





RESEARCH ARTICLE

Unifying Coral Reef States Through Space and Time Reveals a Changing Ecosystem

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Received: 8 February 2024 | **Revised:** 13 September 2024 | **Accepted:** 20 September 2024

Handling Editor: Jonathan Belmaker

Funding: This work was supported by the Fondation pour la Recherche sur la Biodiversité (CESAB: SCORE-Reef) and the Office Français de la Biodiversité (OFB).

Keywords: alternative stable state | Anthropocene | ecosystem function | global change | herbivory | marine protected area | overfishing | phase shift | reef resilience | regime shift

ABSTRACT

Aim: Ecological state shifts that alter the structure and function of entire ecosystems are a concerning consequence of human impact. Yet, when, where and why discrete ecological states emerge remains difficult to predict and monitor, especially in high-diversity systems. We sought to quantify state shifts and their drivers through space and time in the most ecologically complex marine ecosystem: tropical coral reefs.

Location: Worldwide.

Time Period: 1987–2019.

Major Taxa Studied: Coral reef communities.

Methods: Using a global dataset of 3375 coral reef surveys, along with 13 time series datasets ranging between 1987 and 2019, we applied a novel double-dichotomy approach to classify coral reefs into four simplified and discrete states based on the relative contributions of corals versus algae to benthic cover and small-bodied versus large-bodied fishes to fish standing stock. We then

examined state shifts considering a range of spatial predictors and tested whether states have shifted directionally over time, and the nature of the most common transitions.

Results: We show that geographic, environmental and anthropogenic context fundamentally shapes coral reef states at the local scale, which explains disparities among case studies, and stakes out critical baseline expectations for regional management efforts. We also reveal clear multi-decadal state shifts on coral reefs: over time, systems dominated by reef-building corals and small-bodied, planktivorous fishes tend to have been replaced with reefs characterised by algae and larger-bodied fishes.

Main Conclusions: Our results suggest a previously unrecognised transition from systems that harness external subsidies through small-bodied consumers associated with structurally complex live corals, to herbivore-dominated systems with stronger bottom-up dynamics. Overall, the partitioning of complex reef ecosystems into a small suite of discrete ecological states suggests that spatial context-dependency, shifting baselines and changes in reef functioning are crucial considerations for coral reef management in the 21st century.

1 | Introduction

System-wide state shifts that alter the structure and functioning of entire ecosystems are a concerning consequence of human impact on Earth (Scheffer, Carpenter, et al. 2001). Such state shifts are commonly characterised by transitions between foundation species that induce feedback loops among multiple taxa and can lock systems into alternative regimes (Scheffer, Straile, et al. 2001; Knowlton 2004). Sustained monitoring of multiple taxa is expensive, highly heterogeneous in its methodology, spatial, and temporal scale, and inherently incomplete (Magurran et al. 2010), which can make the precise determination of the causes and effects of state shifts difficult to determine.

In this context, tropical coral reefs are particularly challenging. Complex ecological interactions among countless organisms are a defining feature of coral reefs (Rowan and Knowlton 1995; Pozas-Schacre et al. 2021), but these interactions are increasingly altered by anthropogenic stressors, sometimes resulting in catastrophic ecosystem collapse (Knowlton and Jackson 2008). The most notorious state shift on coral reefs involves transitions from reef-building corals to algae (most commonly, fleshy macroalgae) (Gardner et al. 2003; Bruno and Selig 2007; Bruno, Côté, and Toth 2019). Such ‘phase shifts’ are facilitated by combinations of heat stress, storms, overexploitation, disease and nutrient pollution, which harm corals, promote algal growth, reduce grazing and shift reefs towards microbial energy pathways (Done 1992; Haas et al. 2016; Bruno, Côté, and Toth 2019; Reverter et al. 2020). While these shifts in benthic communities have unequivocally occurred, their frequency, nature, drivers and reversibility have been vigorously debated (Bruno et al. 2009; Bruno, Côté, and Toth 2019; Alves et al. 2022; Baumann et al. 2022; Crisp, Tebbett, and Bellwood 2022; Tebbett, Connolly, and Bellwood 2023). A valuable knowledge base has resulted from this discourse, but uncertainties arising from spatial context dependency, unknown baseline levels of coral dominance, and idiosyncrasies in benthic organismal categorisations limit our ability to predict when, where and why shifts in benthic communities occur.

Although causal relationships between fish community structure (primarily herbivorous fishes) and benthic composition (primarily coral cover) have proven tenuous in large-scale analyses (Russ et al. 2015; Bruno and Valdivia 2016; Bruno, Côté, and Toth 2019), numerous links between the benthos and fishes

have been documented at local and regional scales (Stuart-Smith et al. 2018; Wismer et al. 2019). For example, benthic composition and structural complexity can impose bottom-up effects on fish communities by providing shelter and prey (Taylor et al. 2018), often disproportionately affecting small-bodied fishes (Wilson et al. 2010; Alvarez-Filip, Gill, and Dulvy 2011; Brandl, Emslie, and Ceccarelli 2016). Conversely, direct exploitation of reef fishes has led to widespread extirpations of large-bodied coral reef fish species (Graham et al. 2005; Lefcheck et al. 2021), which can (but not always does) alter the benthic community through reduced top-down herbivore grazing, bioerosion and nutrient provision (Bellwood, Hoey, and Hughes 2012; Rasher, Hoey, and Hay 2013; Shantz, Ladd, and Burkepille 2020). Thus, state shifts on coral reefs may unfold through a variety of top-down and/or bottom-up mechanisms that necessitate the simultaneous examination of fish and benthic communities.

Recent work has identified coral reef states across benthic and fish communities at regional scales (Cresswell et al. 2017; Donovan et al. 2018; Jouffray et al. 2019) (including, for example, herbivore-dominated systems or coral-bacterial mat states), but global drivers and temporal dynamics of coupled fish-benthic reef states have remained largely unexplored (Strain et al. 2019). In other words, while there is rich evidence for univariate state shifts on coral reefs and their proximate drivers—most prominently, from coral-dominated to macroalgae-dominated [due to climate change (Schutte, Selig, and Bruno 2010; Graham et al. 2015; Crisp, Tebbett, and Bellwood 2022)] and from large to small-bodied fishes (due to overfishing (Graham et al. 2005; Cinner et al. 2016))—system-wide shifts in fish and benthic communities combined are only documented in isolated case studies, which can be affected by local variability and temporal mismatches (Jouffray et al. 2015; Donovan et al. 2018; Bruno, Côté, and Toth 2019; Wismer et al. 2019).

A simple, novel approach for addressing this knowledge gap is through a double-dichotomy approach (i.e., an orthogonal arrangement of two axes) (Caprihan et al. 2021), where two opposing configurations of benthic and fish communities combine for four discrete ecological states, defined by coral versus algal dominance and fish community size structure (Figure 1). Among these simplified reef states, those characterised by high coral cover and large-bodied fishes are conventionally perceived as ‘healthy’, while reefs dominated by algae and small-bodied fishes typically indicate ecosystem degradation (Graham

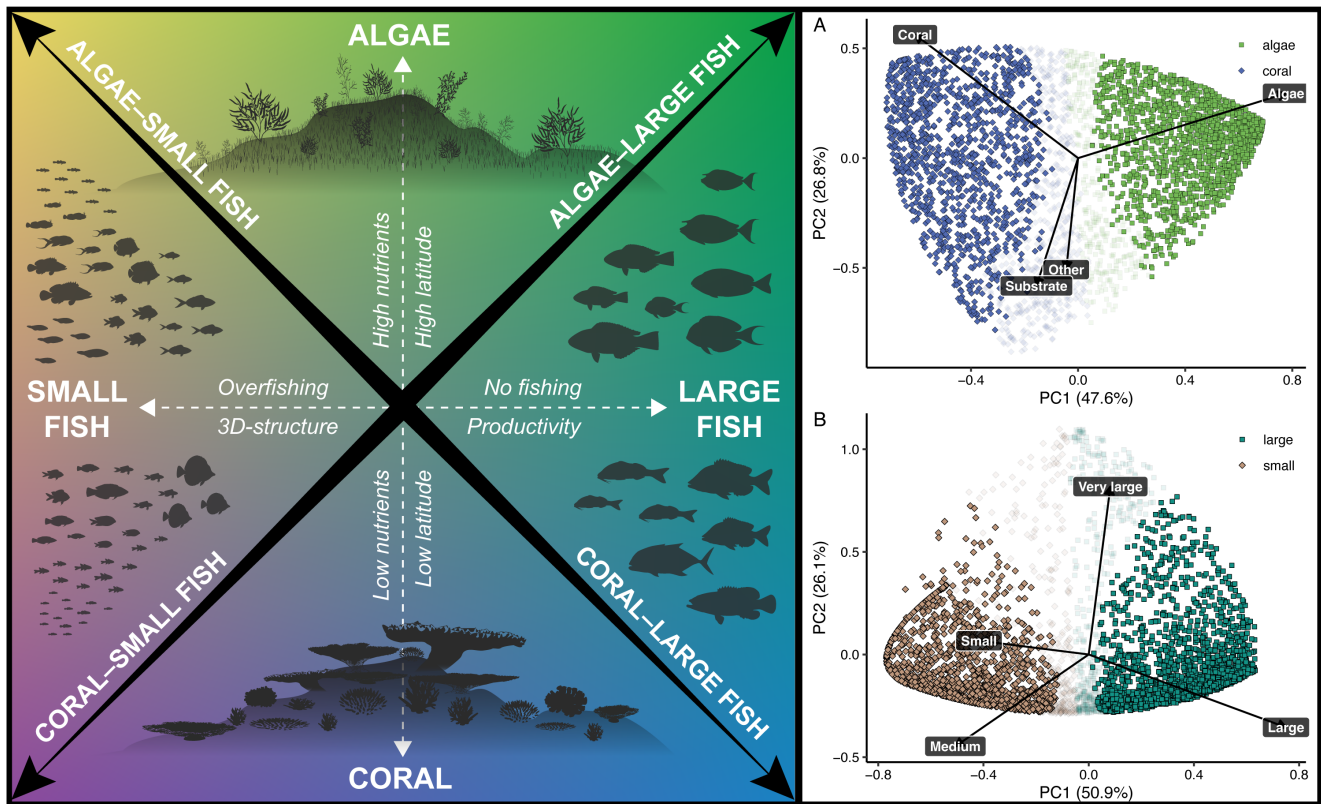


FIGURE 1 | A double dichotomy approach to identifying coral reef states based on benthic and fish communities. Using the proportional composition of benthic cover and fish size classes, reefs can be divided into state-dyads dominated by coral versus algae (y-axis) and small-versus large-bodied fishes (x-axis). This creates four distinct states along the four diagonal axes (black arrows), denoted as: Coral–large fish, algae–large fish, algae–small fish, and coral–small fish. Known and hypothesised key drivers that cause shifts towards each state are provided in white italics. (A) and (B): Ordination plots displaying the spread of surveys (from the Reef Life Survey dataset) in the first two dimensions for the benthos (A) and fishes (B). Colours denote classifications obtained from the fuzzy-clustering method, while positioning in multivariate space is based on the relative contributions of the four categories for benthic and fish communities, respectively. Variance explained by the first two PC axes is provided in parentheses. Points with low opacity denote surveys for which state assignments were <95% confident.

et al. 2005; Mumby et al. 2021). By integrating producers, habitat providers and mobile consumers into a single framework, this approach may yield insights into system-wide dynamics rarely considered in the context of state shifts on coral reefs.

We use a global dataset of coral reef communities (the Reef Life Survey [RLS]) in combination with 13 time series datasets to examine spatial and multidecadal trends in coral reef states based on the described double-dichotomy. Specifically, we (1) classify reefs into four discrete states, (2) examine spatial determinants of reef states across a global dataset and (3) examine temporal trends in reef states across 13 time series datasets. The panoramic perspective arising from our framework places all coral reefs into a unified context to guide management strategies and track our progress towards conservation targets.

2 | Materials and Methods

Our analyses consist of two main parts. First, we use the RLS dataset (Edgar and Stuart-Smith 2014; Edgar et al. 2020) to create a global coral reef state space based on a double-dichotomy approach. This allows us to examine the spatial prevalence of the obtained reef states and interrogate their potential drivers.

Second, we use this global state space to assign surveys across a compilation of 13 time series datasets of the benthos, fishes, or both, across 12 broad locations (two datasets from Mo’orea, French Polynesia) and ranging between 1987 and 2019, to the different reef states, which allows us to trace changes in reef state assignments over time. Time series ranged in their spatial and temporal spread from more than 20years of monitoring at a single site in French Polynesia, to surveys over shorter time spans at a wide range of reefs across Ningaloo Reef in Western Australia (Table S1). While we compiled 13 total time series datasets, only 10 of them were synchronised between fish and benthic surveys to permit analyses of all four states (with a total of 109 distinct sites across locations). All datasets (RLS and the time series) consist of diver-based survey protocols for fish (>5cm total length) and benthic communities. While the RLS database employs a standardised protocol throughout (Edgar and Stuart-Smith 2014), time series datasets used variable implementations of diver-based surveys (Supporting Information).

Using the RLS data, we tested whether coral reefs globally split into pre-conceived states (coral- vs. algae-dominated and small fish- vs. large fish-dominated). To do so, we computed the aggregated cover of benthic groups across four coarse categories: corals (all hard and soft corals across all growth forms, including

bleached corals), clean calcareous substrate (bare structures suitable for coral settlement, including bare rock and crustose coralline algae [CCA]), algae (all red, green, brown and calcified macro- and microalgae, including rubble and dead coral, which are covered by turf algae and microorganisms, but not including CCA), and all other categories (e.g., all sessile invertebrate taxa, sand, seagrass) (Table S2).

For fishes, we allocated all surveyed fishes to four size classes, based on their body size recorded in situ: small ($S \leq 10$ cm TL), medium ($M > 10$ – 20 cm), large ($L > 20$ – 40 cm) and very large ($XL > 40$ cm). We then computed the relative contribution of the four fish size classes to overall biomass using recorded size estimates of fishes in the field and conversions to weight via length-weight relationships (Kulbicki, Guillemot, and Amand 2005). For fish species that did not have species-specific estimates for length-weight relationships, we used averaged genus or family-level estimates. Since cryptobenthic fishes are not reliably surveyed by visual methods and generally contribute little to total standing biomass values (Brandl et al. 2018, 2019), they were not included in this study.

Our double-dichotomy approach based on coarse categories undoubtedly simplifies a complex ecological system. Algae, for instance, are often divided into short, productive, filamentous turf algae and fleshy, upright macroalgae, with the former often considered a healthy part of many reefs, while the latter are commonly considered to be a sign of degradation (Steneck and Dethier 1994; Bruno et al. 2014). Nevertheless, within both groups, numerous important and nuanced divisions can be made: for instance, turf algae can be divided into ‘beneficial’ short, productive forms, and ‘detrimental’ long, sediment-laden mats (Goatley and Bellwood 2013; Tebbett and Bellwood 2020), while macroalgae can include benign species that actively contribute to calcium carbonate production [e.g., *Halimeda* spp. (Castro-Sanguino, Bozec, and Mumby 2020)], and harmful, allelopathic algae that can lead to swift overgrowth of other benthic organisms (Rasher et al. 2011). However, field surveys rarely monitor these groups with comparable resolution and accuracy, which renders attempts to synthesise large-scale dynamics across datasets (such as the second step in the present study) reliant on broader groups that obscure fine-scale functional variability.

Our high-level classifications provide the necessary simplicity to analyse inherently heterogeneous datasets and rigorously test existing paradigms. Specifically, rather than tying benthic organisms to a specific role in the degradation of reefs, we build on characteristics that unite coral and algal categories. Corals are long-lived, mixotrophic animals with relatively low productivity that provide a rigid (Scleractinia) or semi-rigid (Octocorallia) reef framework that is likely to persist for years, while turf algae, macroalgae and cyanobacteria represent relatively short-lived and often ephemeral, autotrophic organisms (macroalgae, turf algae and cyanobacteria) that contribute little to reef structural complexity but have high primary productivity. As such, despite pertinent functional heterogeneity within each group, our birds-eye analysis captures important system-wide attributes that allow us to interpret past changes and infer future trajectories. Importantly, our approach provides only one avenue to simplify an inherently

complex system; various other methods, such as trait-based approaches, may offer fruitful complementary insights to the results presented below.

2.1 | Classifying Reef States

Our analytical approach relied on the clustering of reefs into discrete states. To assign reefs to different states, we ran a fuzzy-clustering analysis based on c-means (FCM) with two mobile centres (i.e., two state categories, in this case representing coral- vs. algae- dominated states and small vs. large fish-dominated states) and a fuzziness exponent of 1.2 for both the benthic and fish data, which we normalised using the Box–Cox-chord transformation (De Cáceres, Font, and Oliva 2010). This analysis was chosen based on its successful application in plant ecology, and its ability to reveal archetypal regimes and their associated assignment uncertainties (De Cáceres, Font, and Oliva 2010). To visualise the clustering outputs, we performed a principal components analysis (PCA). The ordination revealed that the clusters largely corresponded to the expected orthogonal states along PC1, identifying clusters dominated by coral and algae for the benthic communities and clusters dominated by small- and medium-sized fishes and large fishes for the fish communities (Figure 1). We incorporated the uncertainty of state assignments in all analyses, and tested the sensitivity of our results to pooling turf and macroalgae for the state assignments (see Figures S1 and S2). An alternative aggregation scheme for benthic groupings (following the RLS_coarse category in Table S3) was also used as a sensitivity analysis, which showed broad agreement in state assignments between classification schemes (Figure S3).

2.2 | Modelling Reef States Across Space and Conditions

We calculated the probabilities of being assigned to each of the four states (coral-large fish, coral-small fish, algae-large fish, algae-small fish) for each survey by multiplying the respective assignment probabilities (e.g., $P_{\text{coral}} \times P_{\text{small fish}} = P_{\text{coral:small fish}}$). We then examined the geographic prevalence of state types using a Bayesian model with *Realm* (Eastern Indo-Pacific, Tropical Eastern Pacific, Tropical Western Atlantic, Western Indo-Pacific and Central Indo-Pacific; Kulbicki et al. 2013) as a fixed effect using the Dirichlet distribution for the multinomial response variable (Hijazi and Jernigan 2009).

To examine the potential drivers of reef states globally, we then tested the predictive power of six environmental and anthropogenic covariates for state assignments: absolute latitude (in degrees, to incorporate the well-known tendency of reefs to flourish near the equator), depth (in m), significant wave height as a proxy of wave exposure (in m, remotely sensed from 2011 to 2019 based on Wavewatch III global model estimates; Cheung 2010), chlorophyll *a* concentration (in mg m^{-3} , remotely sensed from the Bio-ORACLE; Assis et al. 2018), human gravity (dimensionless, a composite metric of human impacts in a given location based on population density and distance; Cinner et al. 2018) and fishing restrictions (open or restricted fishing vs. no-take zones). We parsed the dataset down to surveys for which data across all

six covariates existed, resulting in a total of 3375 datapoints. We then again ran a Bayesian regression model with the four state probabilities specified as multinomial outcomes modeled with the Dirichlet distribution, and each of the six predictor variables specified as fixed effects. To account for spatial non-independence within survey sites (i.e., single reefs or reefs in close vicinity), we specified *Site* as a random effect. Finally, we sought to gauge how the model outcomes may inform our expectations for reef states under varying conditions. To do so, we predicted reef states for two hypothetical scenarios (reefs with minimal human impact at 3° absolute latitude and 20° absolute latitude), obtaining estimated probabilities for the four state types based on the specified conditions.

2.3 | Modelling Reef States Through Time

To examine trends in reef states over time we used the state assignments from the RLS data—a comprehensive, standardised dataset of reef communities—as a training algorithm to categorise reefs throughout the time series datasets. Using the mobile centres obtained from the spatial FCM, we assigned each datapoint (i.e., year) in the time series datasets to one of the respective states, again conserving the probability of each assignment to ensure consideration of uncertainty. Because time series differed vastly in their temporal spread, we standardised them based on their start ($t=0$) and end ($t=1$) date, with every intermediate survey year corresponding to the respective value between 0 and 1 (i.e., the halfway point of each time series would be 0.5), while accounting for time series length in the models.

Since there was no perfect overlap between the benthic and fish time series data (i.e., some datasets contained only fish or only benthic data), we first ran two Bayesian mixed models with beta distributions and log-link functions to test the effect of time on state probabilities in benthic communities and fishes (Figure S4). For both models, we specified an interaction effect between chronology (i.e., years in the standardised time series) and the length of the time series, as well as a random slope for each location (a spatial descriptor for a suite of reefs), and a random intercept for each site (usually corresponding to a single or small number of surveyed reefs within a location). We then combined the surveys that monitored the benthos and fish communities in synchrony at the same site (10 time series datasets, spanning a total of 109 sites) and ran a Dirichlet Bayesian mixed model, examining the effect of time on the probability of belonging to one of the four state types, again specifying a random slope for *Location*, and a random intercept for each *Site* within a location. Since the length of the time series had only weak effects on the benthic states and no effects on fish states through time (see Figure S4), we omitted time series length as a predictor due to the demanding nature of the model. To complement this analysis, we also explored the likelihood of discrete state shifts over time using discrete-time Markov chains (DTMCs). DTMCs are an ideal analytical framework for analysing the probability of transitions between discrete states based on a sequence of categorical events. Their stochastic nature means that only the current state influences the transition probability, making them well-suited for our analysis of discrete state shifts (as opposed to the continuous analyses previously). Additional information about the DTMCs is provided in the [Supporting Information](#).

Finally, to briefly explore hypothesised changes in fish functional structure (from small-bodied planktivores towards large-bodied herbivores), we examined changes in biomass through time for fish genera classified as either herbivores (*sensu lato*) or small-bodied planktivores (Table S4). This was based on previous research that has suggested negative responses of planktivorous species to loss of coral cover (Brandl, Emslie, and Ceccarelli 2016) and increases in herbivores following disturbance (Taylor et al. 2020), and correlations among their respective functional traits [planktivory and small body size as well as herbivory and large body size (Floeter et al. 2018)]. We ran a Bayesian mixed model on transects as the replicate unit, using a random slope for *Location* and a random intercept for *Site* within *Location*. We log-transformed biomass estimates (in grams per 100 m²) to normalise the data, and ran the model using a Gaussian error distribution. Details on model specifications are provided in the [Supporting Information](#).

3 | Results

3.1 | Reef Classification

The PCA of the RLS data revealed the predicted double-dichotomy (Figure 1). For the benthos, there was a clear distribution of reefs along the first axis (which explained 47.6% of the total variability) that parsed reefs into systems dominated by either corals or algae. PC2 split reefs based on the presence of clean, calcareous substrate and other benthic organisms and substrates. Likewise, the PCA for fish communities revealed a clear distribution along the first axis (explaining 50.9% of the total variability), with fish biomass being either concentrated in the small and medium size classes, or large and very large size classes (Figure 1). Notably, the gravity of very large fishes was weak on PC1, which correlated with increased uncertainty of state assignments with high biomass of very large fishes (likely due to the more random occurrence of these large-bodied species) (Figure S1). Across the full dataset, reef state assignments displayed weak correlations between coral-dominated and small fish-dominated states, and algae-dominated and large fish-dominated states (Pearson correlation coefficient: 0.084).

3.2 | Global Distribution and Drivers of Reef States

State assignments displayed considerable spatial heterogeneity across scales, with all biogeographic realms harbouring reefs across the four states (Figure 2). Coral reefs in the Tropical Eastern Pacific and Tropical Western Atlantic were more likely to be in the algae-large fish or algae-small fish states, while reefs throughout the Western and Eastern Indo-Pacific showed high probabilities of being in coral-dominated states. Reefs in the Central Indo-Pacific were most likely to be in the algae-large fish or coral-large fish states.

We found strong correlations between the four coral reef states and environmental and anthropogenic drivers (Figure 3). Nearer to the equator, reefs were most likely in the coral-large fish state (mean predicted posterior probability estimate: 29.6% [26.9, 32.3; lower and upper 95% credible interval]), while reefs at the highest latitudes (20°–30° absolute latitude) were most

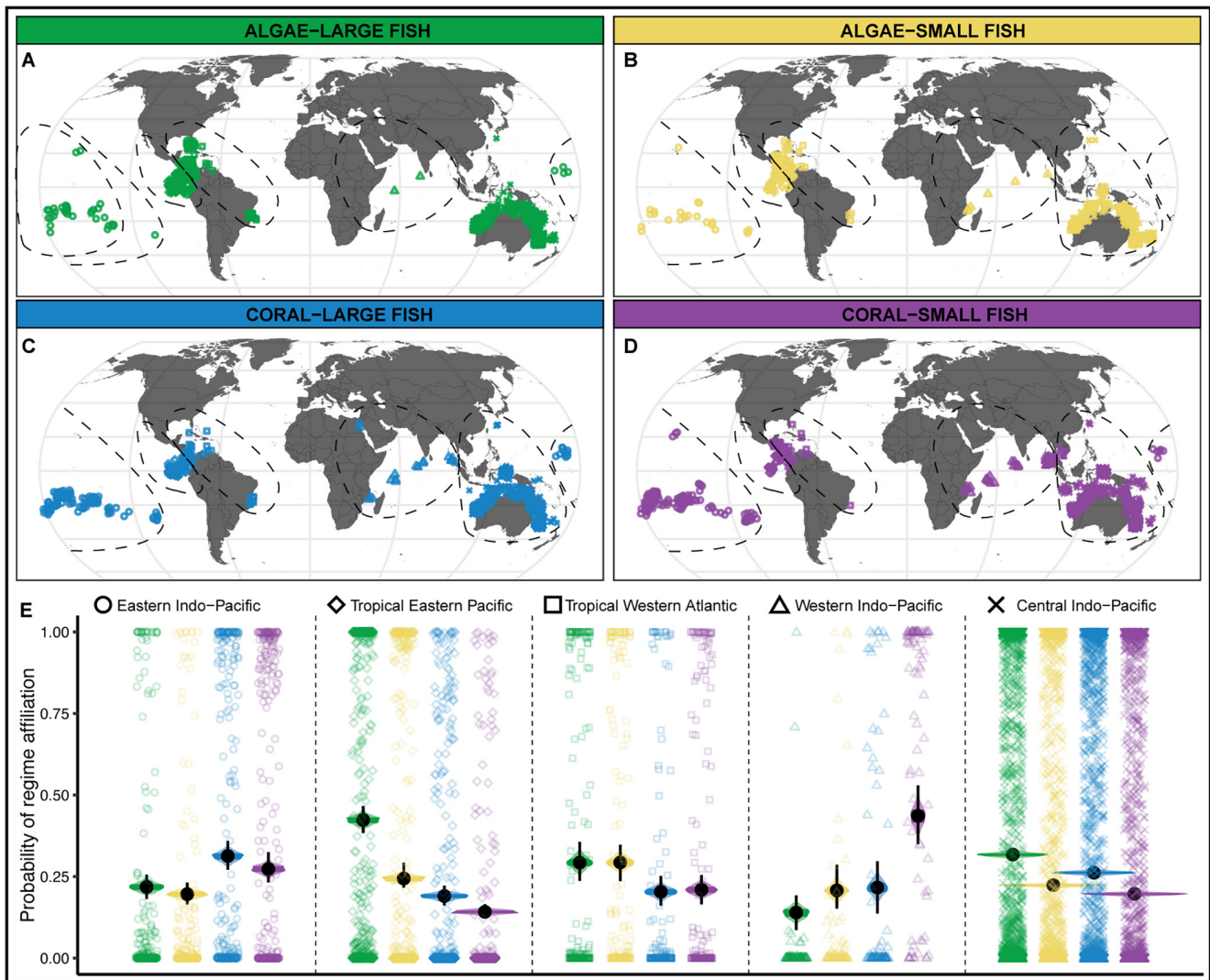


FIGURE 2 | Biogeographic patterns in coral reef states. The four states are ubiquitous at a global scale, resulting in limited discernable differences among biogeographic realms (A–D). Yet, probabilities of being in the four respective states varied substantially across five biogeographic realms (E). Points in A–D represent individual surveys and are jittered for display purposes. Slab and caterpillar plots in (E) represent the distribution of 1000 fitted draws from the Bayesian posterior, marking the mean predicted value (black circle), its 50% and 95% confidence intervals (shaded slabs), and full range of predictions (black line and lightest shading), and with colours matching the four state colours. Points at the extremes of the y-axis (0 and 1) indicate very high probabilities in their state assignment.

likely to be in the algae-large fish state (33.7% [31.4, 36.2]). At the shallowest depths, reefs were equally likely to be in either of the four states, but with increasing depth, state probabilities increased for coral-large fish (36.2% [29.2, 42.9]) and algae-large fish states (32.0% [25.6, 38.7]). In the most oligotrophic waters (minimum mean chlorophyll *a* values), the four states had similar probabilities, but at high chlorophyll *a* values, the combined likelihood of reefs to be in an algae dominated state was > 80%. Low wave exposure favoured large fish states, while high wave energy environments had equal probabilities of reef states. Our additional investigation into the sensitivity of our results to the grouping of turf and algae indicated that high exposure slightly favoured coral-dominated states (Figures S5 and S6).

Even intermediate human impact dramatically decreased the probability of being in a large fish state, with very low probabilities of both the coral-large fish (2.6% [1.0, 4.5]) and algae-large

fish state (7.9% [4.0, 14.5]) at the highest human impact (although there were only very few observations at the highest human impact values). Both fished and unfished reefs were most likely to be in either of the two large fish states, but this probability increased strongly in no-take zones, where the algae-large fish state was the most likely (34.9% [33.1, 36.7]) and the coral-small fish state was the least likely (17.9 [16.9, 18.9]). Separating turf and macroalgae in the initial classification resulted in higher assignments of coral-large fish states both inside fished and no-take zones (Figure S5), suggesting some ecologically relevant effects of MPAs on the relative prevalence of turf versus macroalgae.

3.3 | Temporal Trends in Reef States

While our spatial decomposition provides a useful indication of recent reef states (average survey year = 2013), our

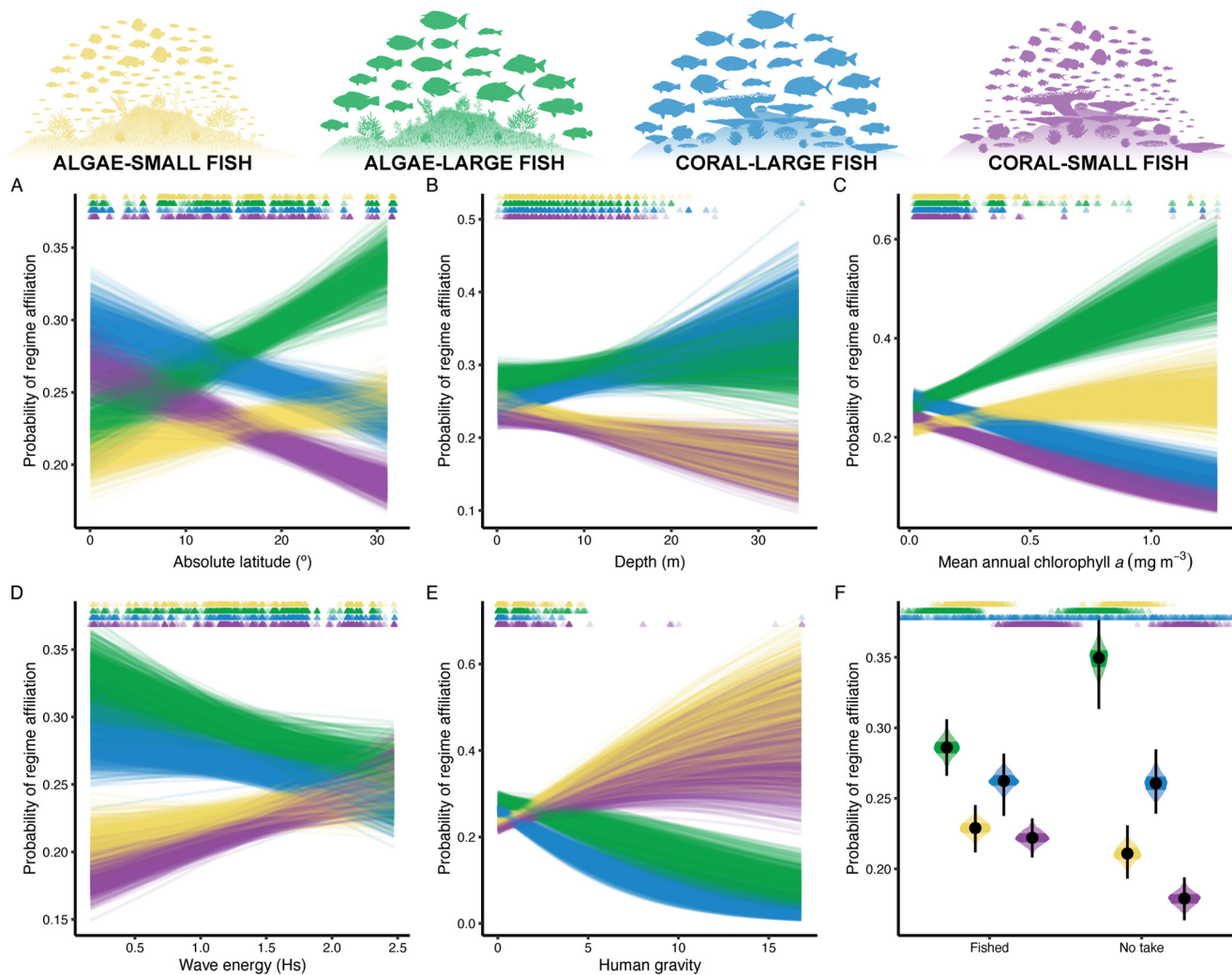


FIGURE 3 | Relationships between six explanatory variables (A–F) and the probability of reefs falling into one of the four states. Lines show posterior predicted fits ($n=1000$) from the Bayesian regression model for each state type (green=algae-large fish; yellow=algae-small fish; blue=coral-large fish; purple=coral-small fish), with all other predictors held at their median. Points at the top of the plots represent the raw state assignments along each subpanel's x -axis. Slab intervals in (F) mark the mean predicted values (black dot), its 50% and 95% CIs (darker shades), and full prediction range (black line and lightest shade).

global baselines of coral reefs may have already shifted due to long-standing human impact. Indeed, we detected substantial changes in reef states over time. For benthic states (12 datasets), the likelihood of algal states increased over time (Bayesian parameter estimate: time=0.69 [0.22, 1.16]) (Table S1) and showed a clear decrease in the intercept for time series length, suggesting that longer time series had lower probabilities of being in the algal state at the beginning (time series length = -0.05 [-0.09 , -0.02]) (Figure S4a). For fishes (11 time series datasets), we found a substantial decrease in the likelihood of being in the small fish state over time (-0.93 [-1.51 , -0.34]), which was not markedly affected by time series length (Figure S4b). In absolute terms, algal cover increased by 13.9% ($\pm 2.0\%$ SE) across all sites, while coral cover decreased by 6.5% ($\pm 1.9\%$ SE). Likewise, the smallest fishes decreased by 1191 g (± 363 g SE) across sites, while the largest fishes increased by 7946 g (± 5180 g SE). There was no relevant change in total fish biomass from the beginning to the end of all time series datasets (-423 g ± 1578 g SE).

Across 10 combined time series spanning an average of 12.2 years (± 6.6 years SD), most datasets showed at least one state shift (88.1% out of 109 time series), while 11.9% of sites remained in the same state throughout the observation period. Of sites that exhibited state shifts, only 21.5% were in the same state at the beginning and the end of the time series (a dynamic interpretable as disturbance and recovery). This was most prevalent when the original state was coral-large fish (7.5% of sites), followed by the two algal regimes (5.4% each) and least likely (3.2%) when reefs were in the coral-small fish state at the onset of the monitoring period. Accordingly, we also found an increasing probability of the algae-large fish state over time (45.2% [38.7, 51.5] at the conclusion of the time series), and a decreasing probability of the coral-small fish state (14.3% [12.0, 16.7%]) (Figure 4). In the DTMCs, discrete shifts were more likely between fish states than benthic states, more likely to occur within the two algal regimes than the coral regimes, and least likely to involve diagonal shifts across benthic and fish states simultaneously (Figure 5). The

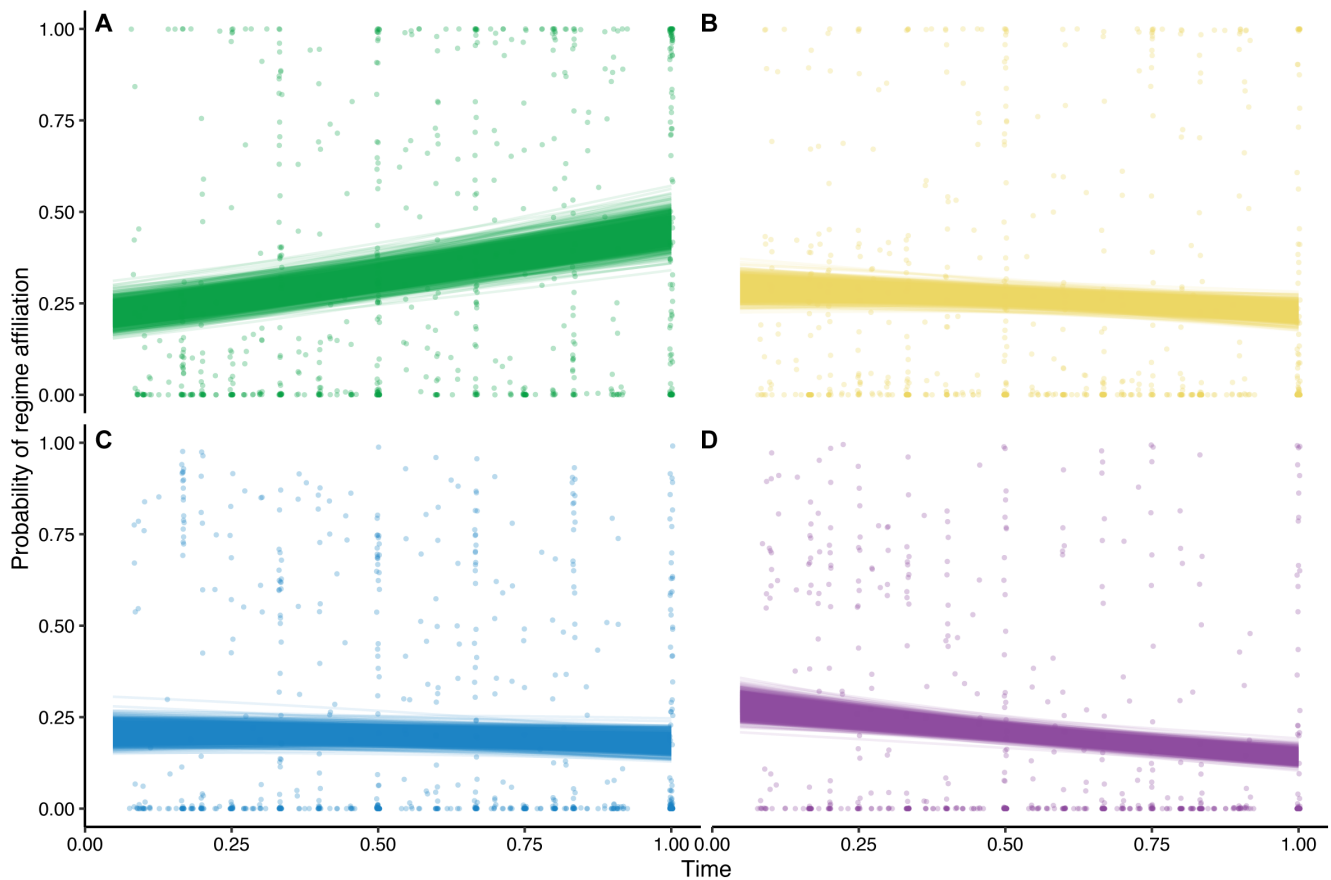


FIGURE 4 | Temporal trends in coral reef states, as obtained from 10 timeseries. The four plots show the probabilities of state assignments (y-axis) for each state (A = algae-large fish; B = algae-small fish; C = coral-large fish; D = coral-small fish) across the standardised length of time series (from t_0 at the beginning to t_1 at the conclusion of the time series; x-axis). Lines represent 1000 predicted draws from the Bayesian posterior, while points represent the raw probabilities of state assignments obtained from the fuzzy-clustering analysis.

most likely state shifts were from small fish to large fish in the algae state (48.5% [39.7, 57.4]) and from the coral-large fish state to the algae-large fish state (45.7% [37.8, 53.7]). Finally, reefs were least likely to shift into the coral-small fish state (average predicted probability: 28.0%).

4 | Discussion

Predicting where, when and why coral reefs shift from one ecological state to another, and whether changes in benthic and fish communities co-occur, remains challenging. By parsing these highly complex ecosystems into a small suite of simplified states, we harness the power of divergent datasets to quantify the prevalence of different reef states globally, their drivers, and their temporal dynamics over the past few decades.

While all geographic realms harboured all four reef states, their respective prevalence varied, reflecting documented differences in environmental conditions and biogeographic history (Roff and Mumby 2012; McWilliam et al. 2018; Parravicini et al. 2021; Reverter et al. 2022; Tebbett, Connolly, and Bellwood 2023): the Tropical Eastern Pacific—such as the Galapagos Islands—can be heavily influenced by cold upwelling that favours algal growth (both turf and macroalgae)

and supplies nutrient rich resources to larger-bodied fishes (Glynn 2001). In turn, the low probability of the coral-large fish state in the Western Atlantic is likely related to the regional decline of corals, loss of herbivorous fishes and urchins, and overfishing of large-bodied fishes (Jackson et al. 2001; Gardner et al. 2003; Schutte, Selig, and Bruno 2010; Shantz, Ladd, and Burkepile 2020). Notably, separating turf and macroalgae resulted in an even probability of reef states in the Tropical Atlantic only, suggesting that correlations between turf and macroalgal prevalence are weaker in the Tropical Atlantic than elsewhere (Figures S5 and S6). For the Indo-Pacific, state assignments are probably influenced—at least in part—by spatial clumping in survey distributions (Reverter et al. 2022). Central Indo-Pacific reefs had high probabilities of being dominated by large fishes (both algae- and coral-dominated). Most surveys were located in Australia, with comparably low human impact, relatively selective fisheries and a long-standing fisheries management system. Conversely, the high probability of coral and small fish states in the Western Indian Ocean may be influenced by comparatively sparse coverage of reefs from more impacted regions of the Indian Ocean, such as India, Sri Lanka, or the Southwest Indian Ocean.

Despite geographic differences, there was high heterogeneity of reef states at local and regional scales, emphasising

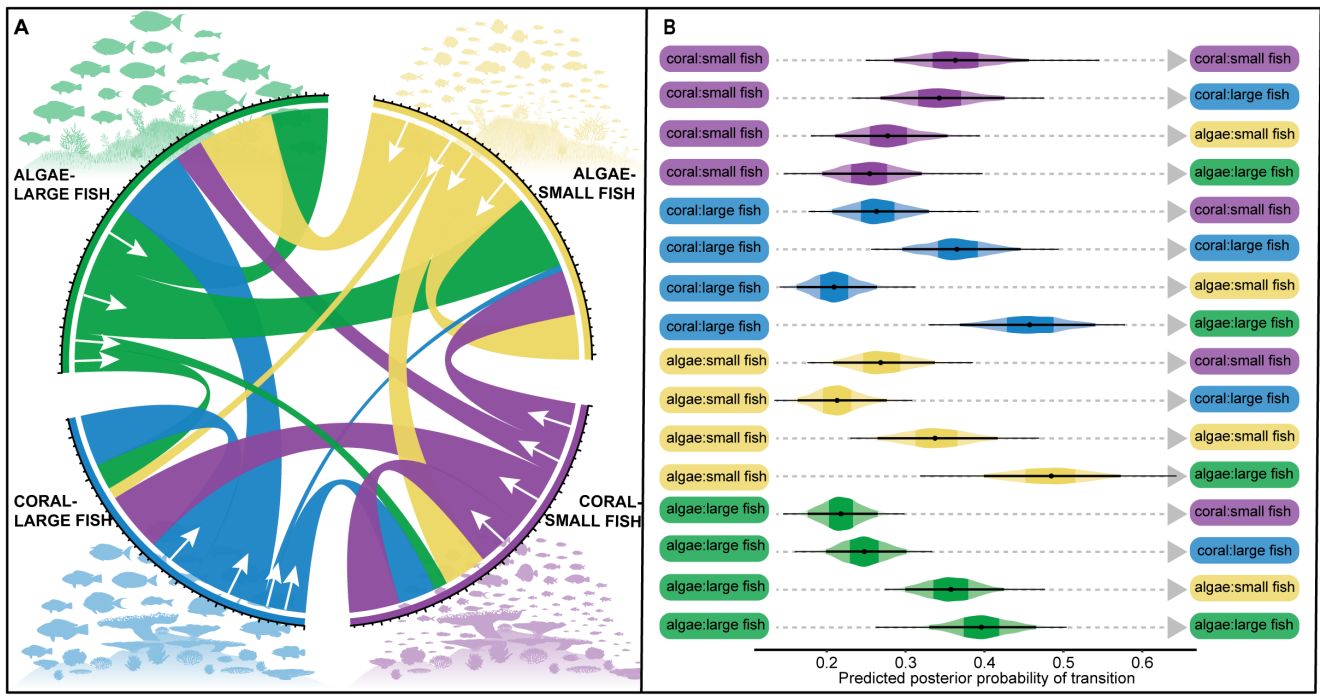


FIGURE 5 | Estimated probability of state shifts between coral reef states across the investigated time series. (A) Chord diagram highlighting the state change probabilities between the four state types. (B) Predicted posterior probabilities of state changes from 1000 random draws based on the Bayesian mixed model. Labels on the left of the y-axis highlight the original state, while labels on the right denote the state shift (including hysteresis, if the state is the same as the one to the left). Slab intervals in (B) mark the mean predicted values (black dot), its 50% and 95% CIs (darker shades), and full prediction range (black line and lightest shade).

the strong spatial context-dependency of reef states (Schmitt et al. 2019; Crisp, Tebbett, and Bellwood 2022). Our results allow us to establish some general, quantitative expectations of reef states based on prevailing conditions, which may help transcend the idiosyncratic nature of case studies. Algal domination at high latitudes is likely driven by lower survival, competitiveness and recruitment of corals in high-latitude environments due to a temperature, light levels, aragonite saturation state, grazing pressure, larval supply and settlement cues (Robinson et al. 2018; Abrego et al. 2021). For coral reef fishes, empirical evidence for latitudinal variability in body size is somewhat equivocal (Taylor et al. 2019; Audzijonyte et al. 2020), but marine fish assemblages tend to have fewer small-sized species at high latitudes (Lindsey 1966; Coghlan et al. 2024). Similarly, given that reef fish species tend to mainly recruit to shallow habitats such as lagoons and back reefs (Adams and Ebersole 2002), the steeply increasing probability of deeper reefs to be in the large fish states appears intuitive. Chlorophyll *a* concentrations (which are often indicative of nutrient availability) does not appear to curtail the abundance of large-bodied fishes (Heenan et al. 2016). However, the sharp increase of algae-dominated states at high chlorophyll *a* concentrations aligns with both the reported negative impacts of coastal nutrient input on corals and high cover of algae in naturally nutrient-rich environments, even where healthy communities of large-bodied herbivores exist (Burkpile et al. 2013; Wiedenmann et al. 2013).

The clear decline of the coral-large fish state at high human impact reflects the rapid extirpation of large reef fishes near

human settlements (Stallings 2009; Cinner et al. 2016; Lefcheck et al. 2021). In turn, the comparatively high probability of the coral-small fish state at high anthropogenic impact (despite considerable uncertainty) supports the notion that local human impact does not inextricably foster algal dominance (Bruno and Valdivia 2016). More specifically, although fishing restrictions increase the likelihood of reefs to be dominated by large fishes, this does not consistently translate to an increased probability of coral dominance. This finding supports suggestions that no-take zones may have little detectable influence on the reef benthos (Bruno, Côté, and Toth 2019; Graham et al. 2020)—in part due to the lack of statistical power and ill-suited metrics to assess benthic community change (Mumby et al. 2021)—and that fish biomass is more readily replenished on macroalgal reefs than on coral reefs after disturbance (Hamilton et al. 2022).

Our results set important expectations concerning present-day management targets for coral reefs worldwide (Figure S7). Coral reefs in ostensibly ‘pristine’ settings (3° absolute latitude, minimal human impact, minimal chlorophyll *a*, and inside a no take zone), would indeed have the highest probability of being in the widely considered ‘healthy’ coral-large fish state, followed by the algae-large fish state. Yet, a reef in these exact same conditions at 20° absolute latitude (which traverses reefs in the Middle East, India, Southeast Asia, Hawaii, Mexico, the Caribbean, the East African Coral Coast, the Southwestern Indian Ocean Islands, Australia’s Ningaloo Reef and Great Barrier Reef, as well as several Pacific Islands) would most likely be in the algae-large fish state. Collectively, these reef systems form a substantive proportion of the global

coral reef area. Thus, even under ideal present-day conditions with minimal human impact (e.g., Ningaloo Reef), many reefs are likely to be in an algal-dominated state with fish biomass concentrated in the larger size classes.

Importantly, several other important predictors were unaccounted for in our analysis, especially recent bleaching events, seascape configuration, or larval connectivity (Berkström et al. 2020; Fontoura et al. 2022). Nevertheless, our analyses provide a non-exhaustive suite of baseline expectations concerning coral reef states worldwide given their local settings, including the notion that benthic dominance by algae may be a common and/or natural state on today's coral reefs, even in areas where present-day local human influence is low.

4.1 | Temporal Trends in Reef States

The observed trend towards algal-dominated states over time supports observations of local coral-algae phase shifts and their—at least regional—ubiquity. Given the coarse nature of our state classification, we are unable to tease apart trends within algal states (turf or macroalgae) (Tebbett, Connolly, and Bellwood 2023) or the prevalence and importance of shifts towards other benthic organisms (Crisp, Tebbett, and Bellwood 2022; Reverter et al. 2022). Nevertheless, our results reaffirm that reefs have generally moved from systems characterised by mixotrophic, structure-building animals to more ephemeral, autotrophic primary producers.

There is little doubt that humans directly reduce fish biomass in the largest size classes (Stallings 2009; Cinner et al. 2016; Shantz, Ladd, and Burkepile 2020; Lefcheck et al. 2021). Yet, fish communities decreased most notably in the relative representation of small fishes over time. There are several non-exclusive explanations for this trend. First, the increased implementation of MPAs over time may bolster fish populations in larger size classes due to the preferential harvest of large individuals by humans (Edgar et al. 2014; Strain et al. 2019), with a large number of MPAs represented in the time series. Second, baseline configurations of reefs in our time-series may represent an already depleted fish community that lacks biomass in the largest size classes, as human impact on reef fish communities significantly predates the beginning of even the earliest time series. Third, salient ecological drivers may have caused the general decrease in small fish-dominated states, related to bottom-up processes mediated by the benthos. In this context, examining fish and benthic state changes simultaneously provides critical insights.

As the primary habitat builders, scleractinian corals provide important fine-scale structural architecture that increases surface area and shelter availability, which disproportionately favours small-bodied reef fish species (Almany 2004). As such, the concurrent demise of corals and small-bodied fishes is intuitive, and supported by case studies (Graham et al. 2007; Wilson et al. 2010; Alvarez-Filip, Gill, and Dulvy 2011). While larger bodied fishes also benefit from structural complexity on reefs (Rogers, Blanchard, and Mumby 2014), strong size selectivity of fishes for shelter holes and the sequential erosion of the reef structure (including rapid disappearance of delicate

branching structures and the persistence of larger, boulder-like structures) suggests that adverse effects of reef flattening due to coral loss will, at least initially, primarily affect small-bodied animals.

This, in turn, may change ecosystem functioning on reefs. In fact, we found a mean 41.1% decrease in the biomass of small-bodied planktivores (from 362.1 g per 100 m² [234.9, 566.6] to 213.4 g per 100 m² [138.5, 326.7]) throughout our time series, suggesting that the increasing rarity of the coral-small fish state coincides with a loss of small-bodied fishes that harness pelagic energy (Figure S8). These fishes frequently occur in high numbers, feed on planktonic resources that arrive on reefs as external subsidies, and sustain a variety of piscivorous predators (Hamner et al. 1988; Morais and Bellwood 2019; Skinner et al. 2021). Thus, the loss of small-bodied, high-turnover species that depend on coral for shelter may compromise coral reef food webs worldwide.

The simultaneous rise of large-bodied fishes in algal-dominated states may, in turn, reflect a bottom-up, resource-mediated effect expressed through increased abundances of large-bodied herbivores and omnivores (rather than predators that depend on small-bodied fishes for food). There is increasing recognition that mobile herbivores actively track their dietary resources (Tootell and Steele 2016), and wide availability of endolithic and epilithic resources following coral mortality may boost the abundance, biomass and growth of large-bodied herbivores in the short- and medium-term (Robinson et al. 2019; Graham et al. 2020; Taylor et al. 2020) to sustain productive fisheries (Robinson et al. 2019). However, our results also show that algae-dominated states show frequent transitions between small and large fish-dominated states, which suggests more seasonal, ephemeral and volatile producer–consumer dynamics than reefs in the coral-large fish state. Accordingly, there was a weaker overall trend of increasing herbivore biomass throughout our time series (Figure S8), from 2652 g [1738, 4056] to 3226 g [2102, 5057] (21.6% mean increase).

4.2 | Coral Reef States in the 21st Century

While there is strong consensus that coral reefs have changed dramatically, the nature of changes, their significance, and our ability to counteract these dynamics through protection or restoration continue to be debated. Our results help to move this debate forward. First, pristine reef conditions on modern reefs are often thought to be characterised by high coral cover and large-bodied fishes (McClanahan et al. 2007; Sandin et al. 2008). Although high human impact often pivots reefs out of the coral-large fish state, the reverse is not inexorably the case: even reefs in relatively pristine conditions can have high probabilities of being dominated by algae, small fishes, or both. Thus, baselines for coral reef management need to be precisely defined with respect to local conditions. Second, while our results support the positive effect of MPAs for large fish species, the most fragile reef state in recent decades appears to be dominated by corals and small-bodied fishes. Neither are likely to benefit directly from MPAs that are designed solely for protecting fisheries species, but may benefit from other restrictions that, for instance, reduce anchoring damage. Thus, well-designed and enforced MPAs can bestow a variety of ecological benefits on coral reef ecosystems, but case-by-case evaluations

of their design and utility in the face of the costs they can impose on local stakeholders are critical (Bruno, Côté, and Toth 2019).

Finally, the revealed temporal state shifts suggest critical shifts in coral reef functioning. While reefs in the coral-small fish state are likely to obtain and recycle energy and nutrients through external subsidies and internal cycling mechanisms (Brandl et al. 2019; Skinner et al. 2021), reefs dominated by algae and large-bodied herbivores exhibit direct paths from benthic primary producers to large-bodied fishes (Hempson et al. 2018). Both high-turnover, small-bodied fishes and herbivorous fishes have played critical roles in the rise of modern coral reefs, their productivity and their capacity to sustain coral reef fisheries (Brandl et al. 2019; Lin et al. 2019; Morais, Connolly, and Bellwood 2020; Siqueira et al. 2023). Yet, the dominance of the algae-herbivore pathway—whether it is turf or macroalgae—may fundamentally reshape energetic pathways on coral reefs. Such systems can offer lucrative, nutritionally rich and potentially resilient fisheries to coastal communities (Robinson et al. 2019; Wilson et al. 2022), but our results also suggest that they are less stable (given their frequent transitions between small and large fish communities). Given this, alongside compromised processes such as reef accretion or diminished aesthetic appeal, systems in algal states may fail to provide some important services to society. Determining how to manage such systems and whether it is feasible or advisable to restore reef states dominated by corals and small-bodied fishes will be a critical challenge in the 21st century.

Author Contributions

S.J.B. and V.P. developed the project with input from M.A., R.D.S.-S., S.A.K., N.A.J.G., G.J.E., R.K. and M.K.D.; R.D.S.-S., G.J.E., N.A.J.G., S.K.W., R.K., R.A., L.B., D.A.E., J.E.A.-G., J.G., T.H., J.-P.M., D.M., C.L.R., J.W. and M.A. provided data; J.W. and J.C. processed time series data; S.J.B. analysed the data, produced the figures and wrote the first draft of the manuscript. All authors contributed by editing various drafts of the manuscript.

Acknowledgements

We thank Sandrine Job, Andrew Baird, as well as Reef Life Survey Divers and all data collectors for their contributions to the paper. We are grateful to Koniambo Nickel SAS and especially Gregory Marakovich and Andy Wright, who made data from New Caledonia available, and Australia's Integrated Marine Observing System (IMOS) for making the RLS data available. This research is a product of the "SCORE-Reef" group, supported by the synthesis center CESAB of the French Foundation for Research on Biodiversity (FRB) and the Office Français de la Biodiversité (OFB).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code are available on [Figshare](https://figshare.com/doi/10.6084/m9.figshare.24264109.v1) (doi: 10.6084/m9.figshare.24264109.v1).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.