al.*, 2015). For instance, metals contained in plankton ingested by the coral host are absorbed by algal symbionts for photosynthesis (Ferrier-Pagès, Sauzéat & Balter, 2018). Similarly, studies applying CSIA-AA to nitrogen cycling in symbiotic corals have demonstrated that essential amino acids present in plankton prey are utilised by the algal symbionts instead of the host, although algae can synthesise essential amino acids (Martinez *et al.*, 2022). Therefore, further research is needed before isotope-based inferences of heterotrophy can be made (e.g. Price *et al.*, 2021) or to understand fully the fractionation pathways of carbon and nitrogen in symbiotic associations. Finally, despite the major role that bacteria can play in providing vitamins or essential trace elements to their hosts, their contribution to their host's diet has been poorly investigated.

At the ecosystem level, our understanding of how energy fluxes in MAF food webs will change in response to future climate is still uncertain. Our current knowledge of the abundance and composition of food sources, and how they change over time and space, is limited and simplified for most MAFs (de Froe *et al.*, 2022; Portilho-Ramos *et al.*, 2022). This is in part due to the high spatial and temporal variability of the physical and biological factors in MAFs, which restricts our understanding of the key processes regulating ecosystem trophodynamics (Bierwagen *et al.*, 2018). In particular, diurnal, tidal, lunar, and seasonal variations are important drivers in zooplankton and organic matter food source concentrations (Palardy, Grottoli & Matthews, 2006) and can cause significant temporal variability of trophic processes across spatial scales (Rossi & Rizzo, 2021). To address trophodynamics in such complex ecosystems, food web metrics (such as those based on stable isotope analysis) should be presented and discussed in a systematic, mechanistic, and hypothesis-driven framework (Pethybridge *et al.*, 2018; Alp & Cucherousset, 2022) allowing a greater focus on ecosystem processes (Streit & Bellwood, 2022). Furthermore, relatively few long-term observational data on food source concentrations are available (e.g. Eriksen *et al.*, 2019), and these data sets are often limited to easily accessible shallow MAFs, while deep MAFs are poorly sampled and less understood (Morais, Medeiros & Santos, 2018). Food quality and its importance for the life cycles and survival of MAF populations under rapidly changing conditions remains unclear (Rossi *et al.*, 2019). To develop reliable models describing changes in MAF composition, it is critical to know (*i*) how food quality and availability are changing; and (*ii*) how these changes affect the overall energy budget of benthic suspension and detrital feeders, particularly in deep waters where the size and dimensions of reefs can affect particle-retention properties (Rossi *et al.*, 2017; Corbera *et al.*, 2022). With this in mind, we propose to focus future research on how heterotrophy affects population dynamics and community resilience (Viladrich *et al.*, 2017).

VI. CONSIDERING HETEROTROPHY IN THE MAFs RESTORATION TOOLBOX

Tropical MAFs (i.e. shallow coral reefs) have attracted the greatest attention in conservation and restoration efforts to date, while temperate and cold-water MAFs have been largely ignored in this regard (UNEP-WCMC, 2022). However, similar recommendations can be applied to all MAF systems. The International Coral Reef Society (ICRS) has defined three key pillars for coral reef conservation and restoration (Knowlton *et al.*, 2021): (*i*) reducing global climate threats (by lowering greenhouse gas emissions and increasing carbon sequestration); (*ii*) improving local conditions and management for coral reef resilience; (*iii*) investing in restoration science and active coral reef restoration. In addition, the success of conservation is intricately tied to governance, whose effectiveness varies in time and space. Effective strategies to conserve and restore coral reef ecosystems (e.g. Baums *et al.*, 2019; Voolstra, Peixoto & Ferrier-Pagès, 2023), as well as temperate and cold-water MAFs (e.g. Ounanian *et al.*, 2017; Montseny *et al.*, 2021), have been proposed in several reviews and studies. However, as Ladd & Shantz (2020) highlighted, restoration efforts often overlook fundamental ecology concepts and only 15% of reef restoration publications consider trophic interactions as a potential contributing factor to restoration success. Also, the importance of heterotrophy for organismal fitness and propagule dispersal remains largely overlooked (Viladrich *et al.*, 2022*a*) (Fig. 3). There are several direct and indirect pathways by which trophic interactions and heterotrophy can be incorporated into conservation and restoration efforts. As with any intervention, the risks and limitations of each of these interventions (e.g. Anthony *et al.*, 2020), as well as their long-term sustainable financing (e.g. Suggett *et al.*, 2023), need to be carefully considered to ensure restoration success (Fig. 4).

Actions at the community and ecosystem levels are those with the lowest potential risks and limitations (Fig. 4). At these levels, food availability (e.g. zooplankton, DOM, POM)

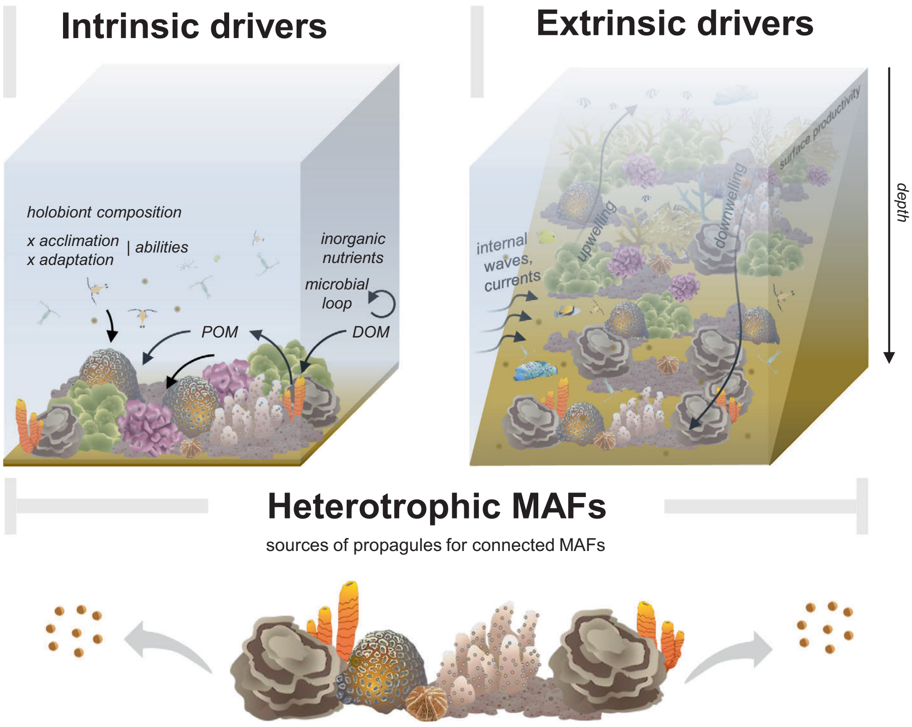
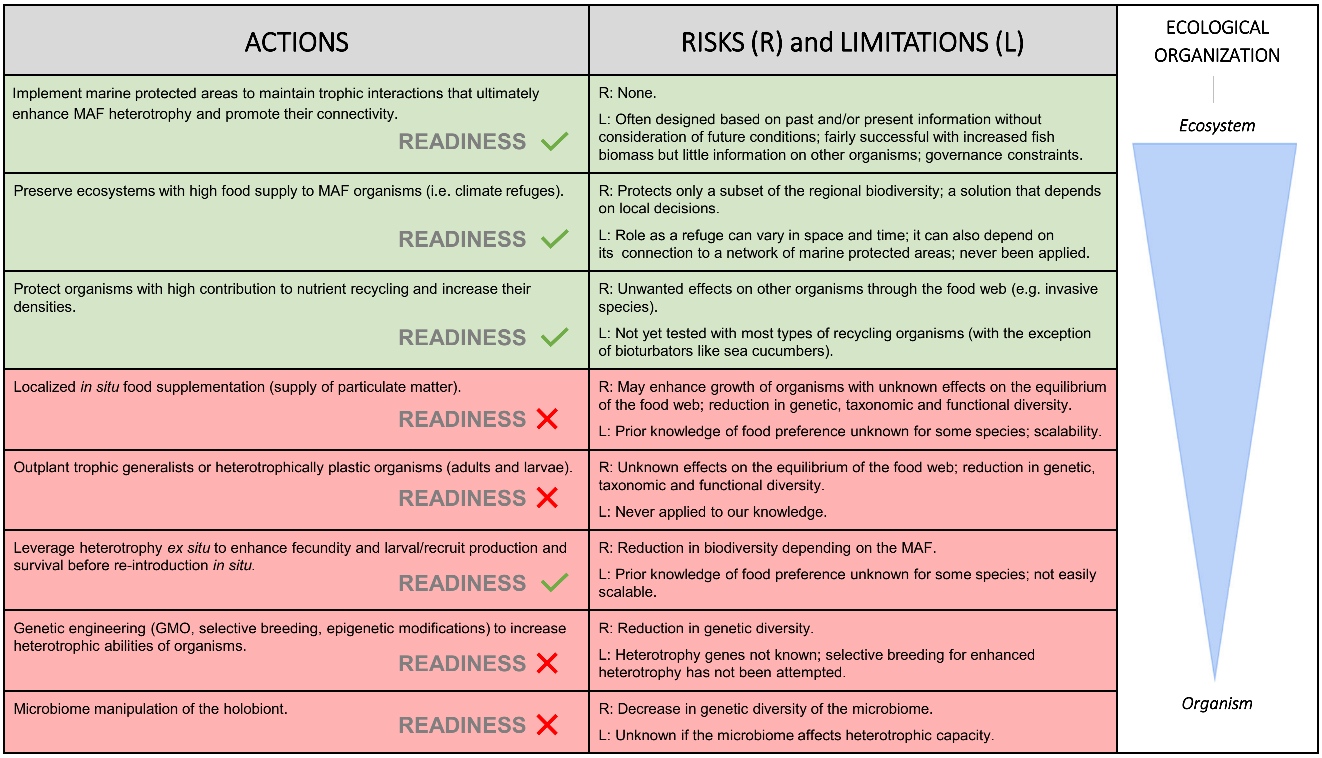


Fig. 3. Intrinsic and extrinsic drivers of marine animal forest (MAF) heterotrophy and their relative importance for sexual reproduction. Several factors affect heterotrophic processes which in turn influence the growth of MAFs. Healthy MAFs can be important sources of propagules within a network of interconnected marine protected areas. DOM, dissolved organic matter; POM, particulate organic matter.



ACTIONS	RISKS (R) and LIMITATIONS (L)	ECOLOGICAL ORGANIZATION
Implement marine protected areas to maintain trophic interactions that ultimately enhance MAF heterotrophy and promote their connectivity. READINESS ✓	R: None. L: Often designed based on past and/or present information without consideration of future conditions; fairly successful with increased fish biomass but little information on other organisms; governance constraints.	*Ecosystem*
Preserve ecosystems with high food supply to MAF organisms (i.e. climate refuges). READINESS ✓	R: Protects only a subset of the regional biodiversity; a solution that depends on local decisions. L: Role as a refuge can vary in space and time; it can also depend on its connection to a network of marine protected areas; never been applied.	
Protect organisms with high contribution to nutrient recycling and increase their densities. READINESS ✓	R: Unwanted effects on other organisms through the food web (e.g. invasive species). L: Not yet tested with most types of recycling organisms (with the exception of bioturbators like sea cucumbers).	
Localized *in situ* food supplementation (supply of particulate matter). READINESS ✗	R: May enhance growth of organisms with unknown effects on the equilibrium of the food web; reduction in genetic, taxonomic and functional diversity. L: Prior knowledge of food preference unknown for some species; scalability.	
Outplant trophic generalists or heterotrophically plastic organisms (adults and larvae). READINESS ✗	R: Unknown effects on the equilibrium of the food web; reduction in genetic, taxonomic and functional diversity. L: Never applied to our knowledge.	
Leverage heterotrophy *ex situ* to enhance fecundity and larval/recruit production and survival before re-introduction *in situ*. READINESS ✓	R: Reduction in biodiversity depending on the MAF. L: Prior knowledge of food preference unknown for some species; not easily scalable.	
Genetic engineering (GMO, selective breeding, epigenetic modifications) to increase heterotrophic abilities of organisms. READINESS ✗	R: Reduction in genetic diversity. L: Heterotrophy genes not known; selective breeding for enhanced heterotrophy has not been attempted.	
Microbiome manipulation of the holobiont. READINESS ✗	R: Decrease in genetic diversity of the microbiome. L: Unknown if the microbiome affects heterotrophic capacity.	*Organism*

Fig. 4. Management actions that can be implemented to increase heterotrophy in marine animal forests (MAFs). Actions are presented across levels of ecological organisation and according to their readiness, with ✓ indicating that a particular action is ready and ✗ indicating that it still needs development. Colours indicate whether the action is scalable (green) or not yet scalable (red) given current knowledge and technology. GMO, genetically modified organism.

should be considered when identifying areas for conservation and restoration efforts. For example, several food-rich ecosystems have been identified as climate refuges for certain MAF organisms under future climate conditions. Corals, sponges, and bivalves living in or near mangroves can exhibit higher levels of heterotrophy and enhanced thermal tolerance, making them more resilient to climate change disturbances (Camp *et al.*, 2019). Tropical corals exposed to internal waves and upwellings also exhibit enhanced heterotrophy and heat-stress resistance, as these physical processes bring cold and nutrient-rich water to the surface and stimulate primary and secondary production (Buerger *et al.*, 2015; Fox *et al.*, 2023). Similarly, some coral species accustomed to living in turbid environments rely more heavily on heterotrophy and are more resistant to stress (Anthony & Fabricius, 2000). Finally, cold-water MAFs in habitats with particularly high food supply and comparatively low energetic costs could provide refuges under climate change conditions, e.g. habitats where high geomorphic relief favours particularly strong currents and particle advection (Soetaert *et al.*, 2016) and which are not likely to be subject to aragonite undersaturation or hypoxia in the near future (Sweetman *et al.*, 2017). These refuges could be used strategically as natural sources of propagules within a network of interconnected marine protected areas (MPAs) taking into account their long-term capacity given spatial and temporal variability and vulnerability (Camp, 2022). Further research is however needed on the full potential of such refuges in MAF conservation.

In MAFs which are not naturally enriched with food, heterotrophy can be stimulated through enhanced biotic interactions such as herbivory. For example, studies have shown that the inclusion of herbivorous snails or sea urchins in coral nurseries can enhance nutrient recycling and increase the growth and survival of adult and juvenile corals (Craggs *et al.*, 2019; Henry, O'Neil & Patterson, 2019). Herbivorous fish may indirectly benefit benthic heterotrophs, by excreting nutrients or controlling algal growth following major disturbances (Holbrook *et al.*, 2016). The role of sea cucumbers in bioturbation has also been identified to be important in the gross production of benthic communities (Uthicke & Klumpp, 1998). These important ecological processes could be leveraged by protecting and restoring MAFs (such as by using MPAs, artificial reefs, larval seeding, or outplanting), ultimately benefiting the entire community through cascading effects. Global change, particularly ocean warming, is however expected to cause significant changes in trophic processes, leading to mismatches between food supply and the benthic community's needs (Rossi *et al.*, 2019). Therefore, increased heterotrophy could offset the decline in food availability.

Actions currently targeted at the organism level present more risk and limitations, notably related to unknown effects on the food web and reduced genetic, taxonomic and functional diversity. Nevertheless, there is increasing evidence of the potentially beneficial effects of increased feeding on the physiological and reproductive performance of MAF organisms under different environmental conditions (e.g. Grottoli *et al.*, 2006; Cox, 2007; Gori *et al.*, 2013; Dobson *et al.*, 2021). Mixotrophic species that are heterotrophically plastic are more resilient to stressors (e.g. Grottoli *et al.*, 2006; Levas *et al.*, 2016). Heterotrophy can be used *ex situ* to increase parental fecundity, larval production, settlement and survival (Gori *et al.*, 2013; Toh *et al.*, 2014; Rodd *et al.*, 2022), resulting in a larger number of new recruits available for outplanting. The re-introduction of small recruits later *in situ* may be an efficient tool for cold-water MAFs, for which restoration actions are limited due to their deep locations. Also, such an intervention does not increase the risk of large biodiversity losses in regions where the MAFs consist of only a few foundational species. This practice might be more limited and limiting for tropical MAFs, which have high biodiversity.

In situ, enhancing feeding opportunities through food supplementation may be a viable intervention to reduce mortality and increase growth of MAF builders locally following stress events or to enhance restoration success. This can be achieved using light traps for capturing pelagic and benthic plankton (Chan *et al.*, 2016). This approach, however, requires determining the best diet for each MAF builder, as well as the species that respond most strongly to increased heterotrophy (Conlan *et al.*, 2018). Obviously, such an action is difficult to scale up to an entire MAF ecosystem, but it may locally and temporally boost foundational species. Restoration of highly degraded sites could benefit from outplanting species with high feeding capacity and/or high heterotrophic plasticity that can rapidly increase benthic cover. The risk of genetic bottleneck effects in this case is outweighed by the risk of complete habitat loss.

Manipulation of the host microbiome (Symbiodiniaceae and other microbes) can, in concert, either enhance host heterotrophic capacity (Leal *et al.*, 2015) or provide essential nutrients during stress events (Bednarz *et al.*, 2021). Finally, heterotrophic traits could be leveraged in assisted evolution approaches through epigenetic manipulation and selective breeding of the most heterotrophic individuals in the population. While the above actions to promote heterotrophy at the organism and population levels have shown some local success, further development is needed to determine if they are deployable at the community or ecosystem level beside existing restoration practices (e.g. Banaszak *et al.*, 2023).

Due to the imminent consequences of climate change, it is imperative to consider sustained food sources for the restoration of MAFs. This entails incorporating strategies and interventions to enhance MAF feeding in the strategic planning of restoration initiatives and MPA designs. The actions presented above are not sufficient to prevent the decline of MAFs, or to diminish the importance of climate change mitigation, but provide a new suite of strategies to add to a comprehensive and integrative approach that could ultimately benefit MAF ecosystems conservation, restoration, and protection.

VII. CONCLUSIONS

(1) MAFs are widespread benthic ecosystems built by suspension feeders. They provide a range of benefits and services that are important to millions of people worldwide. Currently, MAFs are declining due to anthropogenic stressors.

(2) Heterotrophy is a key process for MAF functioning, providing energy and recycled nutrients. In many instances, heterotrophy contributes to the overall stability of MAFs. In particular, increased heterotrophic feeding has been shown to have positive effects on physiological and reproductive performance of MAF organisms, population growth and survival, community diversity, and ecosystem resilience.

(3) A variety of tools exist to assess heterotrophy in MAFs at different levels of ecological organisation. Trophic interactions are key, but overlooked, and could play an important role in restoration and conservation.

(4) Sustaining trophic functioning in MAFs through restoration initiatives could help address the challenges of climate change. Certain habitats may also serve as climatic refuges for MAF organisms and should be priority targets for marine protected areas.

(5) More research is needed to understand nutrient fluxes in MAF food webs better and how they will change under future climate conditions.

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