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A functional perspective on the meaning of the term ‘herbivore’: patterns versus processes in coral reef fishes

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Abstract Herbivorous fishes are a key functional group in coral reef ecosystems and have been the focus of a vast body of research. While substantial progress has been made in research, challenges persist, especially in respect to quantifying patterns versus processes. Despite this challenge being recognised over 40 years ago. To help clarify such challenges, and work towards solutions, in this perspective we explore how the definition of ‘herbivorous reef fishes’ precludes an easy translation between patterns of herbivore abundance and the process of herbivory. Indeed, if herbivorous fishes are defined as, *a fish in which the diet is predominantly based on plant material*, then this encompasses a diverse suite of fishes which all remove primary producers to varying extents and have markedly different impacts on reef functioning. Given this situation, we explore how our approaches to directly quantifying herbivory on reefs have progressed. We highlight how lessons learnt from macroalgal assays could be applied to the direct quantification of herbivory from algal turfs in the epilithic algal matrix (EAM); a community of primary producers that are invariably difficult to work with and quantify. Nevertheless, given the abundance of turfs on coral reefs, and their relative importance in herbivore dynamics, widespread process-based assessment of EAM herbivory represents an avenue

for expanding future research. Recognising the difficulty of translating patterns in herbivore abundance to the process of herbivory, and an enhanced focus on EAM herbivory, will be necessary to comprehensively quantify the process of herbivory on Anthropocene coral reefs.

Keywords Algal turf · Ecosystem function · Epilithic algal matrix · Macroalgae · Parrotfish · Surgeonfish

Introduction

The dynamic balance between the process of herbivory (algal removal) and primary productivity (algal production) is central to the functioning of coral reef ecosystems (Odum and Odum 1955; Carpenter 1986; Done 1992; Brandl et al. 2019). Indeed, the importance of this dynamic balance, and the role of key agents (i.e. herbivores) in maintaining the balance, has long been recognised with a history of reviews by formative coral reef scientists (e.g. Ogden and Lobel 1978; Borowitzka 1981; Hatcher 1983; Hixon 1983; Steneck 1988; Horn 1989; Choat 1991; Hay 1997; Choat and Clements 1998). Moreover, the role of herbivorous fishes as the primary agents of herbivory on tropical coral reefs is widely appreciated (e.g. Randall 1961; Wanders 1977; Lewis 1986; Choat and Clements 1998; Burkepile et al. 2020) as they are considered “*among the most abundant and widespread groups of vertebrate herbivores*” (Choat 1991). Perhaps the overall situation was most eloquently conveyed by Horn (1989) in the opening sentence of his review: “*Fish herbivory in the sea is an important ecological subject because the trophic interactions at the base of food webs, the energetic requirements and physiological capabilities of fishes and the role of fishes in the flow of energy through marine communities are involved.*”

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Since the early recognition of the importance of herbivores and herbivory on coral reefs, appreciation of this importance has grown considerably in the Anthropocene (Hughes et al. 2017; Steneck et al. 2017). The global decline of scleractinian coral cover on reefs and increase in algal cover (Souter et al. 2021; Tebbett et al. 2023a), has ensured that the study of herbivory remains at the forefront of coral reef science. Indeed, herbivorous fishes are now widely accepted as integral to the resilience of coral reef ecosystems, as their capacity to constrain macroalgal growth may facilitate the recovery of corals post-disturbance (Bellwood et al. 2004; Hughes et al. 2010; Graham et al. 2013). As such, identifying the key herbivorous fish species involved, which algal species/forms they remove, and how strong these interactions are, has represented a key area of coral reef research (Burkepile and Hay 2008; Rasher et al. 2013; Dell et al. 2020). Increasingly, it is also recognised that to understand broader ecosystem dynamics in detail we must embrace a functional perspective, in which quantification of processes (e.g. the rate of plant removal) is crucial (Bellwood et al. 2019; Streit and Bellwood 2022). However, this process-based assessment of coral reef herbivory can be challenging.

In respect to the difficulty in quantifying the process of herbivory on coral reefs we may reflect on two insightful thoughts expressed by Steneck (1983) 40 years ago:

Firstly, *“Measurements of percent cover, biomass, or number of individuals when applied to assemblages of reef dwelling herbivores are of dubious meaning for quantifying herbivory. For instance, how many foraging urchins equal the impact of a 20 kg parrotfish? The “apples and oranges” involved here result from trying to force units and techniques which are designed to determine patterns in herbivore abundance on the process of herbivory.”*

Secondly, *“Ecologists are far from agreeing on a method (or methods) for measuring herbivory on reefs. While this does not seem to inhibit publications on the subject, comparisons between reefs are impossible...The only clear message revealed in this study is that quantifying a process is infinitely more difficult than quantifying patterns in the abundance of herbivores. So far we have only scratched the surface and still we are biting off more than we can chew.”*

Importantly, these sentiments remain, in many ways, as true today as they did when they were expressed 40 years ago. While critical progress has been made in the quantification of herbivory in some research areas, in other key areas progress has lagged and we often still attempt to try and quantify the process of herbivory via patterns in herbivore abundance/biomass. To help clarify these issues, and potentially move towards solutions, in this perspective we will expand on the two sentiments outlined above. Specifically, we will highlight why examining processes via patterns is difficult for the simple fact that the very definition

of a ‘herbivorous reef fish’ precludes an easy translation between patterns of herbivores and the process of herbivory. Given this difficulty we then explore how our approaches to directly quantifying herbivory on reefs have progressed and consider how these may need to be recalibrated if we are to comprehensively quantify this process in the Anthropocene.

What is a herbivorous reef fish?

Defining what herbivorous reef fishes are is not a straightforward task and has stimulated the thoughts of scientists for decades (e.g. Hatcher 1983; Horn 1989; Choat and Clements 1998; Wilson et al. 2003; Parravicini et al. 2020; Siqueira et al. 2020). These thoughts suggest that a classic definition of what a ‘herbivore’ is, such as that supplied by the Oxford English Dictionary “*an animal that eats only plants*”, may not be particularly applicable to reef fishes, nor other herbivorous organisms, given the opportunistic consumption of protein-rich animal tissue exhibited by many ‘herbivores’ (e.g. Case and McCullough 1987; White 2011; Dudley et al. 2016). In terms of reef fishes specifically, the term ‘plants’ as it pertains to the marine environment, can encapsulate a plethora of primary producing organisms, including true plants, algae and cyanobacteria (sensu Bolton 2016), that are all targeted by reef fishes as nutritional resources (Randall 1965; Choat et al. 2002; Clements et al. 2017; Nalley et al. 2022). Furthermore, the term *only* in this classic definition is a difficult hurdle to overcome and will be the focus of our appraisal below. To understand why this term is an issue one may ask: does the term *only* imply that the organism does not or cannot ingest any other material other than plants during its life? Obviously, such a restriction would mean most ‘herbivorous’ fishes are not actually herbivores. For example, every herbivorous reef fish has a larval stage that feeds on plankton (Sampey et al. 2007; Llopiz and Cowen 2009). Therefore, considering the need for some degree of flexibility regarding the extent to which plant material is consumed by ‘herbivorous’ fishes, we will explore the merits and shortcomings of three alternative definitions below, as they apply to adult reef fishes, that vary the extent to which plant material is ingested.

Definition 1: A fish that eats plant material Of the three definitions we examine this one is clearly the most inclusive in terms of the extent to which plant material may be consumed by herbivorous fishes. However, under this definition virtually all fishes on coral reefs could be considered ‘herbivorous’ as the vast majority of fishes on coral reefs ingest some plant material (Parravicini et al. 2020). For example, even strict piscivorous fishes ingest fishes whose guts are full of algae and, therefore, by definition, they have eaten plant material, albeit indirectly. A problem that will become

increasingly apparent with the use of metagenomic methods for inferring fish ‘diets’ (Casey et al. 2019). To highlight this major shortcoming with the definition more clearly, perhaps it is best to use an example as it relates to a human consuming a hamburger. Under this definition, if a person ordered a propriety hamburger and chose to discard the bun, the lettuce, the onion, the tomato sauce and retained and ingested only the beef patty with a single pickle on top, then they would still be classed as a herbivore. Is this what we mean when we talk about ‘herbivorous’ reef fishes: a fish that eats (some) plant material?

Definition 2: A fish in which the diet is predominantly based on plant material Following on from the first definition, the second definition places far more restriction on the extent to which plant material is consumed by herbivorous fishes. Indeed, in this definition the term *diet* implies the habitual eating, while the term *predominantly* suggests plants are the most frequent or most abundant dietary items ingested. However, even with such restriction, there is still a remarkable degree of flexibility under this definition. To explore this flexibility let us return to the hamburger analogy. If our person once again orders the hamburger, but this time retains and ingests the hamburger in its entirety, they would have ingested a nutritional resource predominantly derived from plant material (based on volume/area). Indeed, the bun, the lettuce, the onion, the tomato sauce, the pickle, and the oil that the beef patty was cooked in are all derived from plants. Consequently, if we were to analyse the gut contents using an approach that is commonly applied to reef fishes (e.g. Randall 1967; Robertson and Gaines 1986; Kelly et al. 2016; Tebbett et al. 2017) we would quantify the relative frequency of different items and conclude that plant material made up more than 50% of the material ingested. Therefore, under this definition, a person could exist on a diet of hamburgers, and nothing but hamburgers, and still be considered herbivorous. Yet, despite plants being the predominant component of this diet (by volume/area), nutritional resources are undoubtedly being derived by this person from the beef patty. Indeed, despite being less frequent in the gut contents, the beef patty is likely to be the major source of calories and protein in this diet (a point overlooked if we only assign trophic groups based on the frequency of ingested material).

Importantly, in our analogy above, some of the nutrients derived from the beef may also be crucial to the long-term subsistence of this person. How does this differ from a parrotfish which, by feeding on the entire epilithic algal matrix (EAM), ingests thousands of copepods a day (Kramer et al. 2013)? Indeed, ‘herbivorous’ parrotfishes are the greatest consumer of EAM-bound crustacea, eating in the order of 10,000 harpacticoid copepods per m² per day (Kramer et al. 2013). Importantly, this phenomenon is unlikely to be restricted to reef fishes or aquatic environments, as other

herbivorous organisms are likely to ingest animals associated with the plant material they consume (reviewed in Gish et al. 2017). Given a diet of predominantly plant material, but with the possibility that some animal material may also be needed to meet some or even most of the nutritional/energetic requirements, is this what we mean when we describe herbivorous reef fishes or herbivorous organisms more generally?

Definition 3: A fish that feeds exclusively on plant material with this material meeting all of its energetic and nutritional requirements The third definition is the most restrictive and is, in this respect, in-line with that proposed by the Oxford English Dictionary. However, this third definition has the added component that this plant material must meet all the energetic and nutritional requirements of the fish. This component of the third definition builds on the shortcoming of the second definition, by ensuring that herbivorous fishes under this definition do not depend on material from animal origins to survive. In essence, it is the equivalent of a vegan diet which must meet all energetic and nutritional requirements. Given these conditions, this is clearly a very restrictive definition although this definition probably aligns with ‘herbivory’ in the truest sense of the word. However, the restriction of this definition inevitably raises the question: can any reef fish, especially those widely viewed as herbivorous, even be considered a herbivore?

Consideration of definitions

By considering the various definitions above together we can elucidate what is commonly meant by a herbivorous reef fish. In this case, the first definition above would appear to be far too inclusive. Indeed, of the 4554 reef fishes considered in a recent study, 99.1% of species were found to have some degree of trophic interaction with plant material (Paravicini et al. 2020). By contrast, the number of fishes that qualify for inclusion as herbivores under the last definition is very limited. The primary candidates for inclusion at this upper echelon of herbivory on reefs are the various species of kyphosid (Fig. 1c), which have evolved specialised hindguts where they rely heavily on microbial symbionts for fermentation of ingested macroalgal material (Choat and Clements 1998). This means that the second definition appears to represent a good middle ground between being too inclusive versus too exclusive. However, if we define herbivorous fishes based on the second definition, this means that although these fishes are ingesting predominantly plant material, they may be relying on other dietary components (of animal origin) to meet a significant proportion of their nutritional needs. And that this other material may make up 49% of the diet (by volume/area). Furthermore, fishes under this definition habitually consume a wide plethora of plant

Fig. 1 The diversity of fishes that have been considered 'herbivorous' on coral reefs. **a** the surgeonfish *Acanthurus lineatus*, **b** the dwarf angelfish *Centropyge bicolor*, **c** the chub *Kyphosus vaigiensis*, **d** the parrotfish *Scarus psittacus*, **e** the rabbitfish *Siganus corallinus*, and **f** the farming damselfish *Stegastes lacrymatus* (formerly *Plectroglyphidodon*). All photographs F. Libert



material (be this sea grass, algae or cyanobacteria) which composes from 51 to 100% of the material they ingest. This is a large degree of variation, but it ensures most fishes often considered herbivorous (e.g. Figure 1) would retain their current classification. It should be noted that this is probably an unsatisfactory definition from a fish nutrition perspective but appears to be sensible and necessary from an ecosystem perspective. Indeed, given this situation, the term 'herbivore' is perhaps most useful as a convenient phrase, rather than being functionally informative [as was previously recognised by Choat et al. (2002) who described them as 'nominal herbivores'].

Consideration of different perspectives

With a somewhat clarified understanding of what we mean by herbivorous fishes to hand, it is critical to also consider how different perspectives can shape this definition. In this respect, there are two major, but not mutually exclusive, perspectives that have driven scientific investigation into herbivory on coral reefs and shaped how this process is defined: the fish perspective versus the ecosystem perspective. The

fish, or nutritional ecology, perspective of herbivory has received less attention than the ecosystem perspective in recent decades, but it still asks important questions (Choat and Clements 1998; Clements et al. 2009). From this fish perspective one considers what the fish wants to feed on, or needs physiologically, and why? It also involves the plant as a key player, as herbivores have evolved to feed on specific plant material and/or deal with certain plant defences (e.g. Choat and Clements 1998; Hay 1997; Ogden and Lobel 1978).

By contrast, viewing herbivory on coral reefs from an ecosystem perspective, or a plant's perspective, has gained particular momentum in recent decades, especially in respect to reef decline, phase-shifts and the notion of resilience (Bellwood et al. 2004; Littler et al. 2006; Burkepille and Hay 2008; Steneck et al. 2017). Within this context, herbivorous fishes were rapidly identified as critical, with the potential to either prevent or reverse phase-shifts via the removal of algae (Bellwood et al. 2004; Littler et al. 2006; Burkepille and Hay 2008; Steneck et al. 2017). As such, from this perspective, the goal is to understand what the impact of fish feeding on specific plants is, and how much of this

plant material is removed from the ecosystem by fishes. Clearly, these different perspectives have the potential to shape definitions because, from the fish perspective, a fish would only be considered herbivorous if it was specifically targeting plants and needed this plant material to meet its dietary and physiological needs. By contrast, from the ecosystem perspective, a fish would be considered herbivorous if it removes any plant material, regardless of whether it utilises it or not.

Despite the potential conflict arising from these different perspectives, it is critical to note that both are required for a comprehensive understanding of the process of herbivory on coral reefs. A clear demonstration of this has been provided by the study of herbivory on large macroalgae. For example, from an ecosystem perspective, research revealed that most nominally herbivorous fishes removed relatively little, if any, adult macroalgae from coral reefs (e.g. Mantyka and Bellwood 2007; Hoey and Bellwood 2009; Michael et al. 2013; Rasher et al. 2013; Dell et al. 2020). Indeed, very few fishes have been identified as critical to this function (reviewed in Puk et al. 2016; Topor et al. 2019) and, from a plant's perspective, this represents an evolutionary success as herbivory has selected for plant traits such as spatial escapes (Bennett et al. 2010; Brandl et al. 2014; Hay 1984b), temporal growth escapes (Hay et al. 1988) and chemical or morphological deterrents (Hay and Fenical 1988; Paul and Hay 1986; Burkepile et al. 2022) which deter, ameliorate, or resist, herbivore impacts. Importantly, the fish perspective has revealed how the select group of macroalgae-feeding fishes exist on coral reefs. Specifically, macroalgae-feeding fishes were found to have relatively sophisticated guts and associated microbiota to assimilate and subsist on a diet composed largely of a nutritionally poor food item (large macroalgae) (Clements and Choat 1997; Choat and Clements 1998; Choat et al. 2004). In the case of macroalgae-feeding fishes, the two perspectives together provided a more holistic understanding of which fishes were removing what plant material and potentially why. Going forward, it will be necessary to draw on both perspectives to understand complex, changing reef ecosystems.

Implications for using patterns of 'herbivorous fishes' to understand processes

Given the second definition above, it is clear that 'herbivorous fishes' on coral reefs are a highly diverse group targeting an array of primary producers and other nutritional resources to varying extents. Detailed morphological (Bellwood and Choat 1990; Choat et al. 2004; Brandl et al. 2015) and behavioural studies (Robertson et al. 1979; Streit et al. 2015; Adam et al. 2018) have also highlighted that these fishes are removing these resources in fundamentally different ways and, in turn, have fundamentally different impacts

on primary producers. Moreover, different species of herbivorous fishes may remove different algae when selecting for, and feeding on, specific subsets of the algal community (Burkepile and Hay 2008; Rasher et al. 2013). This is likely to result in different species of algae becoming more prominent when impacted by different species, or assemblages, of herbivorous fishes, despite the biomass of herbivores being similar (Burkepile and Hay 2008; Rasher et al. 2013). Clearly, this diversity means that it is very hard to translate data on patterns (i.e. abundance/biomass) of herbivorous fishes to the process of herbivory (i.e. the rate of plant removal).

The challenge of translating patterns into processes is further compounded by scaling impacts (i.e. scaling up small scale observations to ecosystem wide processes) across both spatial and temporal scales. Specifically, fishes are highly mobile organisms which can have a relatively large, diffuse, and spatially heterogenous grazing footprint (Carlson et al. 2017; Streit et al. 2019). Feeding over a relatively large spatial scale means that there is also a larger canvas for factors such as behaviour, habitat structure, and physiology to shape where, which, and how much, plant material is removed by fishes. These scaling impacts are particularly strong in fishes compared to other herbivorous marine organisms, such as urchins and gastropods, which feed over more constrained spatial scales and, therefore, may be more amenable to deriving links between presence and function (Carpenter 1984; Steneck 1997). Similarly, herbivorous fish feeding rates vary across a number of temporal scales including daily (Polunin and Klumpp 1989; Zemke-White et al. 2002) and seasonally (Ferreira et al. 2005; Lefèvre and Bellwood 2010). Importantly, this complexity is further magnified if one wants to scale both plant removal and production rates, to measure actual impact (i.e. production – removal), as plant production also varies considerably including across spatial and temporal scales (Klumpp and McKinnon 1989; Fulton et al. 2014; Pessarrodona et al. 2022a). Yet, measuring actual impacts represents an important endeavour because if production and removal are both small/large than the absolute impact is small, but if these two diverge than the absolute impact may increase. Overall, if fishes that are considered herbivorous are removing plant material to different extents, over varying temporal and spatial scales, in a plethora of different ways, and the production of this plant material is also varying across a number of different axes, than there is no simple formula to translate the presence of fishes to the process of removal, nor to absolute ecosystem impacts.

It should be noted that grouping fishes into 'how' functional groups can simplify the situation [i.e. groups based on how fishes interact with the reef sensu Bellwood et al. (2019)]. However, even with such groupings, a complex suite of links, with varying strengths, exists between functional groups and multiple different process on reefs (Fig. 2).

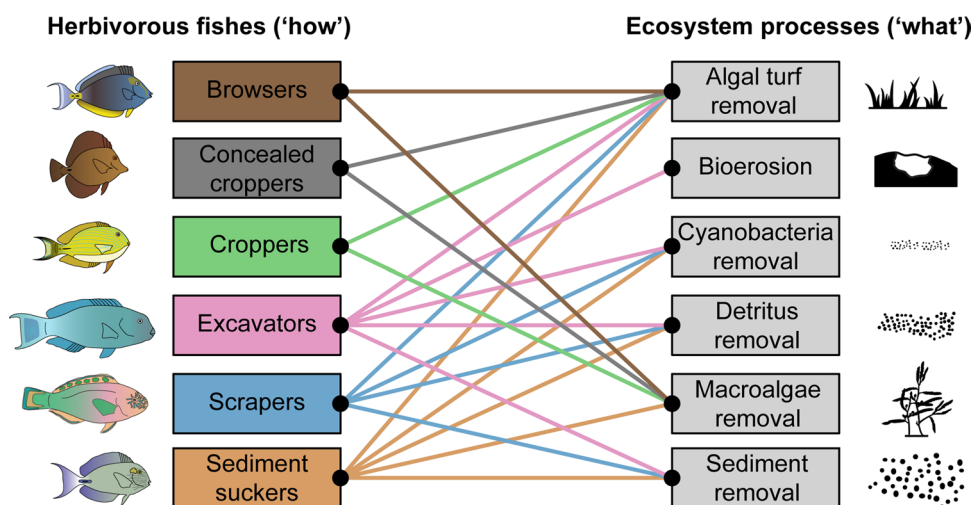


Fig. 2 Conceptual diagram providing an example of the complex links between ‘how’ functional groups of herbivorous fishes [defined based on how they interact with the reef in Bellwood and Choat (1990) and Tebbett et al. (2022)] and six ecosystem processes (i.e. ‘what’ functions they deliver). The coloured lines denote processes

that the different functional groups may contribute to substantially as adults. Importantly, the figure highlights that the ‘how’ classification of herbivorous coral reef fishes does not preclude them from performing multiple functional roles and acknowledges the diversity of nutritional targets/material removed when fishes feed on the benthos

Therefore, if the goal of a research question is to explore and compare the rate at which herbivory occurs on reefs, from an ecosystem perspective (sensu Steneck 1983), then we may need a more direct approach. It is important to note, however, that research into the morphology, behaviour, and physiological capacity of herbivorous fishes is critical in deciphering the ultimate drivers of why and how the process of herbivory is delivered on coral reefs and what material herbivorous fishes can ultimately digest, metabolise, and/or tolerate (e.g. Horn 1989; Choat and Clements 1998; Clements et al. 2009). In this respect, such research is pivotal and complementary to process-based assessments of herbivory.

Quantifying the process of ‘herbivory’

Where substantial progress has been made: macroalgae removal

Despite the direct quantification of herbivory on reefs being more difficult than quantifying patterns of herbivores (sensu Steneck 1983) there has been wonderful progress in recent decades in the direct measurement of a specific form of herbivory. That is, removal rates of upright macroalgae. Nowadays, the use of macroalgal assays have become a standard tool for quantifying herbivory (Littler and Littler 2007), with the origins of this method laying in the early use of *Thalassia* seagrass assays on reefs (e.g. Hay 1981, 1984a). Macroalgal assays have now evolved to commonly utilise a range of different macroalgae to comprehensively quantify the process of macroalgal removal (e.g. Mantyka and

Bellwood 2007; Rasher et al. 2013; Dell et al. 2020; Burkepile et al. 2022). The use of this assay method has, in turn, yielded key insights into the rates of macroalgal removal on reefs across various spatial scales including within and between reef habitats (Lewis and Wainwright 1985; Löffler et al. 2015; Longo et al. 2015), among different reefs (Hoey and Bellwood 2010; Bennett and Bellwood 2011; Michael et al. 2013; Plass-Johnson et al. 2015) and at broader continental or global scales (Vergés et al. 2012; Tebbett et al. 2020) as well as how the process varies under different contexts (Hoey and Bellwood 2011; Vergés et al. 2011; Chong-Seng et al. 2014; Humphries et al. 2015; Catano et al. 2016). These insights were possible because macroalgae assays represent a replicable unit in which the rate of algal removal (i.e. algal mass before versus after deployment) can be quantified under a variety of conditions.

Although there has been marked advances in quantification of macroalgal removal rates on coral reefs it is important to note that this form of herbivory represents a relatively minor component of herbivory on most coral reefs (Steneck 1988; Choat 1991; Choat and Clements 1998) with a limited number of species involved (Choat et al. 2002; Hoey and Bellwood 2009; Topor et al. 2019). This focus on macroalgae removal has been understandable given that the coral-macroalgal phase-shifts documented in the Caribbean became the archetypical example of coral reef degradation in an era of global climate change (Bellwood et al. 2004; Hughes et al. 2010, 2017). Although, it is now clear that macroalgae development is just one of a range of benthic changes experienced (Norström et al. 2009; Jouffray et al. 2015; Reverter et al. 2022) and, outside of the Western

Atlantic, probably does not represent the major trajectory of ecosystem change on coral reefs (Bruno et al. 2009; Roff and Mumby 2012; Crisp et al. 2022; Tebbett et al. 2023a). In addition, upright macroalgae occur on the scale of 10 s of centimetres making such algae easy to manipulate and measure when compared to other primary producers, such as the diminutive turf forming algal species that comprise the EAM on reefs. Yet, it is herbivory on the EAM which represents the major form of herbivory on coral reefs both in the past, and likely into the future. Direct quantification of this form of herbivory, however, has lagged the quantification of macroalgal removal in recent decades, and can still present a dilemma and challenge for scientists despite earlier successes (e.g. Hatcher 1981; Steneck 1983; Carpenter 1986; Russ and McCook 1999).

The challenge for the future: quantifying herbivory on the epilithic algal matrix

In terms of the dynamic balance between primary production and herbivory on coral reefs, the algal turfs/cyanobacteria that comprise the EAM and the fishes that feed on this interface represent the key players. This fact has long been recognised. For example, Marsh (1976) stated: “it seems obvious that workers studying reef productivity should focus more attention on small filamentous forms and the reef zones dominated by them.”. In addition, Steneck (1988) observed that the “general pattern of intense herbivory in shallow reef environments correlated with low biomass, turf-dominated assemblages is global”, while Choat (1991) also noted “most of the plant materials consumed by herbivorous reef fishes are small, structurally simple, and occur in complex assemblages. These can trap sediment and organic detritus and provide a habitat for epiphytic diatoms and bacteria”. Patterns of algae and herbivore abundance support these suggestions. It is widely understood that the EAM is often the most expansive benthic cover on coral reefs (especially compared to upright macroalgae) (e.g. Klumpp and McKinnon 1989; Adey 1998; Vroom et al. 2006; Smith et al. 2016; Tebbett et al. 2023b) (Fig. 3b), while the fishes that feed on primary producers in the EAM numerically dominate herbivorous fish assemblages compared to those that feed on upright macroalgae (Russ 1984; Cheal et al. 2012; Heenan and Williams 2013; Kelly et al. 2017) (Fig. 3a). Importantly, as coral reefs continue to change in the Anthropocene this situation is likely to hold or strengthen given that turfs generally increase in cover following disturbances (Gilmour et al. 2013; Koester et al. 2020; Tebbett et al. 2023a) and the fishes that feed on these turfs also generally increase (Russ et al. 2015; Robinson et al. 2019; Morais et al. 2020).

Since the early recognition of the importance of the EAM in herbivory dynamics we have also come a long way in

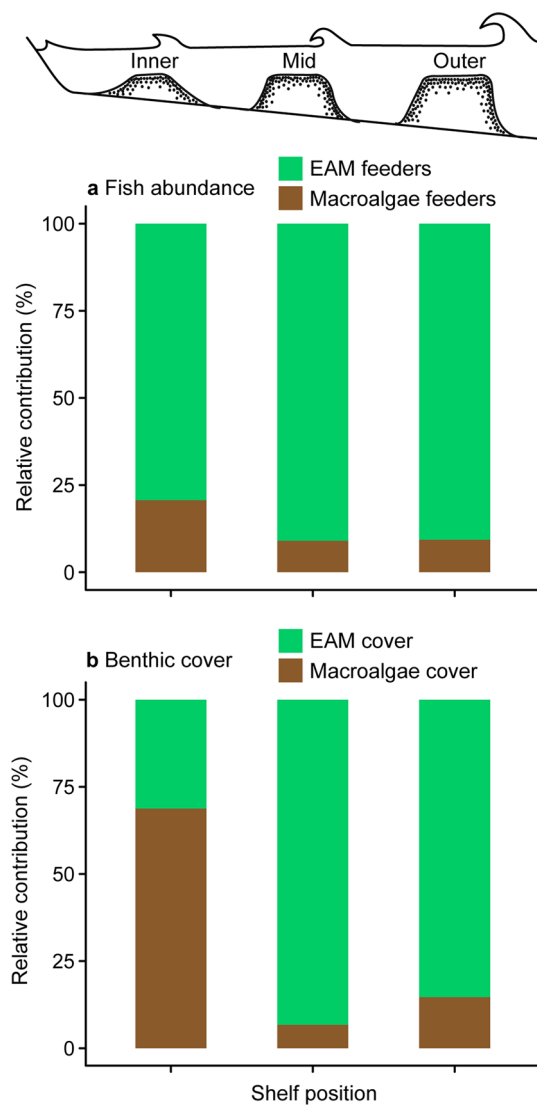


Fig. 3 Relative herbivorous fish abundance and algal cover on inner, mid- and outer-shelf reefs across the Great Barrier Reef, Australia. **a** The relative abundance of key herbivorous fishes (parrotfishes, surgeonfishes, rabbitfishes and kyphosids) that feed on either primary producers in the epilithic algal matrix (i.e. EAM feeders) versus upright macroalgae (i.e. macroalgae feeders). Note, EAM feeders include fishes that feed on hard substrata and target cyanobacteria which are a component of the EAM. Species which primarily target detritus and other nutritional items, or feed primarily over sand, are not considered. **b** The relative cover of the EAM compared to upright macroalgae. Note that EAM feeding fishes and EAM cover generally typify these coral reefs compared to macroalgae feeders and macroalgae cover. Data on fish abundance and algal cover were sourced from Wismer et al. (2009). In all cases, data from different habitats (back reef, flat, crest and slope) in each shelf position were weighted by the average areal extent of each habitat (based on data in Bellwood et al. 2018). Fish categorisation was based on the schemes presented in Siqueira et al. (2019) and Tebbett et al. (2022) and species are listed in Table S1

understanding the nutritional targets of the specific fishes. Early studies suggested that these fishes were predominantly targeting algal material (Hiatt and Strasburg 1960; Hatcher 1983), however, subsequent research has revealed that while this may be true for some species, many EAM feeding fishes are instead targeting the detritus that accumulates in this matrix (Robertson and Gaines 1986; Choat et al. 2002; Wilson et al. 2003) as well as other primary producers such as cyanobacteria (Clements et al. 2017; Nicholson and Clements 2020). This means that EAM feeding fishes are removing plant material to very different extents (as per definition 2 above). Indeed, the fishes that feed on the EAM can be so specialised that despite feeding on the exact same surface they can be removing fundamentally different nutritional items and, in turn, removing/not removing plant material (Choat and Bellwood 1985; Choat 1991; Tebbett et al. 2017). Yet, directly quantifying the rate at which the different material is removed has lagged the quantification of macroalgal removal in recent years. Perhaps this is underpinned by the simple fact that trying to quantify the rate at which a diverse assemblage of fishes remove material from an intricate matrix that occurs on the reef at the scale of millimetres is a challenging task.

Although directly quantifying herbivory on algal turfs is a challenge, it was achieved by pioneering research decades ago (e.g. Hatcher 1981; Steneck 1983; Carpenter 1986; Russ and McCook 1999). In the 1980s and 1990s there was considerable research interest into the direct process-based assessment of both algal turf production and herbivory (i.e. yield of plant biomass to herbivores) on coral reefs with a flurry of key studies (e.g. Hatcher and Larkum 1983; Carpenter 1986; Klumpp and McKinnon 1989, 1992; Russ and McCook 1999). Although, since this time this research topic appears to have fallen out of vogue; highlighted by the fact that 80% of algal turf productivity data on coral reefs was collected prior to 1990 (Tebbett and Bellwood 2021). This may be unsurprising given the increased focus on macroalgal herbivory for the reasons outlined above. Nevertheless, this situation means that the quantification of herbivory may have fallen out of alignment with respect to the relative importance of these two forms of herbivory. For example, if the quantification of herbivory on coral reefs occurred in line with the relative abundance of different algae and herbivorous fishes, the data would suggest that EAM versus macroalgal herbivory would be studied at a ratio of approximately 9:1 (Fig. 3). Importantly, given the plethora of key insights revealed through directly quantifying macroalgal herbivory in recent decades, this suggests that there is an exciting scope for future research on EAM herbivory. Given the sheer abundance of algal turfs (i.e. the EAM) on coral reefs, enhanced process-focused research into herbivory will help inform our understanding of the levels of herbivory required to maintain the balance of production versus

consumption of algal turfs in different contexts and under future disturbance regimes. It will also be key in identifying the relative importance of benthic versus pelagic pathways in supporting reef productivity. However, this research will depend on overcoming the challenges associated with quantifying herbivory from this sub-centimetre matrix.

Potential approaches for quantifying EAM herbivory in the future

Historically, herbivory on reef EAMs has been quantified via measurement of the ‘yield of algal biomass to herbivores’ based on caged and uncaged conditioned tiles or coral plates covered in algal turfs (e.g. Hatcher 1981; Carpenter 1986; Russ and McCook 1999; Russ 2003). This metric, and the utilisation of similar or modified methods appear to represent a promising path forward given their past use (e.g. Humphries et al. 2020). Indeed, the use of experimental substrata such as tiles or coral plates is useful for a range of reasons including the fact that they can represent a standard experimental surface that is relatively easy to manipulate compared to natural reef substrata. Although, careful consideration of a range of factors is necessary to ensure measurements of herbivory on experimental substrata reflect the processes on natural reef substrata. For example, the composition of tiles (Harlin and Lindbergh 1977; Borowitzka et al. 1978; Hixon and Brostoff 1985), as well as the time they are conditioned for (Diaz-Pulido and McCook 2002; Fricke et al. 2011), can influence algal turf community composition, which could shape herbivory dynamics. Likewise, the composition of algal turf communities can vary across a range of spatial scales (from centimetres to 100 s of kilometres) (Scott and Russ 1987; Harris et al. 2015; Arjunwadkar et al. 2022). Such heterogeneity, especially at small scales, can make it difficult to deploy paired replicates that represent the same community composition, which is an important endeavour given that algae vary in both their productivity (Rogers and Salesky 1981; Bruno et al. 2006), and palatability to herbivorous fishes (Wylie and Paul 1988; Littler et al. 1983). Moreover, given that experimental surfaces are generally raised off the substratum, they accumulate lower sediment loads in the EAM relative to the natural benthos (Tebbett et al. 2018). Importantly, as sediment loads in the EAM can shape algal growth rates (Clausing et al. 2014; Tebbett and Bellwood 2020), yield of algae to herbivores (Tebbett et al. 2018), and herbivorous fish feeding rates (Ng et al. 2021; Akita et al. 2022), this could mean that herbivory rates measured on tiles could differ substantially from natural substrata. Ground-truthing herbivory on tiles versus natural substrata would, therefore, be useful in determining how strongly the two approaches are correlated. However, with proper consideration of these factors, large-scale,

replicable quantification of EAM herbivory using such methods appears possible.

Compared to the use of experimental tiles, quantification of yield to herbivores based on natural reef substrata is even more challenging and proportionately more limited in the literature. This is probably because such substrata cannot be easily manipulated, making quantification of the turfs in-situ challenging. Furthermore, the benthos can be very heterogenous even at small spatial scales (e.g. Harris et al. 2015). Nevertheless, through short-term (days) caging, quantification of algal turf growth has been possible (e.g. Afeworki et al. 2013; Bonaldo and Bellwood 2011; Clausing et al. 2014; Tebbett and Bellwood 2020), while longer-term (weeks) caging of natural reef substrata, when combined with scraping and vacuum sampling, offers a possible way to quantify yield to herbivores. However, this latter technique, as for quantification of herbivory from experimental substrata, can be logistically difficult given that cages generally need to be deployed for several weeks (e.g. Russ and McCook 1999; Russ 2003; Tebbett et al. 2018) limiting the efficiency of this method. In addition, the results may be affected by the development of different algal communities over space in response to herbivore exclusion (Scott and Russ 1987). As a result, such data are likely to be highly variable, making it difficult to understand herbivore impacts across space or time. In terrestrial ecology, such as research into grassland herbivory, this ecological noise has been successfully dealt with by substantial levels of replication and/or quantifying relatively large (100 s–1000 s m²) plots (e.g. Bakker et al. 2006; McNaughton 1985). However, similar solutions may not be viable options in coral reef ecology given the logistical constraints of working in these aquatic ecosystems.

One promising method that may offer a more efficient way of quantifying herbivory rates on turfs is through the use of EAM-covered rubble assays (following Bonaldo and Bellwood 2011; Goatley et al. 2016). Using this technique, large pieces of EAM-covered rubble can be transplanted from areas of low-herbivory to areas of high herbivory, in a manner akin to macroalgal assays. If the various components of the EAM (i.e. algae/cyanobacteria, detritus, sediment) on the rubble are subsampled prior to deployment, and then resampled post-deployment, this would result in a measure of yield to herbivores, without the need for prolonged caging. This has already been achieved in terms of variation in algal turf length and particulate mass under different scenarios (e.g. Bonaldo and Bellwood 2011; Goatley et al. 2016). However, while this method would overcome some of the logistical challenges outlined above, careful consideration of the type of rubble used, maintenance of particulate loads during transplantation, and ideally, direct comparisons with naturally occurring consolidated reef substrata, would be necessary to

ground-truth any rates determined with this method prior to its widespread adoption.

In addition to the measure of yield to herbivores it may also be informative to examine the bite rate of herbivorous fishes on the EAM. By filming areas of EAM-covered reef surface the relative, biomass-standardised feeding pressure of different herbivorous fishes, in different contexts, has been revealed, yielding functionally informative insights especially in terms of the key fishes involved (e.g. Bennett et al. 2015; Longo et al. 2015, 2019; Pessarrodona et al. 2022b). Although, it is important to note that the nature of the relationship between feeding pressure (i.e. bite rate) and herbivory rate (i.e. mass of plant material removed) is not currently well resolved for the EAM. It may even be that such a relationship is challenging to resolve accurately given the inherent variability in fish bites on the substratum and the difficulty in measuring fish bite size in fishes that do not leave feeding scars on the benthos. However, if clear relationships can be derived between feeding rate and the mass of plant material or carbon removed per bite, then direct quantification of herbivorous fish feeding rates may offer a realistic way of comparing herbivory across time and space. Such an approach is likely to be better than scaling-up data from fish surveys to reef-wide herbivory (e.g. Ruttenberg et al. 2019; Cinner et al. 2020), which can be useful but often overlooks meaningful functional heterogeneity across space. Indeed, scaling-up patterns of herbivore numbers to the process of herbivory may be useful in indicating relative herbivory but it has major limitations. These include: a) being unable to reveal absolute levels of herbivory, b) overlooking heterogeneity in the locations that receive herbivory, and c) overlooking variability in bite rates/sizes and mass of material removed among locations. Unfortunately, the degree to which this variability could shape results is so extensive that methods involving scaling-up data based on fish presence should be used with caution, especially in large-scale studies. As a result, to comprehensively quantify absolute herbivory on coral reefs, an approach combining both direct measurement of feeding rates and mass of plant material removed/yield to herbivores is likely to yield the most reliable results that provide direct estimates of absolute levels and account for some heterogeneity across space.

Concluding thoughts

Research into herbivorous reef fishes has made substantial progress since Steneck (1983) recognised the difficulty in quantifying the process of herbivory versus patterns in herbivore abundance. Yet, while the process-based assessment of coral reef ecosystem functioning is widely viewed as critical, few studies have met the challenge of directly measuring the process; most document fish abundance patterns and

attempt to translate these into processes. This perspective, however, highlights that the very definition of a ‘herbivorous reef fish’ makes translating patterns of herbivore abundance to the process of herbivory an inherently difficult task. If the research objective is to quantify processes, more direct methods appear necessary. In this respect, we are still looking at the tip of the iceberg when it comes to the quantification of herbivory on coral reefs. Process-based assessments of macroalgal removal have been valuable with several key insights revealed. Nevertheless, this remains a relatively minor component of total herbivory in most coral reef systems. Given the abundance of the EAM, and the herbivorous fishes that feed on it, it may now be time to expand the quantification of EAM herbivory on coral reefs, and in the sense of Steneck (1983) to move beyond ‘scratching the surface’. Indeed, the prevalence of the turfs/EAM on coral reefs now, and likely into the future, offers exciting scope for a plethora of future research directions such as understanding how the budget of production versus consumption varies under different contexts, and if some herbivores are more important than others in maintaining this budget. As the dynamic balance between primary productivity and herbivory represents a core pillar of coral reef ecosystem functioning, process orientated research into the EAM will be key to understanding the functioning of coral reefs in the Anthropocene.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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