

Environmental change and connectivity drive coral reef fish abundance in the Western Indian Ocean

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Abstract

Worldwide, coral reefs are facing risk from climate change. The Western Indian Ocean (WIO) harbours about 16% of global coral reefs with highly reef-dependent local communities. Coastal protection and food security depend on effective conservation management, which requires understanding species abundances. Here, we explore how fish group distribution and abundance across the WIO, categorized by their trophic function, are explained by oceanographic connectivity, sea surface temperature (SST), and chlorophyll *a*. We designed a proportional oceanographic connectivity metric describing the relative strength of connectivity between all WIO coral reefs and each survey site. We created statistical models for four trophic groups: grazers and detritivores, herbivorous excavators, corallivores, and primary piscivores across 51 sites in the WIO. We show that SST and chlorophyll *a* are strong predictors of all trophic fish groups and that the proportional oceanographic connectivity metric improved the model predictions significantly for grazers and detritivores and excavators. For excavators, peak abundances were predicted at medium connectivity, and for grazers and detritivores, at low and medium connectivity, suggesting that larvae dispersal predominates at a local scale. Decision making should include connectivity for efficient conservation area prioritization, for which our proportional oceanographic connectivity metric is a valid and useful parameter.

Keywords: connectivity; coral reefs; environmental drivers; functional diversity; larvae dispersal; marine protected areas; reef fish ecology; spatial structure

Introduction

Indian Ocean sea surface temperatures (SSTs) have increased by 1.04°C during 1950–2015 (IPCC 2022), at a rate of about 0.1°C per decade since the 1950s (Dhame et al. 2020). This is faster than the warming seen in the other tropical oceans and, together with the Western Pacific Ocean, the Indian Ocean is the most vulnerable ocean region to thermal stress (Dhame et al. 2020, Obura et al. 2021). With ongoing climate impacts, it is vital to understand present circulation patterns, larvae dispersal, and fish population dynamics, how these might change, and how this will affect reef resilience and food security (Graham et al. 2015, Hughes et al. 2017, van Hooijdonk 2020). Functionally important fish groups encompass the variety of functional processes critical to reef resilience (Bellwood et al. 2019, Brandl et al. 2019, Sheppard et al. 2023). On coral reefs a major focus for reef persistence and recovery is on different trophic fish groups like piscivores or herbivores that show different feeding mechanisms (Bellwood et al. 2019, Brandl et al. 2019, Sheppard et al. 2023). Herbivorous fish can be divided into sub-groups, such as grazers, detritivores, and excavators by their impact on coral-algal dynamics on reefs (Heenan and Williams 2013, Samoily et al. 2019). Thus, functional diversity is hypothesized to support resilience through complementarity of niches or functional redundancy where several species can perform one ecological function (Fox and Bellwood 2013, Heenan and Williams 2013). Enhancing reef re-

silience by managing trophic fish groups with differing functional roles (Fox and Bellwood 2013, Bellwood et al. 2019) can support the capacity of an ecosystem to withstand and recover from environmental disturbance events (Nyström et al. 2008).

Reef fish are also critical to food security as seen in the yields of small-scale fisheries which can supply up to 99% of protein uptake for coastal communities and around 82% of households' income in the WIO (Barnes-Mauthe et al. 2013). Meanwhile the Indian Ocean coastlines are home to some of the world's poorest communities, who often rely on coral reef resources for their livelihoods (Barnes-Mauthe et al. 2013, Popova et al. 2019, Obura et al. 2021). For the years 2000–2020, these coastlines have seen a striking 33% human population growth within a 100 km radius of coral reefs and a 71% increase within a 5 km radius substantially increasing the pressure on these ecosystems (Sing Wong et al. 2022). Reef degradation and severe annual coral bleaching are expected to occur regionally by 2040 and for most reefs by 2067, therefore actions that help build resilience and mitigate these impacts are urgently needed (Hattam et al. 2020, van Hooijdonk 2020).

Climate change has a predominant effect on larval dispersal with the pelagic larval duration (PLD) of reef fish predicted to decrease by 12%–25% for a 3°C temperature rise due to an increased larvae metabolism, resulting in lower

dispersal and connectivity (Botsford *et al.* 2009, Johansen and Jones 2011, Lloyd *et al.* 2012). Additionally, SST increases lead to coral bleaching and mortality (Hughes *et al.* 2017, Hattam *et al.* 2020) that causes habitat fragmentation (Botsford *et al.* 2009, McMahon *et al.* 2012). Oceanographic currents are predicted to change under future climate change scenarios which will likely have large impacts on species population persistence because of the effects on larvae dispersal (Coleman *et al.* 2017, Gennip *et al.* 2017). Small-scale patterns are difficult to model, but understanding the relative importance of currents compared to other local environmental variables can help prioritize decision-making in marine conservation (Gennip *et al.* 2017, Mayorga-Adame *et al.* 2017, Hidalgo *et al.* 2019, Obura *et al.* 2021). Chlorophyll *a* is an environmental variable that is predicted to change with ocean warming altering biological productivity which can impact fish larvae and trophic group composition dynamics (Kaunda-Arara *et al.* 2009, Beaulieu *et al.* 2013, Samoilyis *et al.* 2019). Remotely sensed SST and chlorophyll *a* data are commonly used for large scales but limitations in sensor algorithms and coastal areas resulting in inaccuracies and low resolutions need to be considered (Chen *et al.* 2013, Sathyendranath *et al.* 2019, Lahiri and Vissa 2022, Sudre *et al.* 2023).

Connections between different coral reef regions and self or non-self-recruiting populations remain mostly unstudied—especially in the WIO (Crochelet *et al.* 2016, Gamoyo *et al.* 2019, Obura *et al.* 2021). Limited resources, infrastructure, local expertise, and security issues lead to poor ecological knowledge of how species abundance and PLD are impacted by environmental factors in the WIO (Gennip *et al.* 2017, Popova *et al.* 2019, Obura *et al.* 2021). High connectivity and strong currents with high larval inflow can strengthen reef resilience and predict persistence of species across regions and temperature scenarios (Mayorga-Adame *et al.* 2017, McManus *et al.* 2021). However, these factors may also disturb acclimatization and thus, impact coral sensitivities to temperature anomalies (Roche *et al.* 2018). Furthermore, high levels of connectivity may have negative side effects, such as spread of pollutants, invasive species and pathogens or limited asynchrony of species (Hughes *et al.* 2010, Mayorga-Adame *et al.* 2017).

Quantifying connectivity is complex and, depending on the type of connectivity being considered, different factors play important roles. In the case of fish, which have a meroplanktonic stage early in their lifecycles, connectivity is a function of transport, larval survival, settlement, and post-larval survival (Pineda *et al.* 2007). The latter three variables mean that oceanographic transport alone is a proxy for true ecological connectivity, as connectivity is also influenced by traits of the species in question (Balbar and Metaxas 2019, Virtanen *et al.* 2020). Passive dispersal by ocean currents is a key mechanism driving the transport of organisms (Jönsson and Watson 2016), but other mechanisms include active migratory connectivity (Cowen *et al.* 2006, Popova *et al.* 2019).

We utilized a subset of trajectories from pre-existing Lagrangian particle tracking experiments (Popova *et al.* 2019) to define and develop a metric called ‘proportional oceanographic connectivity’ describing the strength of ocean circulation connectivity between all WIO coral reefs (UNEP-WCMC, WorldFish Centre, WRI, TNC 2021) and each fish survey site (Fig. 1). Lagrangian particle tracking involves releasing virtual ‘particles’ into the (pre-calculated) time-evolving velocity field of an ocean general circulation model and tracking them ei-

ther forwards in time (downstream) to their destinations or tracking them backwards in time (upstream) to their sources. To assess connectivity among the fish survey sites we used the connectivity from backtracked passively transported particles, which is the transport of particles along ocean currents (Gennip *et al.* 2017, Popova *et al.* 2019).

There is a need for linking ocean circulation model predictions with ecological population models as ocean currents are a major driver of pelagic larval dispersal (Botsford *et al.* 2009, Mayorga-Adame *et al.* 2017, Vaz *et al.* 2022). This is a novel approach that can inform reef management by identifying key areas of interconnectivity and source reefs for conservation prioritization through MPA networks (Gamoyo *et al.* 2019, Hidalgo *et al.* 2019, McManus *et al.* 2021, Figueiredo *et al.* 2022). Current models of trophic fish group abundances often lack larval dispersal and oceanographic connectivity parameters, which are critical factors that influence the fate of reefs after disturbance events such as bleaching (Graham *et al.* 2015, Magris *et al.* 2016, Mayorga-Adame *et al.* 2017).

Our broad aim is to explore how trophic reef fish groups are impacted by their environment and how they respond to variations in oceanographic connectivity, SST, and chlorophyll *a*. SST and chlorophyll *a* changes have been shown to be two of the four main stressors under global change for marine species along with ocean acidification and de-oxygenation (Gennip *et al.* 2017, Samoilyis *et al.* 2019, Obura *et al.* 2021). Chlorophyll *a* concentration shows phytoplankton pigmentation in the oceans and is used as an indicator for ecosystem health and productivity (Feng and Hu 2016). SST measured to a depth of 10–20 m is a critical parameter for coral reefs and reef fish larval development (Hughes *et al.* 2017). For the analysis, we developed generalized additive models (GAMs) to assess how SST, chlorophyll *a*, and oceanographic connectivity relate to trophic group abundance.

Methods

Ecological data

The reef fish data were collected between 2009 and 2015 using a SCUBA-based underwater visual census along five 50 × 5 m transects per fish survey site (Samoilyis *et al.* 2019). Fish transect surveys were completed for 51 sites across coral reefs in Comoros, Madagascar, Mozambique, and Tanzania (Fig. 1). The survey sites are standardized fore reefs between 0.5 and 33 m depth, with most between 7 and 15 m (Samoilyis *et al.* 2019). Four trophic groups essential for reef resilience were chosen and encompassed six taxonomic families (Table 1).

Environmental data

SST and chlorophyll *a* were extracted as monthly mean data series from NOAA’s Environmental Research Division Data Access Program archive (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>) at a spatial resolution of 4 × 4 km (Supp. Figs S1 and S2). The monthly mean data were summarized to annual means and matched to the site and year of the ecological data (Supp. Table S1).

Modelled oceanographic connectivity

Our proportional oceanographic connectivity metric gives the percentage of total WIO reefs that are connected to each survey site within 30 days, according to pre-existing

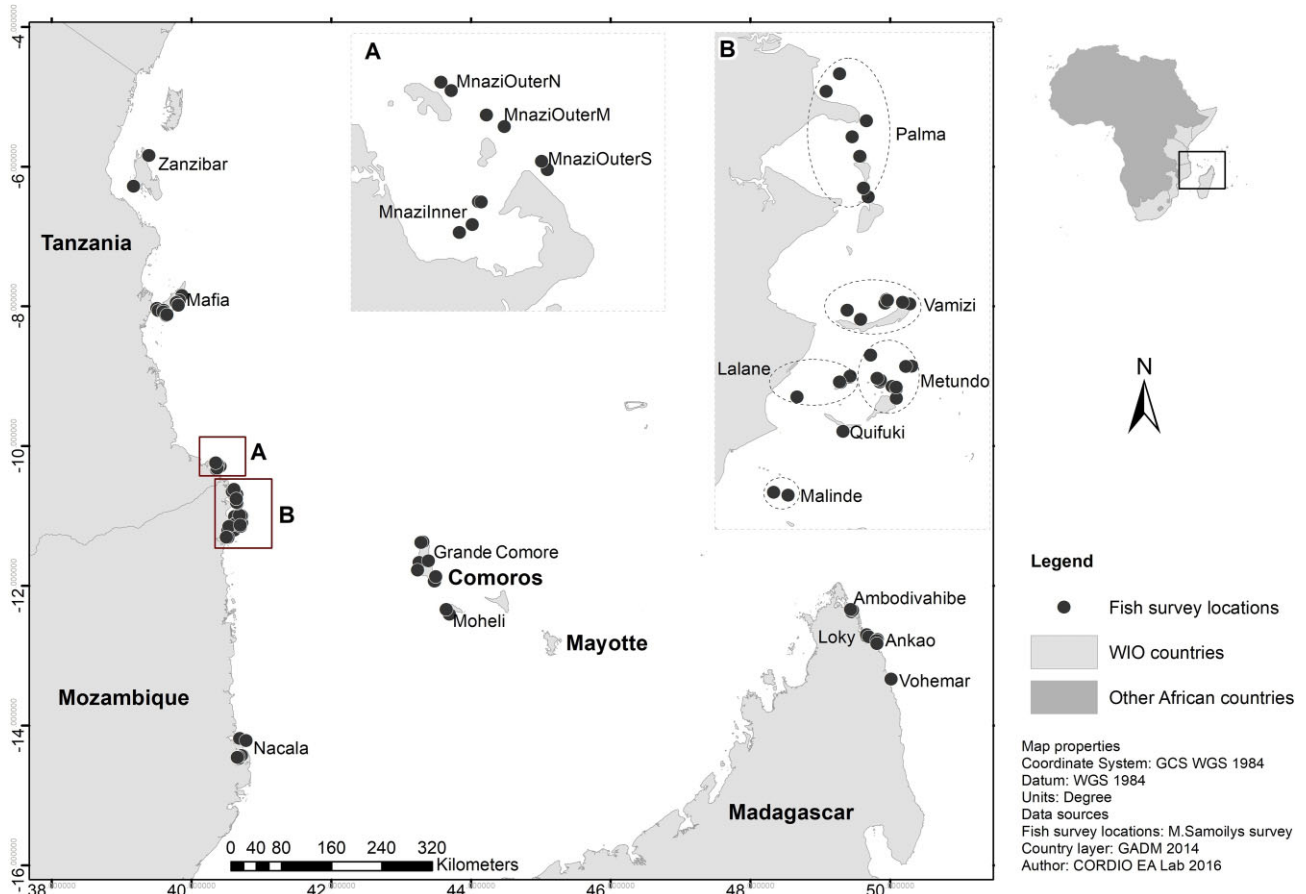


Figure 1. Map of the Western Indian Ocean (WIO) showing the locations of the 51 fish transect survey sites in Comoros, Madagascar, Mozambique, and Tanzania (source: Samoilys et al. 2019).

Table 1. Trophic groups of coral reef fish families used in this research describing their biology and impacts on coral reefs.

Trophic group	Biology and impacts on coral reefs
GRAZERS AND DETRITIVORES	
Families (<i>Acanthuridae</i> , <i>Siganidae</i>)	Feed on algal turf by searching the epilithic algal matrix for detritus, act as indicator for number of algae (Marshall and Mumby 2012, Heenan and Williams 2013)
LARGE AND SMALL EXCAVATORS	
Families (<i>Labridae</i> : <i>Scarinae</i>)	Actively bite pieces off the reef, which results in settlement space for corals and crustose coralline algae, can enhance resilience, play key role in bioerosion, limit fleshy and turf algae due to their higher amount of feeding off the reef matrix (Heenan and Williams 2013, Hussey et al. 2014)
CORALLIVORES	
Families (<i>Chaetodontidae</i>)	Feed on corals, abundance linked to coral cover (Heenan and Williams 2013, Hussey et al. 2014)
PRIMARY PISCIVORES	
Families (<i>Lutjanidae</i> , <i>Serranidae</i> : <i>Epinephelinae</i>)	Prey on lower trophic level fishes, indicators for fishing pressure (Hussey et al. 2014)

Lagrangian trajectories of the coastal zones of four countries (Comoros, Madagascar, Mozambique, and Tanzania) taken from (Popova et al. 2019) (Fig. 2). To calculate this connectivity metric each individual polygon from the WIO (30°S, 12°N, 30°E, 70°E) was extracted from the UNEP-WCMC database (UNEP-WCMC, WorldFish Centre, WRI, TNC 2021), yielding 18 981 reef polygons. A bounding box with a 0.25°-buffer was added to each polygon to define a “reef-associated” area (Supp. Fig. S3). Equivalent boxes were considered around

each of the fish survey sites. For each fish survey site, the Lagrangian particles initialized within that site’s bounding box were considered, which amounted to between 300 and 848 particles per site. These particles were backtracked upstream for 30 days, and if their trajectories intersected with one of the reef polygon bounding boxes, that reef was deemed to be connected to the survey site. The fraction of all WIO reefs connected to each survey site was used as the metric for proportional oceanographic connectivity for each site

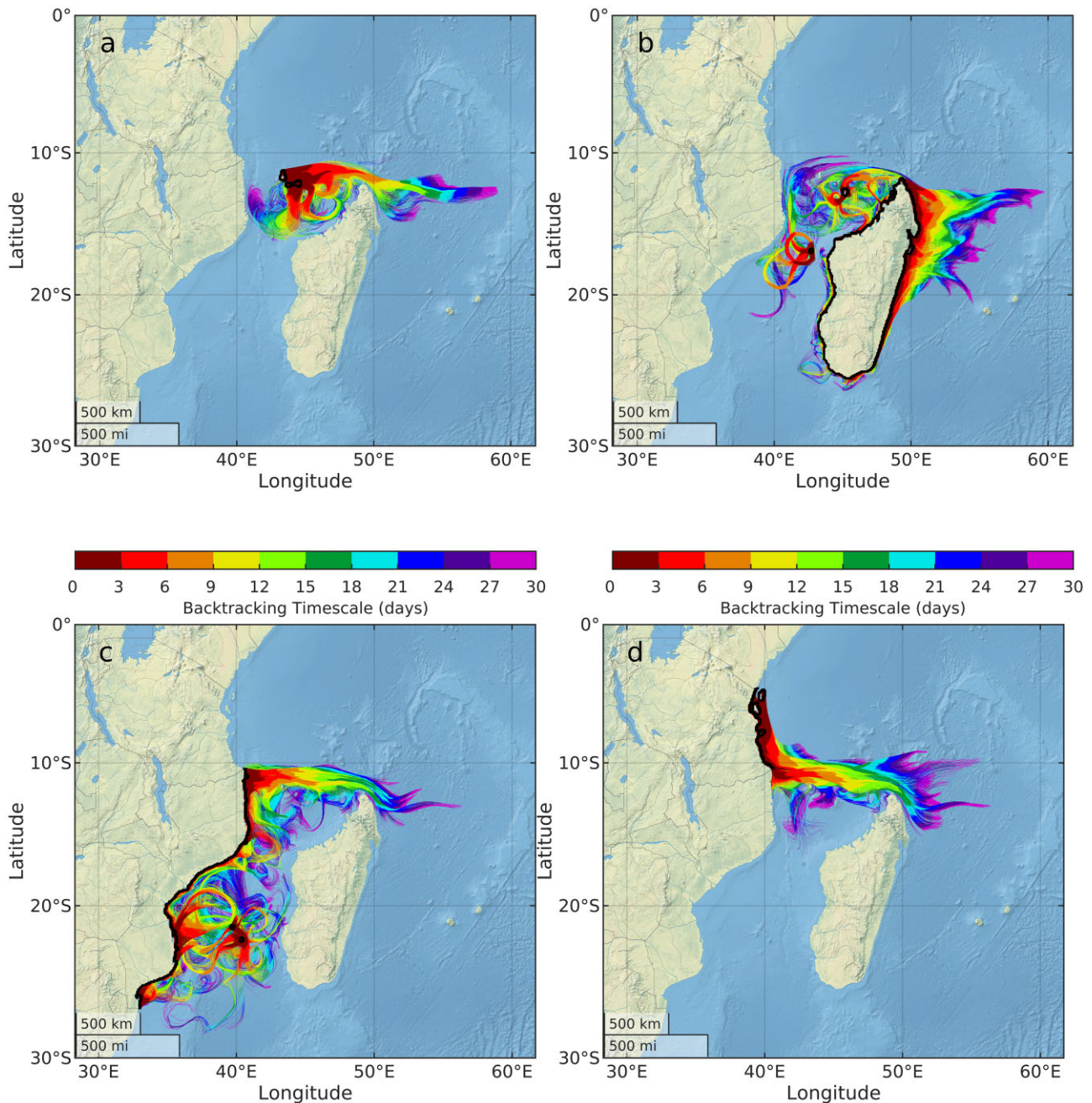


Figure 2. Oceanographic connectivity backtracking model for (a) Comoros, (b) Madagascar, (c) Mozambique, and (d) Tanzania for the year 2010. Particle release locations along the coast are plotted in black and the duration of time elapsed is colour coded such that, for example, a particle starting at the easternmost tip of the orange line would take 30 days to arrive at the initialization site marked in black. Trajectories are showing every 10th particle for each country.

(Fig. 3). For each particle, the first 30 days of backtracking were used to represent a weighted mean for the reef fish taxa most common in our data from the families *Acanthuridae*, *Scaridae*, *Serranidae*, and *Lutjanidae* with annual spawning phenologies (Victor and Wellington 2000, Lester and Ruttenberg 2005, Kulbicki 2015, Roberts et al. 2021).

Our setup used the trajectories from Popova et al. (2019) that were generated with the ARIANE Lagrangian software (Blanke and Raynaud 1997) to perform particle tracking simulations based on modelled ocean hydrodynamics. The hydrodynamic results came from a $1/12^\circ$ horizontal resolution run of the Nucleus for European Modelling of the Ocean (NEMO) general circulation model (Madec 2014), forced with hind-

cast data from the DRAKKAR Forcing Set (DFS) version 5.2 (Brodeau et al. 2010). $1/12^\circ$ is state of the art for global circulation models and sufficient for mesoscale eddies to be well resolved at the latitudes relevant to the simulations performed here (Holt et al. 2014, Biastoch et al. 2018). Particles were traced back in time for up to one year, with particle releases initialized quarterly (January, April, July, October) over a decade (2005–2014). Particle trajectories were calculated, and the particles' locations were recorded at daily frequency. With herbivorous reef fish having maximum travel distances in one direction of up to 10 km and piscivorous reef fish up to tens of kilometres we allow for a 0.25° (~ 28 km) buffer around the reef polygon or fish survey sites to capture all

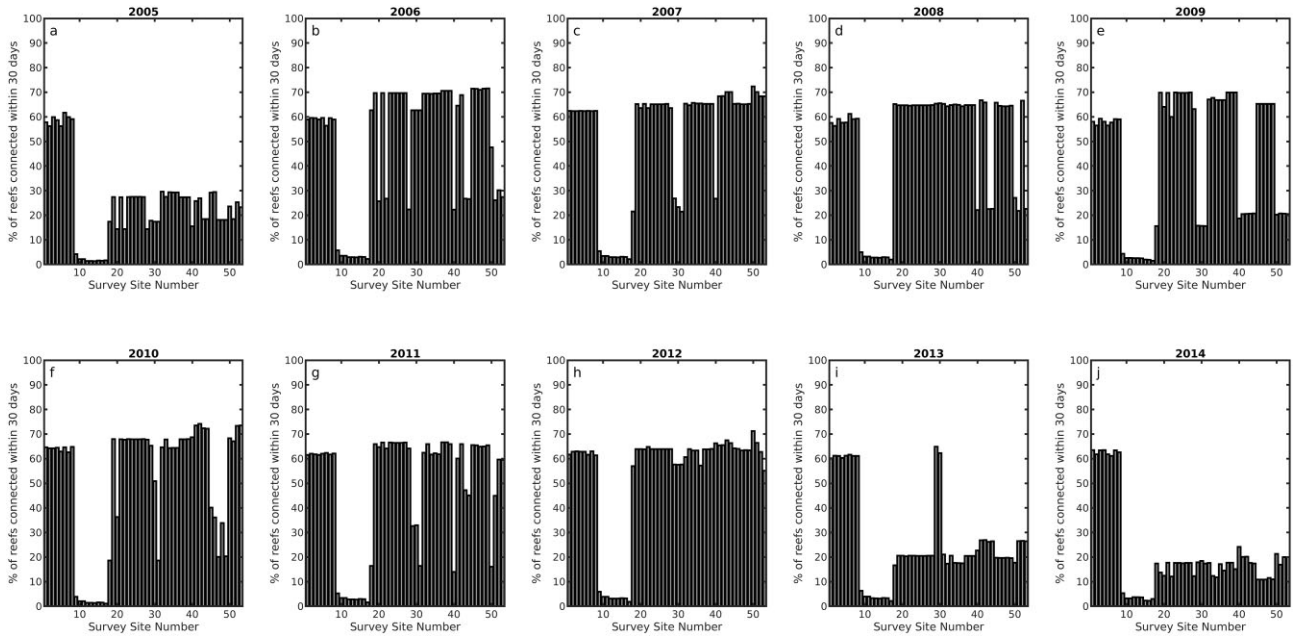


Figure 3. Bar plots for the proportional oceanographic connectivity metric for each year and for all 51 sites.

Table 2. Variance explained in the abundance of trophic groups of coral reef fish by environmental variables in the Western Indian Ocean.

Model	Deviance explained (%)	AICc	edf	Δ AICc
GRAZERS AND DETRITIVORES				
mean sea surface temperature + mean chlorophyll <i>a</i> + connectivity ($K = 14$)	89.9	880.7195	37.33163	0
mean sea surface temperature + mean chlorophyll <i>a</i> ($K = 14$)	63.3	1142.161	26.15785	261.4415
LARGE AND SMALL EXCAVATORS				
mean sea surface temperature + mean chlorophyll <i>a</i> + connectivity ($K = 10$)	73.8	702.8713	26.17412	0
mean sea surface temperature + mean chlorophyll <i>a</i> ($K = 10$)	53.4	892.5468	17.07838	189.6755
CORALLIVORES				
mean sea surface temperature + mean chlorophyll <i>a</i> ($K = 10$)	57.1	471.3942	15.3773	0
mean sea surface temperature + mean chlorophyll <i>a</i> + connectivity ($K = 10$)	66.6	482.8149	22.28583	11.4207
PRIMARY PISCIVORES				
mean sea surface temperature + mean chlorophyll <i>a</i> ($K = 16$)	61.9	318.9211	17.21521	0
mean sea surface temperature + mean chlorophyll <i>a</i> + connectivity ($K = 16$)	62.8	323.8636	17.69656	4.9425

Top-ranked models (bold) of environmental condition and coral reef fish trophic group abundance. AICc = Akaike information criterion corrected for small sample size, edf = estimated degrees of freedom, Δ AICc = difference of AICc relative to the best-fit model.

modelled particles that are reef-associated whilst limiting overlap of the boxes (Green et al. 2015).

Data modelling

We used GAMs to evaluate the relationship of the abundance of the four trophic reef fish groups—grazers and detritivores, excavators, corallivores, and primary piscivores—with the annual mean of both SST and chlorophyll *a* as well as proportional oceanographic connectivity. Visual data inspection showed non-linear relationships for most predictors and thus, GAMs were fitted with the modelling package *mgcv* (1.9–0). Poisson distribution was selected for the abundance data and model assumptions were confirmed through inspection plots. To avoid multicollinearity issues, predictor variables with significant Pearson correlations were not included in the same model. All models were fitted with the Maximum Likelihood method, which performs more robustly under smoothing (Wood 2017). The models were selected based on Akaike's information criterion for small sample sizes (AICc) (Akaike 1998, Wood et al. 2013, R Development Core Team 2018).

The final models were run with different numbers of smooth functions (between $k = 4$ and $k = 16$; default $k = 10$) and the final k parameter was chosen based on capturing the dimensionality of the underlying function and a resulting stable model fit confirmed via AICc values (Wood 2004, 2017, Wood et al. 2013) (Table 2; Supp. Table S2), k -index values, and visual diagnostics plots (Supp. Figs S4–S7; Supp. Table S3–S6).

Results

The proportional oceanographic connectivity metric is below 75% across all sites and the same sites exhibit high or low connectivity patterns throughout the years with the exception of 2013 and 2014 (Fig. 3). Hence, the most highly connected fish survey sites are linked to 75% of coral reefs whereas the least connected sites are linked to just under 5% of coral reefs in the WIO region.

For grazers and detritivores and large and small excavators, models including connectivity were favoured in model

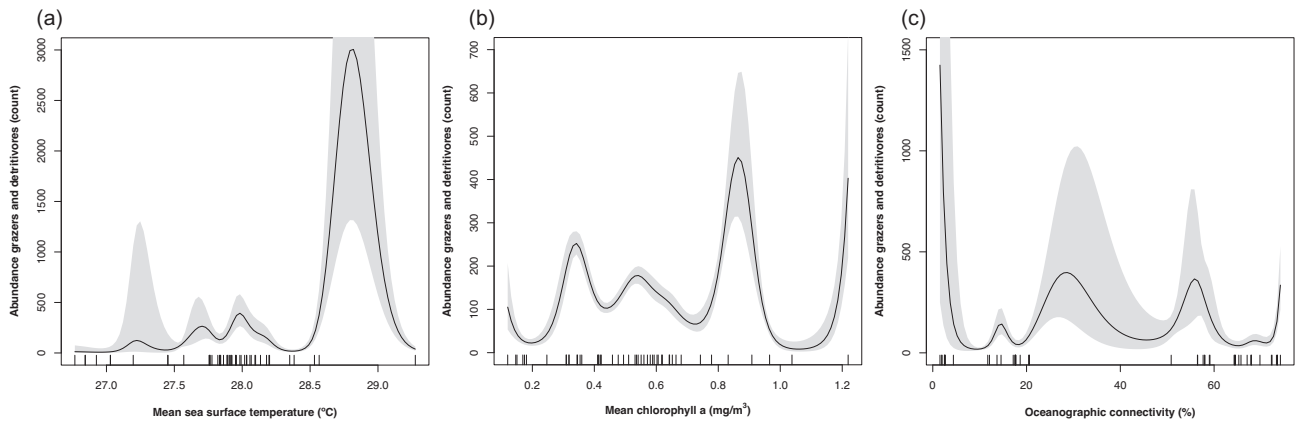


Figure 4. Relationship between the abundance of grazers and detritivores with (a) mean sea surface temperature, (b) mean chlorophyll *a*, and (c) oceanographic connectivity. The best-fit functions are shown with 95% confidence interval in grey and standard errors of both a partial effect combined with the model intercept. The x-axis shows the amount of data points, and the y-axis was shifted to include the intercept.

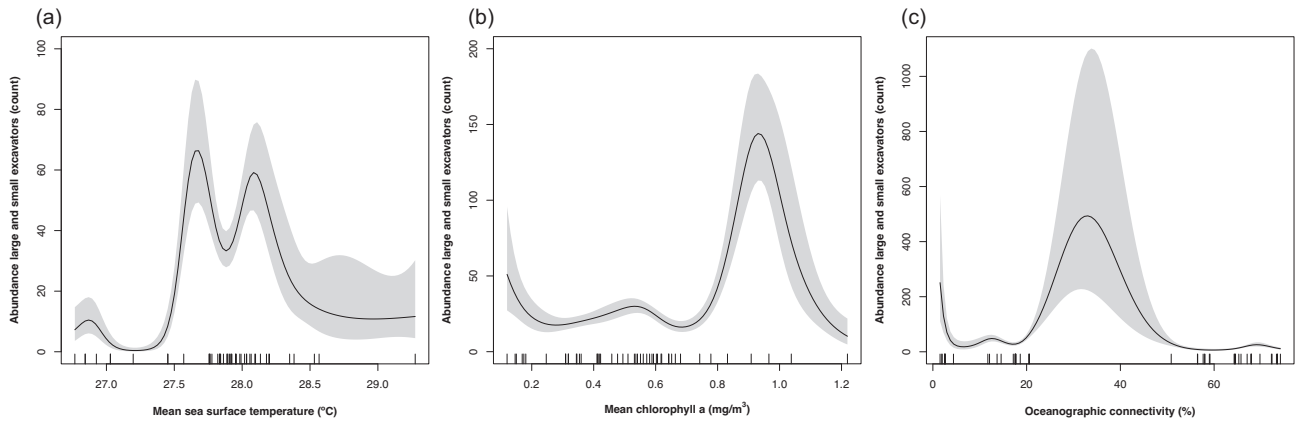


Figure 5. Relationship between the abundance of large and small excavators with (a) mean sea surface temperature, (b) mean chlorophyll *a*, and (c) oceanographic connectivity. The best-fit functions are shown with 95% confidence interval in grey and standard errors of both a partial effect combined with the model intercept. The x-axis shows the amount of data points, and the y-axis was shifted to include the intercept.

selection (lowest AICc) with the best fits ranging from 89.9% deviance explained for grazers and detritivores to 73.8% deviance explained for excavators (Table 2). For corallivores and primary piscivores, the best-fit models include SST and chlorophyll *a* but the models, including connectivity have only minor AICc differences of 11.4 or 4.9, respectively. For grazers and detritivores and excavators all three variables were highly significant (P -value < 0.001). For corallivores and primary piscivores, the best-fit models did not include connectivity, but the other two parameters (SST and chlorophyll *a*) were highly significant (P -value < 0.001).

The abundance of grazers and detritivores peaked at 28.5°C–29°C, the highest peak temperatures of all groups, (Fig. 4a) and at levels of 0.8–1 mg/m³ and above 1.2 mg/m³ chlorophyll *a* (Fig. 4b). For proportional oceanographic connectivity highest abundances were predicted at the connectivity levels of below 5%, between 20% and 40%, and at 55% (Fig. 4c).

Higher SST led to higher excavator abundances with peaks at 27.5°C–28.2°C, whereas for chlorophyll *a* the pattern is more extreme with a sudden peak at 0.9 mg/m³ which then dropped sharply (Fig. 5a, b). For proportional oceanographic connectivity, a peak of excavator abundance appeared between levels of 20% and 50% (Fig. 5c).

The relationship of corallivores with mean SST shows highly non-linear patterns with predicted abundance peaks at 27.3°C and 28.2°C (Fig. 6a). The model indicates a clear trend predicting higher corallivore abundances with chlorophyll *a* levels greater than 1 mg/m³ (Fig. 6b).

Primary piscivore abundances were variable with SST, with a peak at 27.2°C, lower than the other three groups, but a second peak above 28.7°C (Fig. 7a). Primary piscivore abundances show a strong peak in abundances at chlorophyll *a* levels between 0.8 mg/m³ and 1 mg/m³ (Fig. 7b).

Discussion

Here we have shown oceanographic connectivity plays an important environmental role in driving abundance of herbivorous fish groups such as grazers and detritivores and excavators. Connectivity is accounting for 26.6% variation in abundance levels of grazers and detritivores and 20.4% for excavators (Table 2). The best-fit models for corallivores and primary piscivores included only SST and chlorophyll *a* and connectivity explained less than 10% of deviance (Table 2). However, connectivity can still be considered an important driver of their abundances as the difference in AICc values between models with and without connectivity is minor

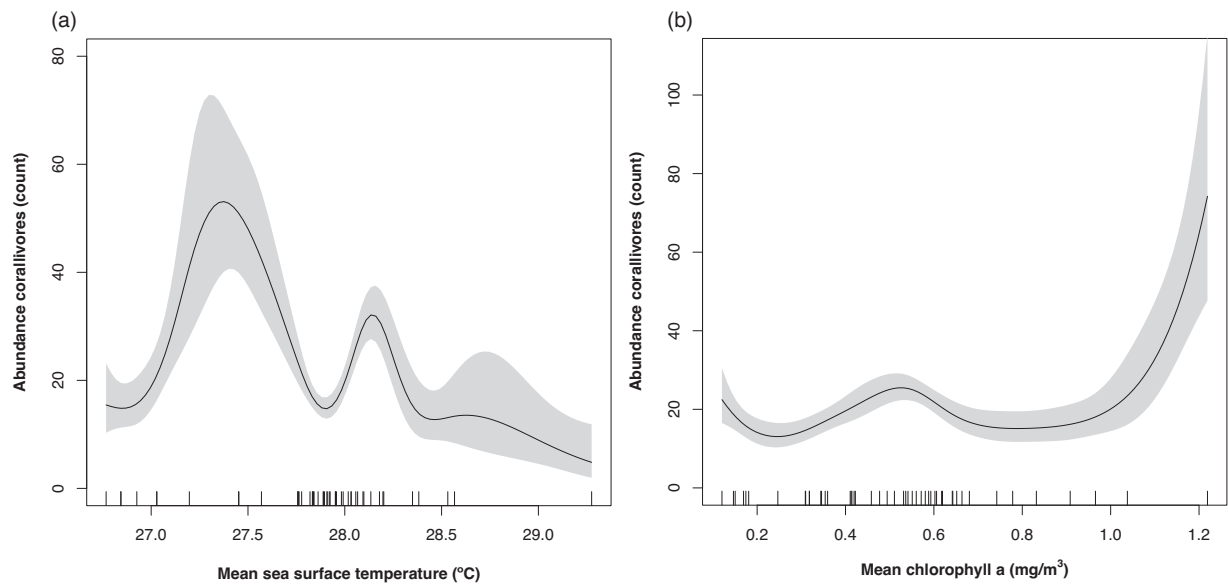


Figure 6. Relationship between the abundance of corallivores with (a) mean sea surface temperature, and (b) mean chlorophyll *a*. The best-fit functions are shown with 95% confidence interval in grey and standard errors of both a partial effect combined with the model intercept. The x-axis shows the amount of data points, and the y-axis was shifted to include the intercept.

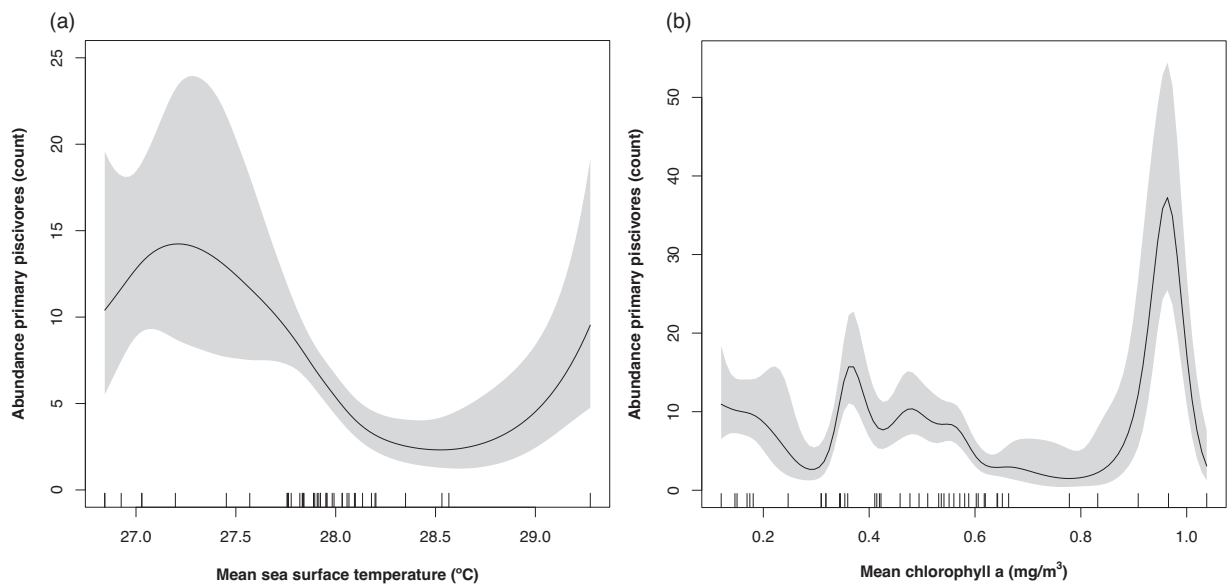


Figure 7. Relationship between the abundance of primary piscivores with (a) mean sea surface temperature, and (b) mean chlorophyll *a*. The best-fit functions are shown with 95% confidence interval in grey and standard errors of both a partial effect combined with the model intercept. The x-axis shows the amount of data points, and the y-axis was shifted to include the intercept.

(Δ AICc <12). Interestingly, different trophic groups were found to have different relationships with oceanographic connectivity. This may in part be due to different movement patterns and habitat confidentiality (Roberts and Ormond 1992, Green et al. 2015, Mayorga-Adame et al. 2017, Roberts et al. 2021). Grazer and detritivore and excavator abundances peaked at medium connectivity levels. Hence, sites with intermediate connectivity can play a larger role in supporting grazers and detritivores and excavators than ones with high levels of connectivity. This may suggest that population size for species within these trophic groups is driven by reproduction and larvae dispersal at a local scale. This is consistent with findings of limited home ranges for herbivorous reef fish (Mumby and Wabnitz 2002, Welsh and Bellwood

2014) but contradicts the idea of herbivores as linking organisms between habitats (Nyström et al. 2008). High connectivity can also come with side effects, such as stronger wave exposure or increased pollutant dispersal, which may have adverse impacts on population sizes (Hughes et al. 2010, Mayorga-Adame et al. 2017). The sharp abundance increase at very low connectivity for grazers and detritivores could be due to statistical issues (e.g. overfitting—see below) (Wood 2008, Marra and Wood 2011, Wood et al. 2016). While a range of smooth functions and model fits were compared, the amount of available data can result in such patterns and limits the model interpretations to large-scale dynamics (Wood et al. 2013, 2016, Wood 2017, Yates et al. 2018).

Grazers and detritivores exhibit patterns of increased abundance with higher temperatures and higher chlorophyll *a* levels and a large drop in abundance after certain thresholds. For excavators (parrotfishes) higher abundances were predicted with medium SST (27.5°C–28.2°C) and high chlorophyll *a* levels (0.8–1.0 mg/m³). It is known that reef fish abundances are negatively impacted by increasing SST above a certain threshold, although fish are more resilient to temperature anomalies than corals when reef structural complexity is maintained (Lloyd *et al.* 2012, Graham *et al.* 2015, Brandl *et al.* 2019). All trophic group models show abundance increasing with higher chlorophyll *a* up until 1 mg/m³ with further increases for grazers and detritivores and corallivores. This is consistent with a previous study (Samoilys *et al.* 2019) and supports evidence that fish species in the WIO might have adapted to changes in SST or chlorophyll *a* due to monsoon seasons (Kaunda-Arara *et al.* 2009, Marshall *et al.* 2014, Mayorga-Adame *et al.* 2017). As chlorophyll *a* is used as a proxy for nutrient levels in seawater, it is not surprising that higher productivity along the east African coast results in higher fish abundance due to higher food availability (Williams *et al.* 2015, Samoilys *et al.* 2019). This trend has also been shown for higher fish biomass across the Pacific (Williams *et al.* 2015). However, there are still drawbacks in the algorithms of sensors and performance of remotely sensed chlorophyll *a* data in ultra-oligotrophic, eutrophic, and optically-complex waters, limiting the conclusions that can be drawn from these data (Williams *et al.* 2015, Zheng and DiGiacomo 2017, Sathyendranath *et al.* 2019, Lahiri and Vissa 2022). Corallivores may not be as impacted by connectivity due to their shorter PLDs, limited home ranges mostly under 1384.9 m², and territorial behaviour (Booth and Parkinson 2011, Mayorga-Adame *et al.* 2017, Roberts *et al.* 2021, Takagi *et al.* 2023). However, their abundances decrease with higher temperatures confirming their dependency on live coral for food (Roberts and Ormond 1992, Stuart-Smith *et al.* 2021). Primary piscivores (largely groupers) are the most sensitive group to fishing and hence can be used as an indicator for fishing impacts (Hussey *et al.* 2014). The models show a non-linear relationship with temperature with predicted abundance peaks at lower temperatures compared to the other groups suggesting higher temperature susceptibility of piscivores or of their prey (Clark *et al.* 2017, Stuart-Smith *et al.* 2021). Piscivore abundances were not significantly influenced by connectivity, which supports the notion that these bigger fish with larger home ranges travel further and hence, the number of connections of their reef habitats to other reefs through ocean currents is less critical (Mayorga-Adame *et al.* 2017).

Our mean SST data has a range from 26.78°C to 29.28°C. For equatorial regions, this is considered large and rising temperatures above 28°C will alter future trophic fish communities through habitat degradation and decreased metabolic or swimming capabilities of adult fishes (Johansen and Jones 2011, Stuart-Smith *et al.* 2021, Samoilys *et al.* 2022). Further, higher temperatures will accelerate fish larval development shortening dispersal durations and thus, altering fish abundance and distribution patterns (Johansen and Jones 2011, Álvarez-Noriega *et al.* 2020). Local and seasonal upwelling patterns affect remotely sensed SST data, which often overestimate temperatures in coastal regions (Ramanantsoa *et al.* 2018, Meneghesso *et al.* 2020, Lahiri and Vissa 2022, Spring and Williams 2023). Hence, our model predictions are less

suitable for local contexts but focus on large-scale impacts of SST on fish abundances (Samoilys *et al.* 2019, 2022, Hochberg *et al.* 2020, Obura *et al.* 2021). Chlorophyll *a* levels ranged in our study from 0.4 to 1.2 mg/m³ and high levels can indicate reduced water quality (Feng and Hu 2016). Since in-situ data are costly across large spatial and temporal scales, we used remotely sensed ocean colour chlorophyll *a* data for our standardized fore reef sites across the WIO (Samoilys *et al.* 2019, 2022, Hochberg *et al.* 2020, Keighan *et al.* 2023). Remote data quality is consistent with less turbidity at fore reefs and ocean colour technologies capture temporal and spatial variations better than other methods (Gohin *et al.* 2008, Samoilys *et al.* 2019, Lahiri and Vissa 2022). Positive relationships of fish larvae with chlorophyll *a* have been reported before in a Kenyan field study and this might change if chlorophyll *a* levels alter with ocean warming (Kaunda-Arara *et al.* 2009, Benyounes *et al.* 2017). This could be investigated with future work linking abundance patterns with climate projections. Trophic groups in our study followed this trend for fish abundance, with the exception of piscivores which showed a weak negative trend for chlorophyll *a* (Williams *et al.* 2015, Samoilys *et al.* 2019).

The statistical modelling presented here gives insight into how trophic group abundances are impacted by environmental variables and oceanographic connectivity. The results show some clear trends that connectivity is an important driver for herbivorous reef fish, alongside SST and chlorophyll *a* concentrations across the WIO. Including reef characteristics, such as wave exposure, structural complexity, self-recruitment, fishing pressure, and in-situ measurements of environmental data may help to expand our modelling study and further explain variation in species abundances in future. We aim to develop the connectivity metric further to capture more fine-scale patterns using higher resolution models or smaller boxes with less overlap around fish sites. Since PLDs are predicted to decrease with climate change leading to a reduction in larvae dispersal distances we could test for different PLDs and other larvae characteristics such as mortality and settlement competency in future (Tremblay *et al.* 2015, Gamoyo *et al.* 2019, Álvarez-Noriega *et al.* 2020). The limitations of statistical connectivity modelling can be overcome to some extent with validation from other approaches such as genetic markers and developments in biophysical modelling (Mertens *et al.* 2018, Vaz *et al.* 2022, Wilcox *et al.* 2023). Despite testing different numbers of smooth functions (*k*) and selecting this final number of functions based on a stable model fit, AICc values, *k*-index values, and visual diagnostics plots, there is a potential excess of non-linearity with using the smooth functions (Wood 2008, Marra and Wood 2011, Wood *et al.* 2016, Yates *et al.* 2018). This could lead to an overestimation of the model fit to data when there are a limited number of observations (Wood *et al.* 2016, Yates *et al.* 2018). Small sample sizes can influence both the statistical fitting and biological interpretation of GAMs (Wood *et al.* 2016, Wood 2017, Yates *et al.* 2018). It is important to note that statistical limitations such as overfitting with these sorts of models are a potential bias and we are cautious about making strong ecological inferences given the low sample sizes (Marra and Wood 2011, Wood *et al.* 2016, Yates *et al.* 2018). However, since our main conclusions draw on large-scale patterns and environmental drivers of fish abundance, these interpretations are not affected by sample size (Marra and Wood 2011, Wood *et al.* 2016, Yates *et al.* 2018, Samoilys *et al.* 2019). Limiting the number of smooth functions might lead to clearer ecological relationships but could

oversimplify complex dynamics (Yates et al. 2018). Further research and data is needed to make small-scale, ecological predictions.

In summary, by using a proportional oceanographic connectivity metric and incorporating this into ecological modelling we show that connectivity plays a role in driving abundances of herbivorous trophic fish groups. Herbivorous fish are an extremely important trophic group for reef resilience because of their role in algae control on reefs (Fox and Bellwood 2013, Heenan and Williams 2013, Brandl et al. 2019). Therefore, ideally oceanographic connectivity should be considered in reef management, such as MPA planning, to increase reef resilience, and our proportional oceanographic connectivity metric is one proven way to do this. This is especially critical in the WIO, which is under high anthropogenic pressure and is predicted to undergo annual bleaching on most coral reefs by 2064 even under optimistic RCP4.5 scenarios (van Hooijdonk 2020, Obura et al. 2021). Consideration of connectivity in MPA design, for instance, to protect the most important source reefs, would help build reef resilience to these threats by aiding reef recovery through larvae dispersal.

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Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

The data and code underlying this article are available in Zenodo, at <https://doi.org/10.5281/zenodo.8111570>.

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