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RESEARCH

Contrasting tropical marine herbivorous fish catches between the Indo-Pacific and Western Atlantic

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Abstract Ensuring food security in the Anthropocene presents a significant socio-ecological challenge, especially in rapidly changing coastal seascapes that sustain critical fisheries. Herbivorous fishes are essential for food and financial security through fisheries, however, their contributions to regional catches, and the factors influencing them, are not well understood. Analysing reported and reconstructed catch data across 69 Exclusive Economic Zones, we identify shallow-reef area and coastal population density as significant predictors of herbivorous fish catches. However, between-realm (i.e. Indo-Pacific vs. Western Atlantic) differences are marked, with rabbitfishes contributing disproportionately to herbivorous fishery catches. While rabbitfishes have the potential to support productive fisheries due to their relatively faster life-history traits, a 60% decline in catch-per-unit-effort suggests that their production potential, along with parrotfishes and surgeonfishes, may be decreasing globally. Our study highlights contrasting social-ecological outcomes for human populations in the Western Atlantic vs. Indo-Pacific; a difference primarily driven by rabbitfish catches.

Keywords Coral reefs · Fisheries · Parrotfishes · Rabbitfishes · Surgeonfishes

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Introduction

Sustaining food security in an era of global change represents a critical socio-ecological challenge (Willett et al. 2019; FAO et al. 2020). This challenge is multifaceted given that the growing human population increasingly demands nutritional benefits from nature, while human activities continue eroding the ecosystems' capacity to deliver benefits for humans (Steffen et al. 2011; Folke et al. 2021). These issues are epitomised in the world's coastal seascapes, especially on coral reefs (Hughes et al. 2017; Fulton et al. 2019; He and Silliman 2019). Globally, the connection between humanity and near-shore seascapes has intensified, particularly among coastal communities that rely on these ecosystems to secure livelihoods and nutrition through subsistence and artisanal fisheries (Canty and Deichmann 2022; Wong et al. 2022; Viana et al. 2023). However, these coastal seascapes are also among the most threatened ecosystems on the planet, as a range of stressors, especially global climate change, are reshaping the composition of these systems (Hughes et al. 2017; He and Silliman 2019; Tebbett et al. 2023). Ultimately, as the condition of coastal seascapes declines, their capacity to sustain fisheries yields is expected to follow (Lam et al. 2020; Eddy et al. 2021; Canty and Deichmann 2022).

Habitats within coastal seascapes display highly heterogeneous and patchy distributions, resulting in scale-dependent characteristics for associated fish assemblages and fisheries (Taylor et al. 2015; Heenan et al. 2016; Sambrook et al. 2019; Wilson et al. 2022). The influence of bottom-up effects (e.g. habitat quality and availability) and top-down effects (e.g. fishing pressure) can vary across local, regional, and biogeographic scales (Williams et al. 2015; Samoilys et al. 2019; Campbell et al. 2020; McClure et al. 2021). Given the limited availability of comprehensive small-scale fishery-dependent data across larger scales (Zeller et al. 2015; Grafeld et al. 2017), fish biomass often serves as a valuable fishery-independent indicator of potential yield (Campbell et al. 2020; McClure et al. 2021; Zamborain-Mason et al. 2023). Fish biomass is used to track changes in fish stock availability over time and to facilitate cross-stock comparisons, particularly in multi-species coral reef fisheries (Nash and Graham 2016; Birkeland 2017). Recent research has linked fishery-independent data, including coral reef fish biomass, with environmental and socioeconomic time-series data (e.g. Samoilys et al. 2019; McClure et al. 2021; Morais et al. 2023). Such studies often highlight that coral reef fish biomass is driven by bottom-up factors, including habitat quality, primary productivity, and reef geomorphology, which can lead to increased catch volumes (Samoilys et al. 2019; McClure et al. 2021; Morais et al. 2023). However, in large-scale studies, the role of habitat availability in influencing coral reef fish biomass yields may have been overlooked (Williams et al. 2015), potentially due to its seemingly obvious relationship. This omission means that relationships between fisheries catches and habitat area are not fully explored, and might lead to an underestimation of the importance of habitat area in supporting fish biomass.

At local scales, fishing has also been found to exert a pronounced top-down influence, leading to a significant reduction in reef fish biomass (Jennings and Polunin 1996a; Taylor et al. 2015; Robinson et al. 2017; Carvalho et al. 2021). Notably, in small-scale coral reef fisheries, which are characterised by diverse species, habitats, and gear types, there are a limited number of species that often dominate a significant portion of the total catch (Jennings and Polunin 1996b; Samoilys et al. 2017; Rassweiler et al. 2020). In this respect, herbivorous fishes represent a key group of fishes that lay at the junction of coastal ecosystem declines and small-scale fisheries yields (Robinson et al. 2023). Herbivory is considered a critical ecosystem function on coral reefs (Bellwood et al. 2004; Adam et al. 2015) as it may limit the dominance of algae via top-down control, potentially facilitating recovery of corals after disturbance (Bellwood et al. 2004; Hughes et al. 2007). This has led to calls for the protection of herbivorous fishes in coastal seascapes via ecosystem- and stock-based management approaches (Rogers et al. 2015; Williams et al. 2016; Chung et al. 2019). Yet, herbivorous fishes are also a key component of coastal fisheries in nations such as Indonesia, French Polynesia, the Seychelles, the Philippines, and Jamaica (Lingard et al. 2012; Bejarano et al. 2013; Edwards et al. 2014; Humphries et al. 2019; Rassweiler et al. 2020; Fulton et al. 2020; Robinson et al. 2023). Herbivorous fishes are typically targeted once higher-trophic level fish stocks have been overfished (Pauly et al. 1998; Mumby et al. 2012). Indeed, Robinson et al. (2023) concluded that herbivorous fishes are now the primary contributors to fisheries services across varying reef habitats.

Despite the attention herbivorous fishes have received from an ecological perspective (e.g. Bellwood et al. 2004; Adam et al. 2015; Bruno et al. 2019), our understanding of the biogeographical, ecological, and socioeconomic factors that influence variation in catches of herbivorous fishes across different regions and realms remains limited. Fishery-independent data, such as underwater estimates of fish abundance, indicate that reef fish distribution patterns can be primarily influenced by habitat effects at larger scales (Bellwood and Tebbett 2024). These broader habitat impacts can often overshadow more localised fishing-related effects on biomass reduction (Taylor et al. 2015; Heenan et al. 2016). However, fishery-dependent datasets, specifically assessments of total catch data, are typically restricted to local studies. Nevertheless, at the local scale, herbivorous fishes can contribute over 50% of the total catch in coral reef fisheries (Houk et al. 2012; Bejarano et al. 2013; Samoilys et al. 2017; Rassweiler et al. 2020; Cook et al. 2024). This substantial contribution is influenced by various factors affecting catch success, including environmental conditions, wave-exposure regimes, and fish behavioural traits (Houk et al. 2012; Samoilys et al. 2017; Humphries et al. 2019). Moreover, herbivorous fishes are captured using diverse gear types, including hook and lines, traps, spears, and nets, rendering them susceptible to a wide array of fishing methods (Bejarano et al. 2013; Campbell et al. 2014; Samoilys et al. 2017; Humphries et al. 2019).

Given the ecological importance of herbivorous fishes in coastal seascapes (Bellwood et al. 2004; Hughes et al. 2007; Adam et al. 2015), and their potential to be a productive nutritional resource to people (Robinson et al. 2019, 2023; Hamilton et al. 2022), a better understanding of their fishery, at larger scales, is clearly important. Previously, this endeavour has been constrained by the scarcity of large-scale fishery-dependent datasets. However, the Sea Around Us (SAU) project has been pivotal in overcoming this limitation, with this project now providing global time-series data on reported and reconstructed fisheries catches (Pauly et al. 2020). The SAU project conducts taxon and fishery-specific catch data reconstructions by analysing fisheries, socioeconomic, and population data sources, offering both total catch (in tonnes) and fishing effort (kW) estimates for various fishing sectors at the country/territory scale, with reporting conducted at the Exclusive Economic Zone (EEZ) level (Pauly and Zeller 2016). These large-scale fishery-dependent data have previously been instrumental in identifying the data-poor and under-reported nature of small-scale fisheries across Pacific islands (Zeller et al. 2015) and the possible global decline in the production potential of coral reef fisheries (Eddy et al. 2021).

Here, we utilised large-scale catch estimates from the SAU project focussing on three archetypical tropical fish groups that are predominantly considered nominal herbivores (i.e. surgeonfishes, parrotfishes, and rabbitfishes; Fig. 1), to examine how yields are related to biogeographic, ecological, and socioeconomic correlates. Our analyses involved fishery-dependent data, including total catches (in tonnes), and an indicator of relative abundance, namely catch-per-unit-effort (CPUE), from the EEZs of 69 nations (i.e. countries and territories), spanning the period from 1950 to 2019, with an emphasis on the most recent and best-documented decade (2009 to 2019). We also examined temporal changes in harvest estimates (e.g. total catch per reef area). In addition, for the most recent decade, we investigated whether the average total fish catch (in tonnes) of each

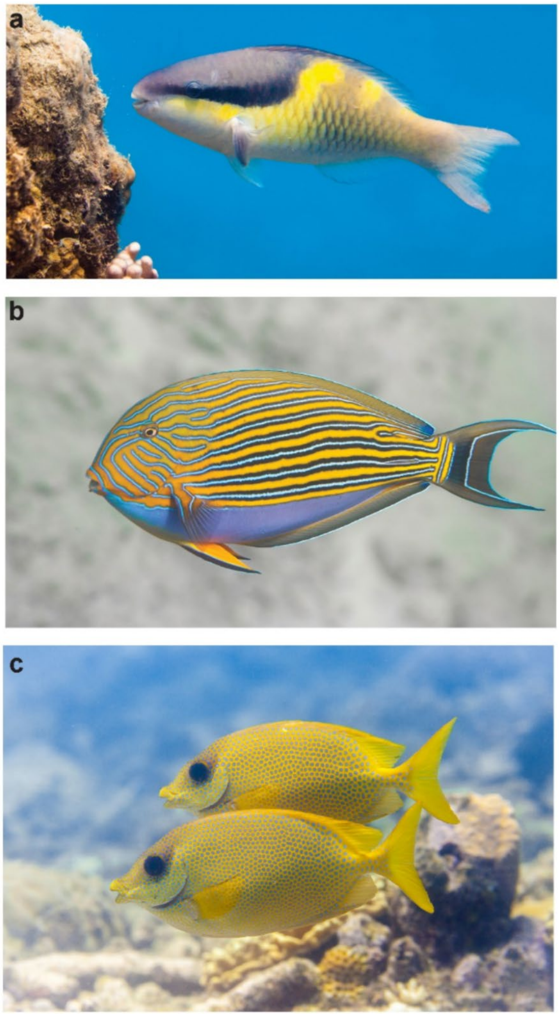

Fig. 1 Species from the three focal herbivorous fish groups. The **a** parrotfish (*Scarus oviceps*), **b** surgeonfish (*Acanthurus lineatus*), and c) rabbitfish (*Siganus corallinus*) (images V. Huertas)

herbivorous fish group and the average CPUE (as an indicator of fish abundance/biomass), were related to habitat availability (i.e. reef area, the principal habitat of most herbivorous fish species) and socioeconomic factors (i.e. human population density per km^2 of reef; Houk et al. 2012; Brewer et al. 2013), Ocean Health Index (OHI; Halpern et al. 2012), and Marine Dependency Score (MDS; Selig et al. 2019) using generalised linear models (GLMs). Moreover, given the biogeographic differences in fish distributions (surgeonfishes and parrotfishes are globally distributed; rabbitfishes only occur in the Indo-Pacific; Siqueira et al. 2019a), we considered how catch estimates of the three groups varied individually between the Indo-Pacific and Western Atlantic realms. This enhanced understanding of how fishery estimates relate to biogeographic, ecological, and socioeconomic factors may be crucial for informing strategies to manage the production potential of herbivorous fisheries, benefiting both ecosystems and coastal communities.

Materials and methods

Catch data collation

Our study focused on three groups of fishes: parrotfishes, surgeonfishes, and rabbitfishes, which are widely recognised as the primary tropical nominal herbivorous fish groups (Tebbett et al. 2024). These three groups are ecologically important (Bellwood et al. 2004; Adam et al. 2015) and contribute to numerous artisanal and subsistence fisheries (Robinson et al. 2011; Hicks and McClanahan 2012; Bejarano et al. 2013; Samoilys et al. 2017; Fulton et al. 2020). To examine how the catch of these three nominal tropical herbivorous reef fish groups varied between biogeographic realms, we compiled a dataset using reported and reconstructed catch data from the Sea Around Us Project (Pauly and Zeller 2016; Pauly et al. 2020), which reports landings data (in tonnes) for each taxonomic group (from 1950 onwards) from a nation's Exclusive Economic Zones (EEZ). Here, we included both countries' and territories' EEZs that reported individual landings data; for example, although the Andaman and Nicobar Islands are not an independent state, their landings data were reported separately from those of India and were thus treated as an individual nation in our analyses. It is crucial to highlight that global catch data are limited by what nation's actually report annually to the Food and Agriculture Organization of the United Nations, which can be improved with reconstructions (as done by the Sea Around Us Project; Pauly and Zeller 2016). Although small-scale artisanal and subsistence fisheries are typically underreported (Sale 2008; Teh et al. 2013; Zeller et al. 2015), such as those targeting herbivorous fishes, non-commercial fisheries can contribute up to 80% of the total catch in coastal fisheries in certain countries (Dalzell et al. 1996; Grafeld et al. 2017). For instance, in Indonesia, surgeonfishes and parrotfishes contribute substantially to small-scale fisheries (e.g. Humphries et al. 2019), yet their catches may go unreported due to the absence of mandatory reporting requirements (Sari et al. 2021). Similar gaps in reported catch data occur in other key fishing nations, as summarised in Table S1. Consequently, the use of catch data here, particularly the analyses of average total catch across herbivorous fish groups and average catch-per-unit-effort, are likely to be conservative estimates. True catch values may be even higher.

We generated a list of species and genera for each herbivorous fish group from Acanthuridae, 'Scaridae', and Siganidae from FishBase (Froese and Pauly 2022). Please note that although parrotfishes are taxonomically within the family Labridae, they are still often reported as 'Scaridae' (cf. Bellwood 1994). We then extracted all available taxon-specific catch data for each group at the species, genus, and family level to avoid incomplete catch data due to the variation of taxonomic resolution of reported and reconstructed catches. In addition, SAU provides catch data categorised by 'functional groups', with one of these groups being all reef-associated fishes. Therefore, following the same approach as above, we also extracted catch estimates for all reef-associated fishes from the same EEZs, as well as overall catch by each EEZ per year.

We adapted the methods outlined by Eddy et al. (2021) to calculate catch-per-unit-effort (CPUE) for each group (i.e. surgeonfishes, parrotfishes, and rabbitfishes) from 1950 to 2010. We first determined the proportion of herbivore catch for each group from the total catch of all reef-associated fishes in each EEZ from 1950 to 2010. We then multiplied each EEZ's total fishing effort, which we extracted from the SAU database (Greer 2014), by that proportion. Lastly, we divided the total herbivorous fish catch by the estimate previously calculated (i.e. effort multiplied by the proportion) (Text S1). This produced a comparable relative estimate of CPUE for each herbivorous group per EEZ per year. Fishing effort data were only available for 1950–2010, limiting CPUE analyses to that period.

The fishing effort data from the SAU database are independent of catch data and were compiled using the same reconstruction approach (e.g. Greer 2014; Pauly and Zeller 2016; Greer et al. 2019). First, the number of vessels in a fleet were identified, with vessels categorised by country, sector, gear, length, and motorisation. Engine capacity (kW) per vessel was then assessed based on length and motorisation. Effective fishing effort is calculated as the product of engine capacity (kW) and the number of days at sea for the fleet segment (Greer 2014; Greer et al. 2019). To ensure comparability in effort and associated CPUE calculations, we focused solely on effort expended in the subsistence and artisanal sectors, excluding gear types not commonly used for harvesting herbivorous fishes (i.e. drifting longlines, driftnets, gleaning, lampara, longline not specified, midwater shrimp trawl, pelagic longline, set longline, and trolling).

Both total catch and CPUE offer crucial insights for understanding fisheries dynamics. Total catch provides a comprehensive view of harvesting scale, aiding in the evaluation of fishing's overall influence on aquatic resources (Pauly et al. 2013). In contrast, CPUE assists in assessing the effectiveness and impact of fishing efforts. It may reveal trends that arise from the interplay between harvested biomass and fishing effort expenditure, acting as an indicator of relative biomass (Eddy et al. 2021). By analysing both metrics, our objective is to disentangle trends within small-scale seascape-associated fisheries in a more comprehensive manner, allowing for more informed inferences regarding large-scale drivers. Temporal trends in total catch, fishing effort, and CPUE for each herbivorous fish group were plotted across the entire dataset, which spans from 1950 to 2020 (1950–2010 for fishing effort). It is important to note that these trends serve as an overview of the dataset and were not subjected to formal analysis, as the primary focus of this study was placed on the most recent decade which is likely to have the most robust data (as it consists of less reconstructed catch data; e.g. Christ et al. 2020).

Environmental and socioeconomic variable collation

We used large-scale ecological and social variables to assess the potential drivers of herbivore catches. To explore potential biogeographic differences, we assigned each EEZ a biogeographic location following the general delineation of realms by Kulbicki et al. (2013). Namely, we separated EEZs into the Indo-Pacific and the Western Atlantic. We focused on the Indo-Pacific and Western Atlantic as these areas incorporate the majority of countries bordering coral reefs (Wong et al. 2022), as well as major marine biodiversity hotspots (Roberts et al. 2002). We found that in the Tropical Eastern Pacific (TEP), only Nicaragua and Colombia had available data for reconstructed or reported herbivorous fish catch. However, due to the nature of our covariates, which are primarily country-based, and considering the complexity of differentiating catch estimates between the Pacific and Caribbean sides of these countries, we chose to categorise both Nicaragua and Colombia as part of the Western Atlantic region. This decision was influenced by the fact that a significant portion of their EEZ and shelf area is located in the Caribbean, the inherent evolutionary link between the TEP and Western Atlantic, the relatively depauperate and less diverse fish fauna (compared to the Indo-Pacific or Western Atlantic), and the absence of rabbitfishes in both biogeographic realms (Kulbicki et al. 2013; Siqueira et al. 2019a, b).

Area estimates of each EEZ, as well as a spatial layer of their global distribution, were accessed via the Flanders Maritime Institute (Flanders Marine Institute 2019). Using a global coral reef distribution layer (UNEP-WCMC 2021) and global bathymetry layer (GEBCO Compilation Group 2023), we estimated the area of reef habitat and shallow coastal habitat (0–30 m depth) area within each EEZ using ArcGIS Pro 2.9.0. We limited shallow coastal habitats to the tropics (i.e. between 30 degrees North and South) as we were examining tropical herbivorous fish groups. We intersected global reef and shallow-water habitat distributions with the EEZ spatial layer, after projecting each to the Equal Earth projection (EPSG 1078), to calculate both coral reef area and shallow-water habitat area per EEZ. Importantly, shallow coastal habitat area and reef area were highly correlated (Pearson's r = 0.84; Fig. S1). Moreover, we chose to use reef area as a direct measure of available habitat for herbivores rather than other ecological proxies, such as coastline length. While coastline length may be useful for generalist species, it fails to account for specific habitat affinities. By using reef area, our approach provides a more accurate representation of the habitat available to herbivores. Consequently, in our statistical analyses, we included only reef area as a predictor to avoid collinearity, while also considering it a proxy for shallow coastal habitat availability.

A range of social drivers were included and assigned to each EEZ to determine the potential relationship between socioeconomic factors affecting herbivorous fish catches. Social variables included coastal population density levels, Marine Dependency Score (MDS; Selig et al. 2019), and Ocean Health Index (OHI; Halpern et al. 2012), which were chosen because of their availability at an EEZ level, and their contribution to varying aspects of human dependence on marine resources. The coastal population density for each EEZ was estimated using a 100 km buffer along the coastline of each EEZ and a population density raster from 2010 and 2020 (Center for International Earth Science Information Network - CIESIN - Columbia University 2022). We then calculated population density per reef area by dividing coastal population density by the estimated reef area for each EEZ for both time periods (following Houk et al. 2012; Brewer et al. 2013; Campbell et al. 2014; Samoilys et al. 2019). For modelling purposes, in cases where the population density per reef area was zero (such as isolated island territories like Wake Island, in the northern Pacific Ocean), we assigned a low value (0.1), which corresponds to the lowest 10% of values found in the dataset.

We also used the Marine Dependency Score (MDS) as a standardised measure of the importance of marine-derived services as it encompasses the nutritional, economic, and coastal protection dependency of each nation (Selig et al. 2019). This relatively novel conceptual framework represents a detailed quantitative assessment of the level of human dependence on marine ecosystems based on the value of the benefit, vulnerability to loss, and availability of substitutes (Selig et al. 2019). Although published in 2019, the MDS calculations primarily relied on datasets from 2011, thus reducing temporal disparities between response and explanatory variables in our statistical analyses. Because the Ocean Health Index (OHI) is a framework for assessing the health of marine ecosystems based on ten broad ecological, social, and economic goals (Halpern et al. 2012), it was also included in our analyses. OHI values were available from 2012 onwards. Other social variables like the Human Development Index or Gross Domestic Product (GDP) are only available at a sovereignty (i.e. country) level, whereas OHI and MDS are available for countries and territories. By using both indices in our analyses, we can comprehensively account for both the state of the surrounding marine environment as well as the usage of marine resources.

Statistical analyses

To explore the relationship between our fishery estimates (average total catch and average CPUE) and large-scale environmental and socioeconomic covariates, we employed Generalised Linear Models (GLMs). Renowned for their versatility and effectiveness across various applications (Zuur et al. 2009), GLMs possess a key feature—proficiency in fitting predictors, enabling us to compare the effects of predictor variables on the response variable (Bolker et al. 2009; Harrison et al. 2018). In addition, we centred and scaled all continuous predictors (via *z*-score transformations; i.e. by subtracting the mean and dividing by the standard deviation), a process aimed at enhancing the relative interpretability of regression coefficients across multiple predictors (Schielzeth 2010).

To generate a single estimate of catch for each herbivorous group per EEZ for analysis, we used the average yearly total catch for each group over the most recent decade available (i.e. from 2009 to 2019). To examine the relationship between average total herbivore catches between 2009 and 2019 and the set of explanatory variables, we used GLMs with a Gamma distribution and a log-link from the '*glmmTMB*' package (Brooks et al. 2017) as the average total catch was never zero. Specifically, we assessed if reef area (km^2), realm (i.e. Indo-Pacific and Western Atlantic), and social drivers (i.e. OHI, MDS, and/or coastal population per reef area), were related to average total fishery catches of each herbivorous fish group. We used the average OHI from 2012 to 2019 and population density data from 2020 to ensure close temporal alignment. For all GLMs, average total catch for each group from each EEZ was treated as the response variable, while realm was treated as a categorical fixed effect and all other variables as continuous fixed effects. All continuous fixed effects were transformed via *z*-score transformations as above; reef area and coastal population per reef area were also logged. We specified models with an interaction between realm and reef area, and additive effects between all social covariates (i.e. no interactions). Subsequently, when models were indistinguishable based on Akaike Information Criterion corrected for small sample sizes (i.e. Δ AICc < 2), we chose the most parsimonious model (Table S2).

We also used GLMs with a Gamma distribution and a log-link to assess the relationship between CPUE of all herbivorous fishes and the same set of transformed and standardised explanatory variables. Since effort data were only available until 2010 and only for 62 of the EEZs included in this analysis, we used the average CPUE of all nominal herbivorous groups over the five most recent years available (2005–2010). Although this analysis represents only a subset of those used to assess average total catches, these 62 nations still accounted for 84% of the total catch. Using the average CPUE between 2005 and 2010 of all herbivorous groups, we generated a single, positive estimate of CPUE per EEZ and treated this as the response variable. To ensure consistency in the temporal scales of our explanatory variables, we utilised the OHI from 2012 and coastal population density data from 2010, while keeping the other explanatory variables the same as above. Furthermore, to investigate whether the significant interaction between reef area and realm, as well as the impact of OHI on the average CPUE, was driven by a single outlier (Niue), we used the same GLM structure on a dataset that excluded Niue (Table S3). However, we had no biological nor socioeconomic reason to remove the outlier, so we show the complete analyses and results for full transparency. All model assumptions and fit were assessed using simulated residuals, which were satisfactory in all cases (package: '*DHARMa*'; Hartig 2022). All statistical analyses and data manipulations were performed using the software R 4.2.2 (R Core Team 2022) and '*tidyverse*' package (Wickham et al. 2019).

Results

Herbivorous fish catches–an overview

Between 1950 and 2019, a total of 69 EEZs in the SAU database harvested parrotfishes, rabbitfishes, and/or surgeonfishes (Fig. 2a). During this period, total annual catch of each herbivorous fish group in each realm (i.e. the sum of all reported and reconstructed catch across all EEZs within each realm for each family in each year), per km^2 of reef area, generally increased (i.e. catch was higher in 2019 than it was in 1950) (Fig. 2b). However, the extent of catch increases differed across herbivorous fish groups in each realm. Notably, rabbitfish catch exhibited the largest increase, rising from 0.16 tonnes per km^2 to 0.73 tonnes per km^2. By comparison, in the Indo-Pacific, parrotfish catch increased marginally from 0.12 tonnes per km^2 to 0.14 tonnes per km^2 between 1950 and 2019, while in the Western Atlantic, it increased from 0.2 tonnes per km^2 in 1950 to a peak of 1.2 tonnes per km^2 in 1992, before decreasing to 0.54 tonnes per km^2 by 2019. Surgeonfish catch in the Indo-Pacific rose from 0.1 tonnes per km^2 to 0.17 tonnes per km^2 between 1950 and 2019, whereas in the Western Atlantic, it increased from 0.13 tonnes per km^2 to 0.29 tonnes per km^2 between 1950 and 2019. Importantly, the notable increase in total rabbitfish catches from 1950 to 2019 (Fig. 2b) may reflect a substantial increase in fishing effort for this group, which, in 2010, was almost eightfold higher than parrotfishes and surgeonfishes combined (Fig. 2c). Furthermore, rabbitfishes contributed the most to the total catch of all herbivorous fishes across all years, regardless of reef area (Fig. S2). This pattern remains consistent when considering the catch of herbivorous fish groups relative to catch of all reef-associated fishes (Fig. S3). While the overall contribution of all herbivorous fishes to global reef-associated catches has declined since the 1950s, rabbitfishes have recently increased, now contributing around 6.5% to total reef-associated fishery catches (Fig. S3).

Spatial distribution of herbivorous fish catches

Based on the initial exploration of the data, rabbitfishes appear to disproportionately contribute to large-scale catch patterns. However, to account for habitat impacts and biogeographic differences that

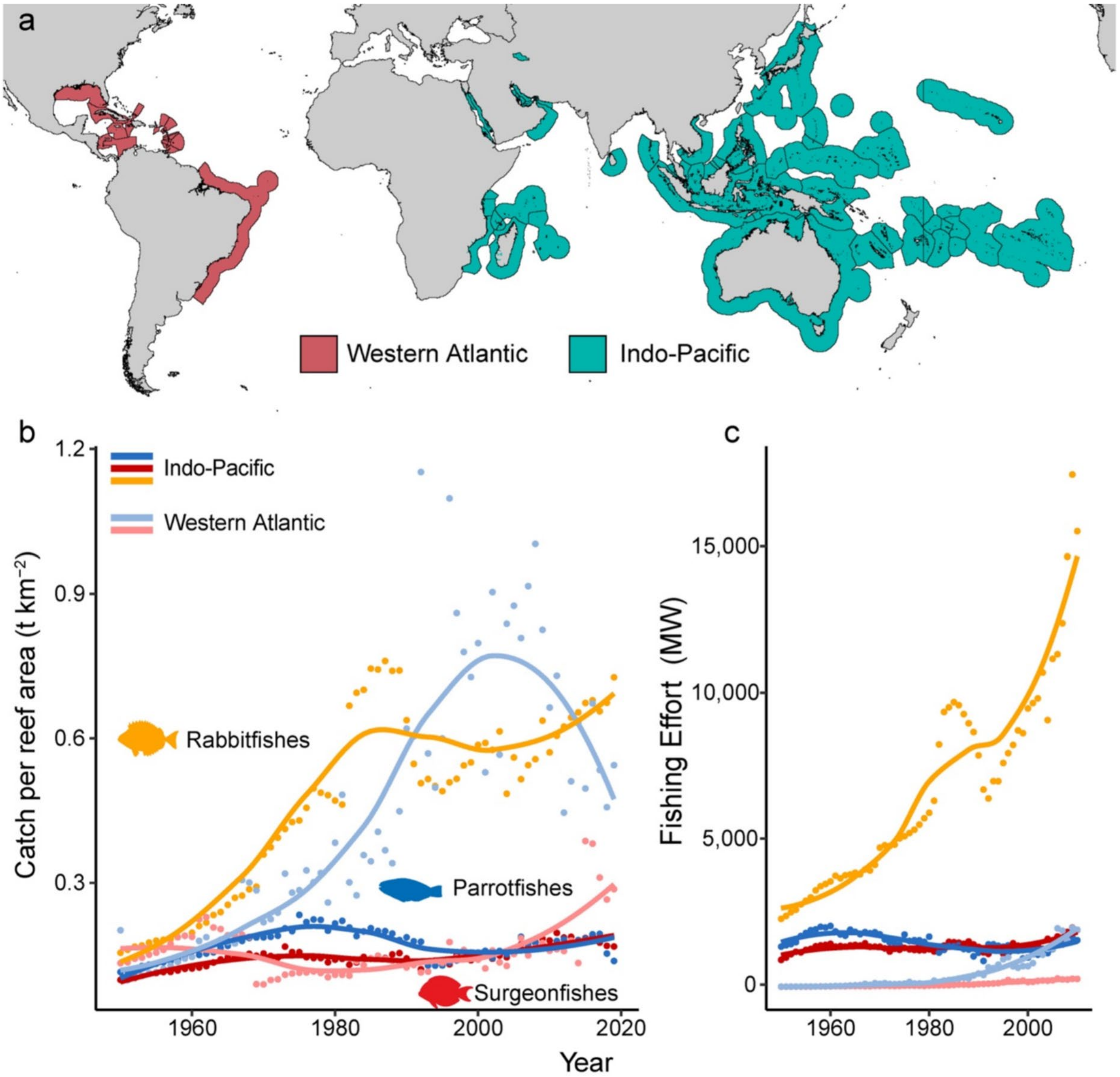

Fig. 2 Temporal patterns of tropical herbivorous fish catch data. **a** Location of the 69 Exclusive Economic Zones (EEZs) included in the analysis, **b** total catches of herbivorous fishes (rabbitfishes [yellow shades], parrotfishes [blue shades], surgeonfishes [red shades]), standardised by reef area, across EEZs in the Indo-Pacific (bright coloured) and Western Atlantic (pale coloured) per year between 1950 and 2019, and **c** the total fishing effort (Mega Watts) for each herbivorous fish group across EEZs in the Indo-Pacific (bright coloured) and Western Atlantic (pale coloured) per year. Differences in fishing effort among herbivorous fish groups likely stem from variations in their occurrence across distinct EEZs with different fleet characteristics, as well as the varying proportions of each group within the total reef-associated catch (see Methods). In all panels, points are the raw data points (i.e. sums of annual estimates across all EEZs in each realm) while the lines were produced by the loess function of the '*stats*' package (R Core Team 2022) and are used for illustration purposes only

may introduce greater variability at smaller scales, we examined how average total herbivorous fish catches (in tonnes) were spatially distributed and how this variability related to key correlates, using data from the most recent 10 years (2009–2019). These data are likely to be the most robust as they consist of fewer reconstructed catch estimates (e.g. Christ et al. 2020) and facilitate more reliable comparisons with recent estimates of both ecological and socioeconomic covariates. During this ten-year period, the average yearly total catches of herbivores in each of the 69 EEZs was spatially heterogenous, ranging from 0.01 tonnes in Eritrea to 22,572 tonnes in the Philippines (Fig. 3a-c). In addition, as expected based on the biogeographic distribution of rabbitfishes (i.e. they are absent from the Western Atlantic; Siqueira et al. 2019a), the data also shows that rabbitfishes were only a major contributor to the herbivore catch in the Indo-Pacific, while both surgeonfishes and parrotfishes were harvested across both realms (Fig. 3a-c).

Correlates of herbivorous fish catches

Given the heterogenous distribution of average total herbivorous fish catches over the most recent decade, we formally tested their variability and correlation with potential covariates using generalised linear models (GLMs) for each herbivorous fish group. Across all herbivorous fish groups, we found that reef area (see Methods) stood out as the sole consistently significant covariate ($p < 0.01$; Fig. 4a-c; Table S3; see Fig. S4 for raw data points). Generally, the GLMs employed to evaluate the relationship between the average total catch (in tonnes) of each herbivorous fish group over the last decade and our large-scale covariates indicated an increase in average total catch across all herbivorous fish groups with greater reef area/coastal habitat availability. Rabbitfishes, in particular, generated the highest average catch for any given reef area (Fig. 4a-c; Table S3). Furthermore, reef area (estimate = 1.50; $p < 0.001$; Fig. 4a; Table S3), coastal human population per km^2 of reef (estimate = 1.54; $p < 0.001$; Fig. S5a; Table S3; hereafter referred to as coastal population density), and OHI (estimate = 0.77; $p = 0.03$; Table S3) explained over 67% of the variability in average total rabbitfish catches across EEZs between 2009 and 2019. Average total catch of surgeonfishes differed between realms, with higher catch in the Indo-Pacific (estimate = -1.27; $p = 0.01$; Fig. 4b; Table S3), and was also positively correlated with reef area (estimate = 0.85; $p < 0.01$; Fig. 4b; Table S3), coastal population density (estimate = 0.89; $p < 0.001$; Fig. S5b; Table S3), and MDS (estimate = 0.54; $p = 0.04$; Table S3). Lastly, reef area alone (estimate = 1.52; $p < 0.001$; Fig. 4c; Table S3) explained over 54% of the variability in parrotfish catch. These results, therefore, highlight that, at a large scale, EEZs that contain larger areas of shallow reef habitat and higher coastal population densities, landed higher catches of herbivorous fishes.

However, it is critical to note that the results suggest clear differences in herbivorous fish yields between realms when reef area is accounted for in the GLMs (Fig. 4). For example, based on an EEZ with an estimated reef area of 1000 km^2, catches in the Atlantic would be in the order of 343 tonnes yr^{-1} (238 t parrotfishes, 105 t surgeonfishes). In contrast, the Indo-Pacific yields would be approximately 4150 tonnes yr^{-1} (238 t parrotfishes, 340 t surgeonfishes, and 3572 t rabbitfishes). Notably, when considering only parrotfishes and surgeonfishes, Indo-Pacific yields are 69% higher, though the differences may be even larger due to potential underreporting in key Indo-Pacific fishing nations (e.g. Indonesia). When rabbitfishes are included, the yields are 1110% higher in the Indo-Pacific compared to the Atlantic. This substantial difference is primarily driven by the relative contribution of rabbitfishes, which constitute approximately 86% of Indo-Pacific herbivorous fish catches (based on an EEZ with an estimated reef area of 1000 km^2).

Herbivorous fishes as fisheries resources

While the analyses above provide insights into ecological and socioeconomic correlates of average total catches across each herbivorous fish group, it is obvious that fishing effort is also likely to play a major role (Fig. 2c). Examining catch-per-unit-effort (CPUE) for rabbitfishes, surgeonfishes, and parrotfishes, which effectively standardises total catch by fishing effort, reveals distinct trends across realms (Fig. 5a). In the Indo-Pacific, rabbitfish CPUE declined by 60% from its 1977 peak, while surgeonfish and parrotfish catches declined by 25% and 47% from their respective peaks in 1973 and 1991. In the Western Atlantic, surgeonfish CPUE steadily declined throughout the entire period, dropping by 91% between 1950 and 2010. Parrotfish CPUE followed a similar trend, decreasing by 94% from its 1950 peak to 2010. We used GLMs to assess how ecological and socioeconomic factors (i.e. reef area, coastal population density, MDS, and OHI) were linked to variability of the average CPUE (tonnes per kW) for all herbivorous fish groups combined for the most recent five years available (2005–2010). In doing so, we

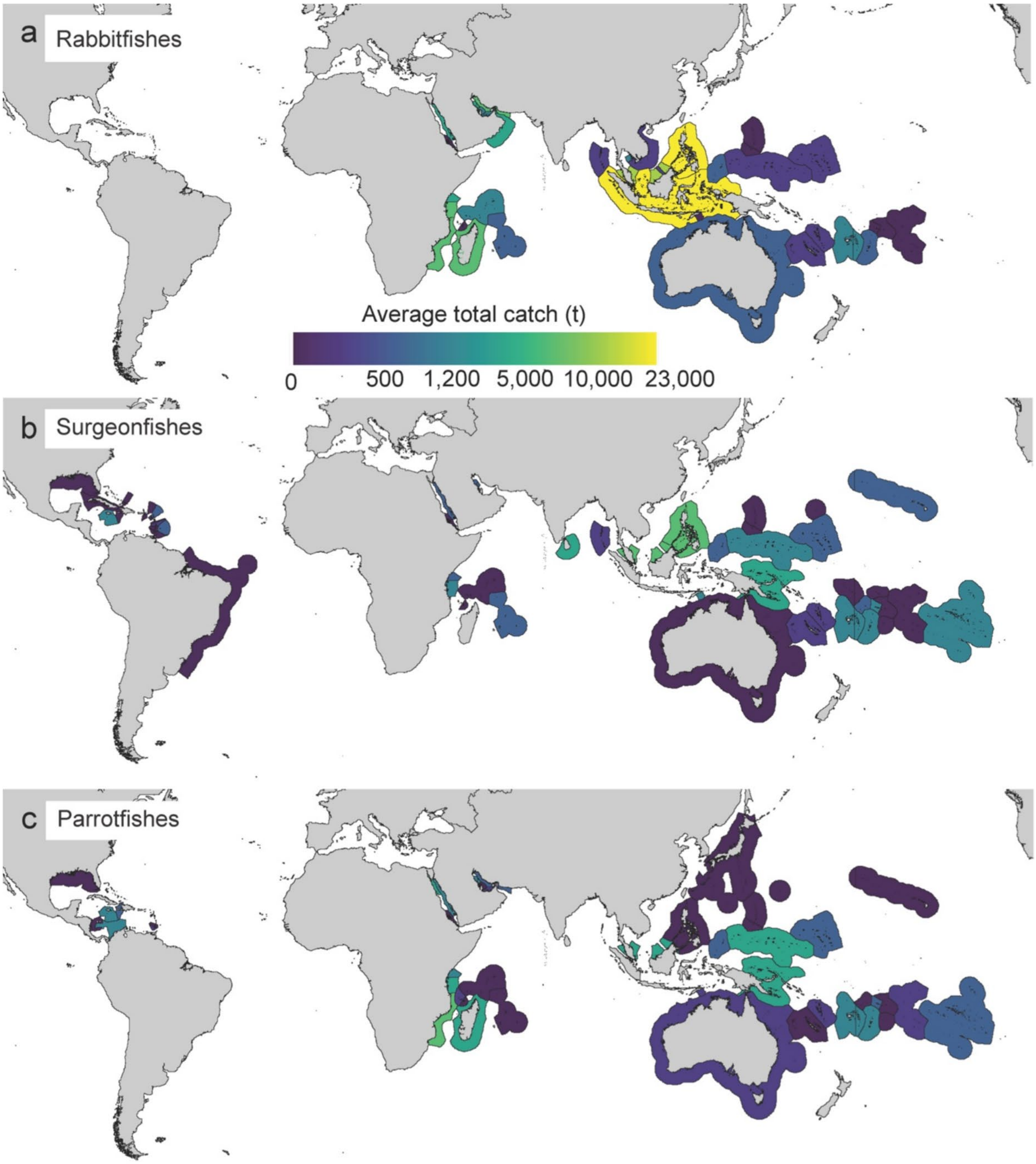

Fig. 3 Spatial distribution of tropical herbivorous fish catches. The average yearly total catches (tonnes; t) of **a** rabbitfishes, **b** surgeonfishes, and **c** parrotfishes across Exclusive Economic Zones (EEZs) between 2009 and 2019. Note that Indonesia did not report surgeonfish or parrotfish catches for this period (refer to Table S1 for an overview of reporting nations for each herbivore group)

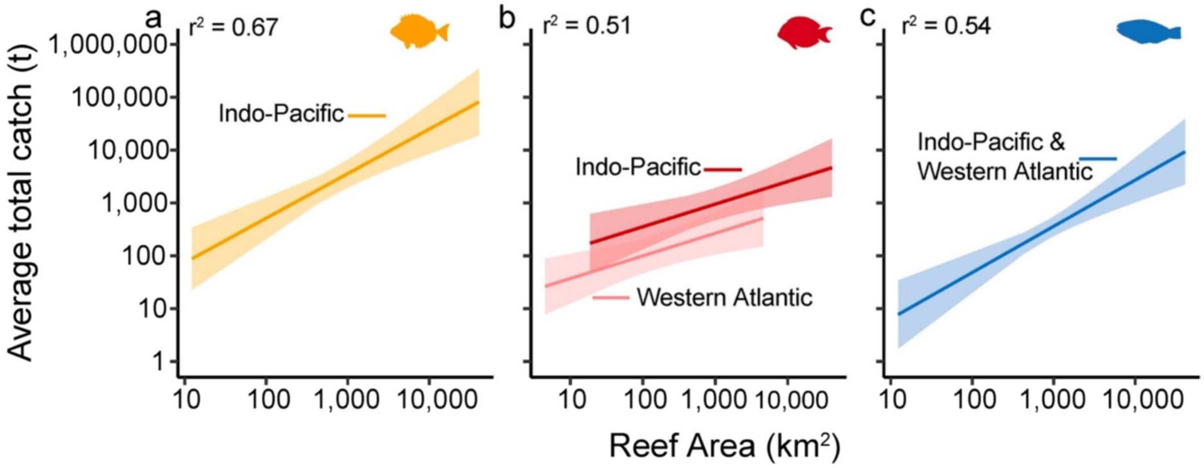

Fig. 4 Herbivorous fish catches between major realms. The relationship between the average yearly total catch (2009–2019) of **a** rabbitfishes ($r^2 = 0.67$), **b** surgeonfishes ($r^2 = 0.51$), and **c** parrotfishes ($r^2 = 0.54$) and the corresponding reef area (km^2) across the Indo-Pacific (darker colours) and Western Atlantic (lighter colour in panel b). Lines show the mean predicted fits from generalised linear models and the shaded ribbons are the 95% confidence intervals. Note the y- and x-axes are on the $\log_{10}$ scale and the r^2 value refers to the fit of the entire model. Also note that there was no significant between-realm difference in parrotfish catches (hence the single fitted line). For a version of this Fig. with raw data points, and separate lines for parrotfishes in each realm, refer to Fig. S4 in the supplemental material

revealed a significant negative relationship between coastal population density and average herbivorous fish CPUE (estimate = -1.08; $p < 0.001$; Fig. 5b; Table S3). Furthermore, average CPUE between 2005 and 2010 was significantly positively correlated with reef area in the Western Atlantic (estimate = 1.22; $p < 0.001$, Table S3), but not in the Indo-Pacific, and was significantly negatively correlated with the OHI (estimate = -0.65; $p < 0.01$, Table S3).

Discussion

Our study explored 70 years of large-scale herbivore catch data from the Exclusive Economic Zones (EEZs) of 69 nations to examine the contributions of parrotfishes, rabbitfishes, and surgeonfishes to fishery catches. As expected, we found that reef area and coastal population density were the strongest predictors of average herbivore catch. However, we also revealed that rabbitfishes were the highest contributor to catches across all herbivorous fish groups. Furthermore, despite increasing average total catches, our study reports a decline in the CPUE for all three herbivorous groups from historical levels to the most recent years. These findings indicate a potential global decrease in the production potential of these functionally important herbivorous fish groups from coastal seascapes in recent years. This has clear implications for the critical ecosystem functions that these fishes deliver across coastal seascapes, as well as for the capacity of these fishes to sustain fishery yields.

We observed that average herbivore catches increased with higher human population density and reef area (which reflects the availability of total shallow coastal habitat area). However, when standardised for fishing effort, the GLM revealed a negative relationship between CPUE of all herbivorous fish groups and coastal population density, indicating that higher human densities may contribute to a decrease in the production potential of herbivorous fishes through increased fishing effort. These results suggest that: (a) there may be a habitat area-dependent baseline level of catch that is consistent across large-scales, irrespective of social drivers, (b) that coastal fishers in tropical seascapes catch the fishes available to them in accessible habitats (Samoilys et al. 2017; Robinson et al. 2020), and (c) that more people lead to higher herbivorous fish catches, but CPUE is lower when human populations are high, which is likely due to a reduction in fishable biomass (Edwards et al.

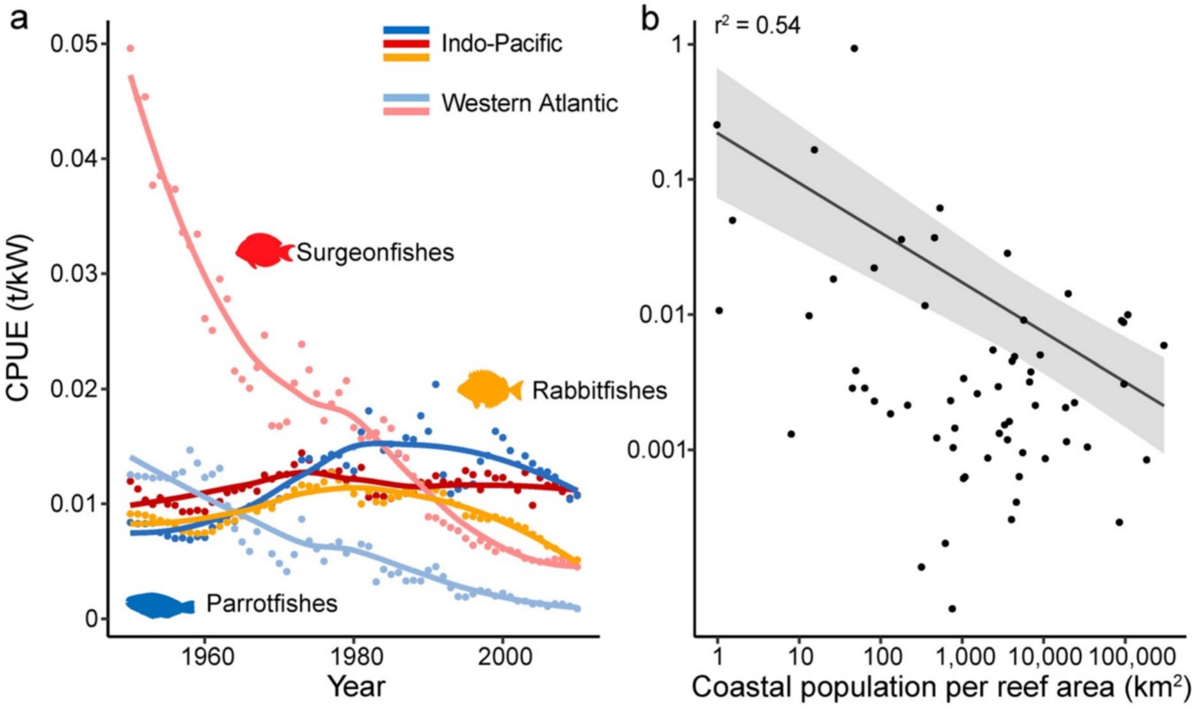

Fig. 5 Tropical herbivorous fish catch-per-unit-effort. **A** Catch-per-unit-effort (CPUE; tonnes per kW) of each herbivorous fish group (rabbitfishes [yellow shades], parrotfishes [blue shades], surgeonfishes [red shades]) across all EEZs in the Indo-Pacific (bright coloured) and Western Atlantic (pale coloured) between 1950 and 2010, and **b** the relationship between average CPUE of all herbivorous fish groups in each EEZ between 2005 and 2010 vs. coastal population density ($r^2 = 0.54$). In panel a), points are the raw data points (i.e. sums of CPUE annual estimates across EEZs) and the lines were produced by the loess function in the '*stats*' package (R Core Team 2022) and are used for illustration purposes only. In panel **b** the points represent the raw data points (i.e. the average yearly CPUE of all herbivorous fish groups between 2005 and 2010 in each EEZ) and the line denotes the mean predicted fit from a generalised linear model, the shaded ribbon shows the 95% confidence intervals. Note the y- and x-axes are on the $\log_{10}$ scale (which is why the majority of points appear to fall below the fitted line) and the r^2 value refers to the fit of the entire model

2014; Heenan et al. 2016). Consequently, nations with larger shallow coastal habitat areas may be better positioned to extract more fishable biomass, whereas smaller nations with limited access to large coastal habitat areas may face challenges in meeting their resource demands (Robinson 2020).

While it is well established that human activities have a significant impact on coastal habitats and their capacity to provide ecosystem services (Brewer et al. 2013; Cinner et al. 2016; Seguin et al. 2023), our results indicate that social correlates, other than human population density (i.e. OHI or MDS), had a limited relationship with large-scale herbivore catch patterns. This finding is consistent with previous studies in the Indo-Pacific region that also found distinct relationships between human density and reef fish trophic structure, but limited relationships with other social variables (Ruppert et al. 2018). However, it is important to note that the manner in which links between fisheries catches, social correlates, and habitat area manifest in the data could be dependent on the scale examined. For example, a study in Timor-Leste found that the availability and distribution of shallow reef habitat can play a critical role in determining the success of livelihood strategies that rely on them (Grantham et al. 2021). Human engagement with ecosystems can, therefore, be influenced by the constraints and resources arising from the type and extent of shallow reef habitat (Grantham et al. 2021). Hence, at smaller scales, an interconnection between reef area and social correlates could dictate the nature and extent of human-nature interactions in coastal areas. However, at a regional or national scale, the availability of shallow coastal habitats and the density of human populations able to exploit them appear to be the primary correlates explaining most of the variability in herbivore catch data. In this respect, at a between-realm scale, it is also important to consider the types of fishes available to fishers in different areas.

Fish communities across tropical seascapes in the Atlantic and Indo-Pacific differ fundamentally in composition and diversity (Kulbicki et al. 2013), with significant implications for what is available to fishers. In terms of herbivorous fishes, the Western Atlantic has a far less diverse fish fauna than the Indo-Pacific, exemplified by the complete absence of rabbitfishes in the Atlantic (Siqueira et al. 2019a). Interestingly, the high contribution of rabbitfishes to herbivorous fish catches in the Indo-Pacific, which aligns with evidence from smaller scale studies, shows that rabbitfishes can account for up to 60% of total fisheries catch (by weight) in some areas (Hicks and McClanahan 2012; Muallil et al. 2014; FAO 2023). Moreover, previous studies in the Indo-Pacific have highlighted the ability of rabbitfishes to maintain coastal fishery yields even in the face of ecosystem change (McClanahan et al. 2008; Rogers et al. 2018; Robinson et al. 2019; Hamilton et al. 2022). For example, Robinson et al. (2019) found that despite extensive coral reef change caused by a mass coral mortality event and persistent macroalgal regime shifts, fishery yields in the Seychelles were maintained; driven primarily by a twofold increase in the CPUE of rabbitfishes. Together, these lines of evidence suggest that rabbitfishes may have traits that make them more capable of withstanding both ongoing fishing pressure and environmental change, which may be particularly relevant given the multi-decadal global decline of coral reefs and the shift towards altered ecosystem states in the Anthropocene (Hughes et al. 2017; Tebbett et al. 2023).

The life-history characteristics of fishes that can help withstand fishing pressure include shorter generation times and higher somatic growth rates (Jennings et al. 1998; Denney et al. 2002; Zhou et al. 2012; Abesamis et al. 2014). Both traits bolster population growth rates and fishable biomass production, potentially enhancing resistance to overfishing through rapid population turnover (Jennings et al. 1998; Denney et al. 2002; Zhou et al. 2012; Abesamis et al. 2014). Rabbitfishes possess both exceptional life history traits, reaching their asymptotic size twice as fast as parrotfishes and surgeonfishes (Text S2; Fig. S6; cf. Taylor et al. 2024a, b), and demonstrating an ability to reproduce and recruit to fishery sizes within one year (Grandcourt 2002). These faster life-history strategies may be coupled with their remarkable habitat versatility, which enables them to thrive in a diverse range of environments, including clear-water, coral-dominated reefs, and mangrove-dominated turbid estuaries (Sambrook et al. 2019, 2020). With over 50% of rabbitfish species exhibiting this versatility (Sambrook et al. 2019, 2020), and some species having wide home/occupancy ranges (Kaunda-Arara and Rose 2004; Ebrahim et al. 2020), their adaptability to various habitats is evident. The combination of key life-history traits and a capacity to occupy a range of habitats may, therefore, underpin the high contribution of rabbitfishes to fisheries catches.

However, the sustainability of rabbitfish catches, as well as those of parrotfishes and surgeonfishes, within their native ranges remains uncertain. A recent study revealed a significant decline of 63% in CPUE of reef-associated fishes since the 1990s, compromising the production potential of coral reef fisheries (Eddy et al. 2021) and potentially affecting the coastal communities reliant on these fishes (Cinner et al. 2012; Hicks et al. 2021). Our analyses, employing similar methods, show variations in herbivorous fish CPUE across realms: while Indo-Pacific parrotfishes, surgeonfishes, and rabbitfishes exhibit declines below the global average for reef-associated fisheries since the 1980s, their Western Atlantic counterparts have experienced CPUE reductions exceeding 90%.

The relative resilience of Indo-Pacific catches compared to the Atlantic may, however, be temporary. Despite their faster life history strategies and remarkable habitat versatility (which may contribute to greater resilience to fishing pressure), rabbitfishes have still experienced concerning declines. Rabbitfish CPUE has decreased by over 60% since the 1980s, with 2010 levels markedly lower than those in 1950, raising concerns over substantial losses in production potential. Their unique reproductive biology, characterised by benthic spawning (Woodland 1990) and the vulnerability of large spawning aggregations to fishing (Grandcourt et al. 2007; Robinson et al. 2011; Samoilys et al. 2013), may contribute to their susceptibility to unsustainable exploitation.

Although high somatic growth rates can potentially support higher catch rates in rabbitfishes, exploitation before sexual maturity and the targeting of both adult and juvenile specimens have led to growth and recruitment overfishing of rabbitfishes in certain regions (Grandcourt et al. 2007; Hicks and McClanahan 2012). Furthermore, rabbitfishes seem to be more susceptible to specific gear types than other herbivorous fishes; notably nets and traps which account for approximately 38% and 33% of all artisanal rabbitfish catches (values represent the sum across all identified net and trap gear categories; Fig. S7). These findings align with previous local studies that have emphasised the vulnerability of rabbitfishes to various gear types, with nets and traps frequently being the primary contributors to the overall catch (McClanahan and Mangi 2004; Soliman et al. 2009; Hicks and McClanahan 2012; Samoilys et al. 2017; Mbaru et al. 2020). For instance, McClanahan and Mangi (2004) observed that while *Siganus sutor* contributed around 16% to the total catch across all gear types, it displayed the highest susceptibility to gill nets (32% of the total catch) and large traps (21% of the total catch). To ensure the sustainability of rabbitfish fisheries, effective management measures, such as seasonal fisheries and gear modifications, could be effective (Hicks and McClanahan 2012; Gomes et al. 2014; Condy et al. 2015; Osuka et al. 2021; Carvalho and Humphries 2022). These management strategies may be essential to safeguard the potential of rabbitfishes as a resilient and sustainable component of coastal seascape fisheries.

Coastal fisheries are crucial for sustaining food security in the Anthropocene, and herbivorous fishes, which play key ecosystem roles, are an integral part of this equation. By revealing that shallow coastal habitat extent and coastal population densities are large-scale factors that relate to herbivorous fish catches and CPUE, we highlight the potential for a growing mismatch between increasing population levels and habitat area-dependent fisheries productivity. This mismatch has particularly large ramifications for developing countries, such as island nations, which are limited by small available coastal habitat areas. Moreover, given the distinct declines of CPUE across all herbivorous fish groups since the 1980s, particularly in the Western Atlantic, as well as reef fishes more generally (Eddy et al. 2021), the data suggests that these ecologically important fishes may already exhibit decreased production potential at large scales. To ensure the sustainability and resilience of coastal seascape fisheries, it is crucial to advance our understanding of herbivore fisheries, and to implement effective management of diverse tropical seascapes in a changing world.

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Data availability Data availability statement This study used data obtained from publicly accessible databases and past literature. The sources of the data and links to the databases are included in the relevant sections of the manuscript and the data will be made available at Research Data Australia on acceptance of the manuscript. Code availability statement The code used to support the results of this research will be made available upon request.

Code availability The code used to support the results of this research will be made available upon request.

Declarations

Conflict of interests The authors declare no competing interests.

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