Coral reef potential connectivity in the southwest Indian Ocean

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Abstract

The tropical southwest Indian Ocean is a coral biodiversity hotspot, with remote reefs physically connected by larval dispersal through eddies and a complex set of equatorial and boundary currents. Based on multidecadal, 2 km resolution hydrodynamic and larval dispersal models, we find that powerful zonal currents, current bifurcations, and geographic isolation act as leaky dispersal barriers, partitioning the southwest Indian Ocean into clusters of reefs that tend to physically retain larvae (and therefore gene flow) over many generations, despite considerable variability due to marine turbulence. Whilst exceptionally remote, the Chagos Archipelago can broadcast (and recieve) considerable numbers of larvae to (and from) reefs across the wider west Indian Ocean, most significantly exchanging larvae with the Inner Islands of Seychelles, but also the Mozambique Channel region. Considering multi-generational dispersal indicates that most coral populations in the southwest Indian Ocean are physically connected within a few hundred steps of dispersal. These results suggest that regional biogeography and population structure can be largely attributed to recent patterns of larval dispersal, although some notable discrepancies indicate that local adaptation, environmental suitability, and/or palaeogeography also play an important role. The model output and connectivity matrices are available in full, and will

provide useful physical context to regional biogeography and connectivity studies, as well as supporting marine spatial planning efforts.

Keywords: Indian Ocean, Coral Reef, Dispersal, Connectivity, Larvae, Biogeography, Population Genetics, Model

1 Introduction

Long-distance connectivity can be established between remote coral reefs through the process of larval dispersal, transported by ocean currents and modulated by larval behaviour (Cowen and Sponaugle, 2009). The physical transport of larvae between reefs is known as *potential connectivity* (Mitarai et al, 2009), and can be quantified as *explicit connectivity* (the likelihood of larval transport from i to j) or *implicit connectivity* (the likelihood of shared larval sources or destinations for i and j) (Ser-Giacomi et al, 2021). Physical larval transport can drive demographic connectivity, genetic connectivity, and evolution depending on the magnitude and variability of potential connectivity, and post-settlement processes (e.g. Watson et al, 2010; Lowe and Allendorf, 2010; McManus et al, 2021). Quantifying reef connectivity is therefore important for effective marine spatial planning (Beger et al, 2010; Balbar and Metaxas, 2019) and explaining biodiversity and biogeography (e.g. Cowen et al, 2006). However, these data are lacking in the tropical southwest Indian Ocean, a biodiversity hotspot (Obura, 2012; Veron et al, 2015; Kusumoto et al, 2020) home to around 7% of the world's tropical coral reefs (Souter et al, 2021).

At present, there is a basic understanding of reef connectivity in this region. The time-mean surface circulation in the southwest Indian Ocean is to first-order explained by Sverdrup transport, generating southward and northward interior transport north and south of ∼15 °S respectively (Godfrey, 1989). This drives the westward flowing South Equatorial Current (fig. 1). When the South Equatorial Current meets Madagascar, it splits into the Southeast and Northeast Madagascar Currents. The former

flows southward along the east coast of Madagascar before feeding the Agulhas system, whilst the latter rushes past the north coast of Madagascar before forming a westward jet, generating eddies through barotropic instability in the process (Collins et al, 2014). The Northeast Madagascar Current then bifurcates, partially feeding the net-southward but eddy-dominated flow of the Mozambique Channel, but with most water entering the East African Coastal Current, which flows northward along the coast of Tanzania and Kenya (Swallow et al, 1991). The East African Coastal Current crosses the equator throughout much of the year (peaking during the southeast monsoon, from May to August), feeding the Somali Current. During the northwest monsoon (December to March), the Somali Current reverses due to the monsoonal reversal of winds, causing the East African Coastal Current to tend to separate from the coast south of the equator and feed the eastward South Equatorial Countercurrent (Schott and McCreary, 2001), although there is considerable interannual variability (e.g. Sachidanandan et al, 2017).

There is limited data on broadcasting coral spawning in the tropical southwest Indian Ocean, with synchronised mass spawning taking place in September to December in Mozambique (Sola et al, 2016), whilst unsynchronised spawning has been observed or inferred elsewhere from October to April (Kenya, Mangubhai and Harrison, 2008a, 2009) and October to December (Seychelles, Koester et al, 2021). This indicates that most spawning takes place during the northwest monsoon, during which larval dispersal should be largely westward within the region dominated by the South Equatorial Current, with eddy-mediated dispersal across the Mozambique Channel, and strong connectivity along the path of the East African Coastal Current. This is broadly supported by regional coral biogeography (Obura, 2012), coral population genetics (e.g. van der Ven et al, 2022), and global (Wood et al, 2014) and regional (Crochelet et al, 2016; Mayorga-Adame et al, 2017; Gamoyo et al, 2019) larval dispersal simulations. These studies provide valuable insights into the connectivity of the

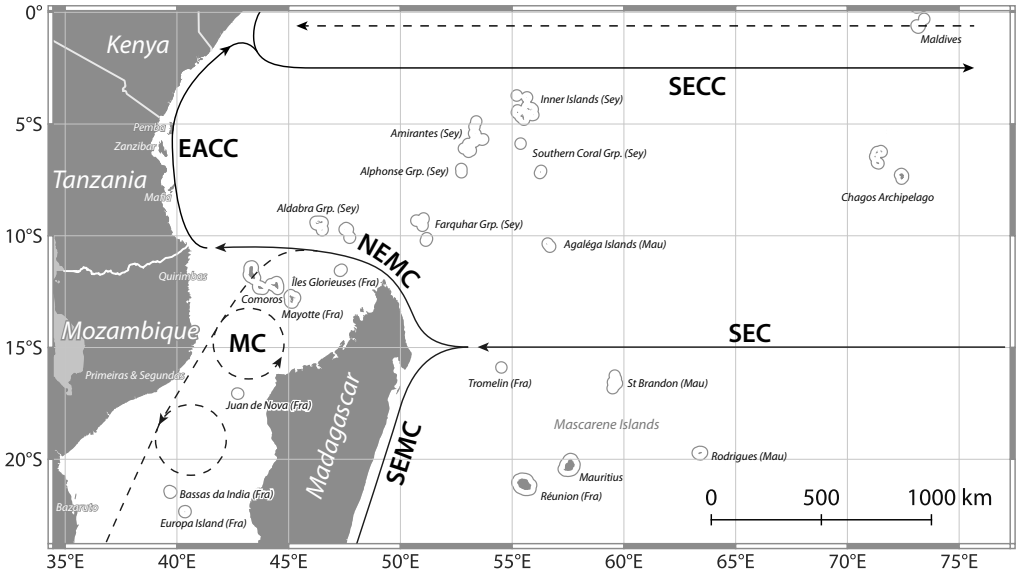

Fig. 1 Map of the tropical southwest Indian Ocean (domain considered by this study), with a schematic representation of surface currents (during the northwest monsoon) based on Schott and McCreary (2001) (**SEC**: South Equatorial Current; **SECC**: South Equatorial Countercurrent; **NEMC**: Northeast Madagascar Current; **SEMC**: Southeast Madagascar Current; **EACC**: East African Coastal Current; **MC**: Mozambique Channel). Dashed lines represent transient surface currents. Note that small islands have been drawn with a halo for visibility.

southwest Indian Ocean, and generally support the existence of well-connected reef clusters in the north Mozambique Channel and along the path of the East African Coastal Current.

However, some genetic studies reveal complex, fine-scale patterns of genetic differentiation around small islands in the path of the EACC (e.g. van der Ven et al, 2016). These observations reveal variability below the scale that can be easily resolved by the large-scale larval dispersal studies conducted to date, which rely on relatively coarse oceanographic data (Wood et al, 2014; Crochelet et al, 2016; Gamoyo et al, 2019). This necessitates the use of higher resolution hydrodynamic models, to investigate to what extent these more localised patterns of differentiation can be explained through physical larval dispersal, as opposed to biological processes such as selection. The importance of high-frequency variability for larval dispersal between remote reefs (Vogt-Vincent et al, in press) also necessitates new approaches. The time-mean

connectivity matrices considered by most previous studies obfuscate the considerable stochastic connectivity variability introduced by turbulence in the ocean, which has important implications for ecology (Watson et al, 2012). Bridging the gap between potential connectivity (from numerical models) and realised connectivity (from population genetics) also has important implications for effective marine spatial planning (Balbar and Metaxas, 2019).

The aim of this study is to describe and physically explain the potential connectivity between all shallow reefs in the tropical southwest Indian Ocean, to support marine spatial planning efforts, and to test to what extent potential connectivity explains regional population structure and biogeography. For this purpose, we simulate daily coral spawning events based on 28 years of surface current predictions at 2 km resolution, representing the highest resolution dataset spanning the entire tropical southwest Indian Ocean, from East Africa to the Chagos Archipelago. In addition to the results presented here, all data from this study and scripts required to reproduce figures, as well as an interactive web app visualising the connectivity network, are available in the associated datasets (Vogt-Vincent et al, 2023).

2 Methods

2.1 Hydrodynamical and larval dispersal models

We modelled coral larvae as passively drifting particles, advected by surface currents, using the SECoW (Simulating Ecosystem Connectivity with WINDS) framework built on OceanParcels (Delandmeter and van Sebille, 2019), as previously described in Vogt-Vincent et al (in press). Young coral larvae are generally positively buoyant, but lose buoyancy with age. However, the vertical swimming speed of coral larvae is significant compared to vertical currents in the open ocean, and they therefore have some capacity to control their position in the water column (Szmant and Meadows, 2006). Larvae of at least some species appear to remain near the surface in response to pressure and

light cues (Stake and Sammarco, 2003; Mulla et al, 2021), which we use to justify our assumption that coral larvae are confined to the upper water column.

We used surface currents from the WINDS model (Vogt-Vincent and Johnson, 2023), spanning the tropical southwest Indian Ocean from 1993-2020, at ∼2 km spatial and 30-minute temporal resolution. Larval dispersal can take place over distances below this spatial resolution, due to asexual reproduction, short larval competency periods, and reef hydrodynamics (e.g. Dubé et al, 2020; Lord et al, 2023; Grimaldi et al, 2022). It is therefore important to note that our analysis will only resolve dispersal over distances of at least a few kilometres. We released 2^{10} particles from each of the 8088 2×2 km coral reef cells identified in the tropical southwest Indian Ocean (Li et al, 2020) daily at midnight between October and March from 1993-2019, for a total of 4920 simulated spawning events. The available evidence suggests that coral spawning in the southwest Indian Ocean is concentrated in these months (e.g. Baird et al, 2021), but it is straightforward to repeat these analyses for alternative spawning seasonality, as the underlying dataset includes year-round spawning.

As in Vogt-Vincent et al (in press), the number of coral larvae represented by each particle is proportional to the surface area of reef within its origin cell (i.e. assuming constant fecundity per unit area of reef). We assumed that larvae gain and lose competency at constant rates following an initial pre-competency period, and die following a time-varying mortality rate (Connolly and Baird, 2010). Finally, we assumed that competent larvae settle with a constant probability per unit time, given that they are above a coral reef, thereby accounting for the possibility that larvae pass over a reef without settling (Hata et al, 2017). Since there is no meaningful information on the flow field below the resolution of the model grid (∼2 km), we scale this probability by the proportion of each grid cell that is occupied by reef. Further details on the larval dispersal model can be found in the supplementary materials (section 1). In this study, we used larval parameters for *Platygyra daedalea*, a broadcast spawning

coral widespread across the Indo-Pacific and commonly used as a study taxon in the southwest Indian Ocean (e.g. Mangubhai et al, 2007; Mangubhai and Harrison, 2008b; Souter and Grahn, 2008; Montoya-Maya et al, 2016), with intermediate pelagic larval duration (Connolly and Baird, 2010). However, our first-order conclusions are robust across species (analogous figures for the other sets of larval parameters described by Connolly and Baird (2010) can be found in the associated datasets, and are described in the supplementary materials, section 2).

2.2 Quantifying potential connectivity

For tractability, we first reduced the 8088 reef cells to 180 reef groups, identified using an agglomerative clustering algorithm. The definition of potential connectivity frequently used in the literature (e.g. Mitarai et al, 2009), i.e. the likelihood that a larva from reef i can physically settle at reef j, corresponds to the single-step *explicit* connectivity described by Ser-Giacomi et al (2021). We computed the long-term single-step explicit connectivity C_{ij} from reef i to reef j as the time-mean proportion of larvae generated at reef i that settle at reef j. We similarly computed the standard deviation of explicit connectivity over time, σ_{ij}. Although explicit connectivity is positively skewed and often dominated by extreme values (Vogt-Vincent et al, in press), we display the mean explicit connectivity here rather than the median, as the latter is zero for most connections.

We also considered *implicit* connectivity, specifically the backward cumulated multi-step implicit connectivity (hereon CMIC), described in Ser-Giacomi et al (2021). In contrast to the single-step explicit connectivity, the CMIC considers ancestral larval sources over multiple steps of dispersal. For a pair of random walks respectively terminating at reefs i and j, $\mathrm{CMIC}_{ij}(k)$ is defined as the probability that the pair of random walks passed through a common reef at least once within k steps. If we assume that gene flow through a reef network can be modelled as a random walk weighted

by explicit connectivity (thereby neglecting all post-settlement processes), $\mathrm{CMIC}_{ij}(k)$ may represent the degree of shared ancestry between two coral populations within k generations of dispersal. Although this assumption is unrealistic, Legrand et al (2022) nevertheless found that CMIC was a better predictor of genetic differentiation between populations than explicit connectivity alone. We estimated the number of generations of dispersal 'separating' two reefs, G_{ij}, by solving for k such that $\mathrm{CMIC}_{ij}(k) = 0.5$.

Due to stochastic oceanographic variability, Vogt-Vincent et al (in press) found that CMIC based on time-varying explicit connectivity (i.e. allowing explicit connectivity to vary between spawning events) was only poorly represented by CMIC based on the time-mean explicit connectivity. We therefore computed G_{ij} separately for 1000 randomly generated temporal subsets of the full time-varying explicit connectivity matrix (each subset representing a random series of spawning events, drawn from the 4920 available events), and took the median across this G ensemble.

2.3 Clustering

Partitioning the reef network into clusters that tend to retain coral larvae is a useful tool for understanding large-scale network structure, and comparing modelled connectivity to observations (e.g. Treml and Halpin, 2012; Thompson et al, 2018). For this purpose, we use the Infomap algorithm (Rosvall et al, 2009; Edler et al, 2023). Infomap partitions flow networks to minimise the information required to describe a random walk (e.g. gene flow through larval dispersal), and identifies clusters of nodes (reefs) that tend to retain flow (gene flow) more effectively than alternative metrics such as modularity (supplementary materials, section 3, Rosvall et al (2009)). However, due to the considerable stochastic variability in reef connectivity (Vogt-Vincent et al, in press), clusters of reefs that tend to retain larvae based on time-mean potential connectivity may not be equivalent to clusters of reefs that tend to retain larvae over a given shorter time interval (thereby affecting short-term population dynamics). We

are therefore interested in identifying clusters of reefs that *consistently* retain larvae over l spawning events.

Similar to our computation of G (section 2.2), we generated 1000 subsets of the full time-varying explicit connectivity matrix (each containing a random series of l spawning events), and computed the time-mean explicit connectivity for each subset over the l events. The value of l depends on the timescale of interest; we took $l = 10$ to investigate dispersal over decadal timescales, to reflect the response of reefs to short-term environmental disturbance. We then individually partitioned the reef network using Infomap for each short-term connectivity matrix, recording the lowest-level cluster assigned to each reef node in a cluster assignment matrix. A principal component analysis (PCA) revealed that over 80% of the variance in cluster assignment across the 1000 possible dispersal histories was explained by the first three principal components (PC1-3). We therefore reduced the cluster assignment matrix to three dimensions, with the closeness between reef nodes in this space representing how consistently reefs were assigned to the same cluster across stochastic oceanographic variability. We objectively assigned reefs to discrete clusters through K-Means clustering based on PC1-3. For illustrative purposes, we focus on the case with $k = 8$ clusters, as this distinguishes most clearly between the clusters emerging from the PCA; however, we note that the optimal number of clusters as identified by the elbow method appears to be around 3, although this is poorly constrained (supplementary materials, fig. S1).

3 Results

3.1 Explicit connectivity

Fig. 2 shows the time-mean explicit connectivity matrix, which is also available as raw data, and presented as an interactive web application in the supplementary materials (Vogt-Vincent et al, 2023). Aside from the general pattern of time-mean explicit connectivity falling with distance, there is considerable asymmetry in the explicit

connectivity, as expected from a region influenced by strong ocean currents (fig. 1). For instance, there is relatively strong explicit connectivity ($> 10^{-5}$) from the Outer Islands of Seychelles to sites in East Africa due to the rapid Northeast Madagascar Current, whereas explicit connectivity in the opposite direction is orders of magnitude weaker as no direct dispersal pathway exists. The weakest connections within Seychelles are not the most distant (the Aldabra Group and Inner Islands, fig. 1), but rather from the Aldabra Group to the relatively nearby Farquhar Group, which would require larval transport in the opposite direction to the Northeast Madagascar Current. Asymmetric dispersal is also pronounced along the path of the northward East African Coastal Current from Tanzania to Kenya.

The strongest connection between the Chagos Archipelago and the rest of the southwest Indian Ocean is predicted to be with the Inner Islands of Seychelles, with mean explicit connectivity that can approach 10^{-6} from some islands in Seychelles, remarkable given the distance of over 1500 km. The eastward South Equatorial Countercurrent influences the Inner Islands of Seychelles during the northwest monsoon, providing an efficient pathway for eastward larval dispersal towards the Chagos Archipelago. Connections between the Chagos Archipelago and most other sites in the southwest Indian Ocean are expected to be principally in the opposite (westward) direction, following an initially slow southward pathway, before entering the South Equatorial Current and being rapidly transported towards the Mozambique Channel (fig. 1).

Explicit connectivity is consistently strong throughout the Chagos Archipelago, unsurprising given the expansive area of reef cover and relatively weak currents (minimising the proportion of larvae being lost to the open ocean). Larval dispersal is also strong within and between the constituent island groups of Seychelles. Due to the dominance of powerful mesoscale eddies within the Mozambique Channel, there is a

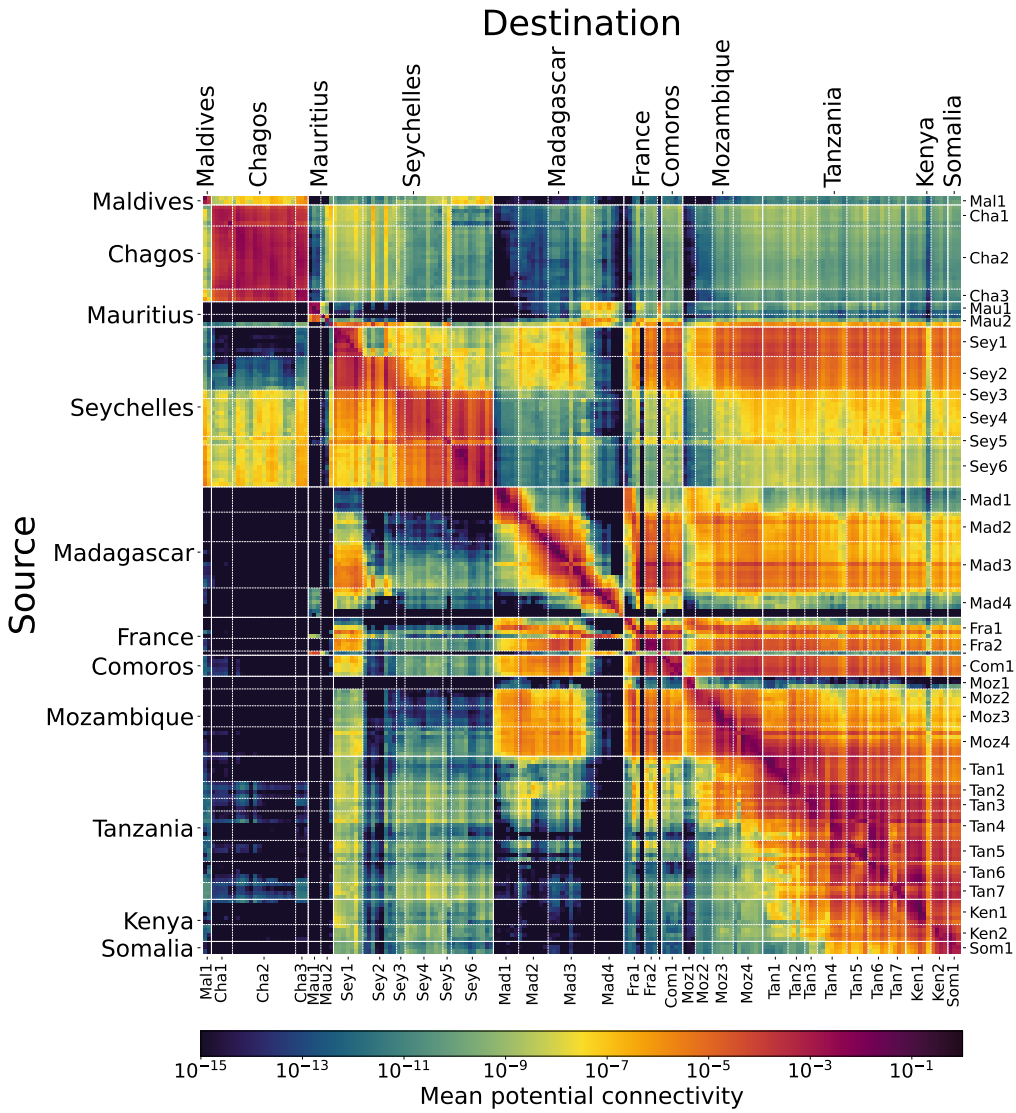

Fig. 2 Time-mean explicit connectivity between pairs of reef groups. Subregion codes are as follows: **Mal1**: Maldives; **Cha1**: S Banks; **Cha2**: Grand Chagos Banks; **Cha3**: N Banks; **Mau1**: Mauritius (Island); **Mau2**: Outer Islands; **Sey1**: Aldabra Grp; **Sey2**: Farquhar Grp; **Sey3**: Alphonse Grp; **Sey4**: Amirantes; **Sey5**: Southern Coral Grp; **Sey6**: Inner Islands; **Mad1**: SW Madagascar; **Mad2**: NW Madagascar; **Mad3**: N Madagascar; **Mad4**: E Madagascar; **Fra1**: Scattered Islands; **Fra2**: Mayotte; **Fra3**: Réunion (not labelled); **Com1**: Comoros; **Moz1**: S Mozambique; **Moz2**: Primeiras & Segundas; **Moz3**: N Mozambique; **Moz4**: Quirimbas; **Tan1**: S Tanzania; **Tan2**: Songo Songo; **Tan3**: Mafia Island; **Tan4**: Dar es Salaam region; **Tan5**: Zanzibar; **Tan6**: Tanga; **Tan7**: Pemba; **Ken1**: S Kenya; **Ken2**: N Kenya; **Som1**: S Somalia. Please see supplementary materials, fig. S2 for a geographic key to subregion codes.

fairly strong and symmetric exchange of larvae between west and north Madagascar and Mozambique, with explicit connectivity exceeding 10^{-6} between many sites.

The time-mean explicit connectivity matrix does, however, obfuscate the enormous temporal (and largely stochastic) variability in connectivity (supplementary materials, fig. S3). The standard deviation of explicit connectivity across daily spawning events is greater than the mean for practically all pairs of reef groups, with this ratio frequently exceeding 10, and even 100 for distant connections. Short-distance dispersal is generally associated with lower temporal variability, as is northward larval dispersal within Kenya and Tanzania due to the effects of the East African Coastal Current, and westward dispersal from the Outer Islands of Seychelles, Comoros, and north Madagascar due to the Northeast Madagascar Current (Vogt-Vincent et al, in press).

3.2 Implicit connectivity

Simplifying gene flow as a random walk weighted by explicit connectivity, fig. 3 (lower triangle) shows that most pairs of reefs within the southwest Indian Ocean share a common ancestral reef within around 200 steps (or generations) of dispersal (see also the raw matrices in the supplementary materials (Vogt-Vincent et al, 2023)). We expect particularly strong implicit connectivity within the Chagos Archipelago, the constituent island groups of Seychelles, and certain dense clusters of reefs within Madagascar (such as southwest and east Madagascar). Despite strong explicit connectivity, implicit connectivity along the path of the East African Coastal Current (Tanzania and Kenya) is relatively weak. The combination of strong currents and almost continuous reef cover along the coast results in larvae being distributed across a wide range of destination reefs, reducing the likelihood of site pairs sharing a same specific ancestral reef (supplementary materials, fig. S4).

Our simulations predict that the implicit connectivity between the Chagos Archipelago and the rest of the southwest Indian Ocean is strongest with Seychelles,

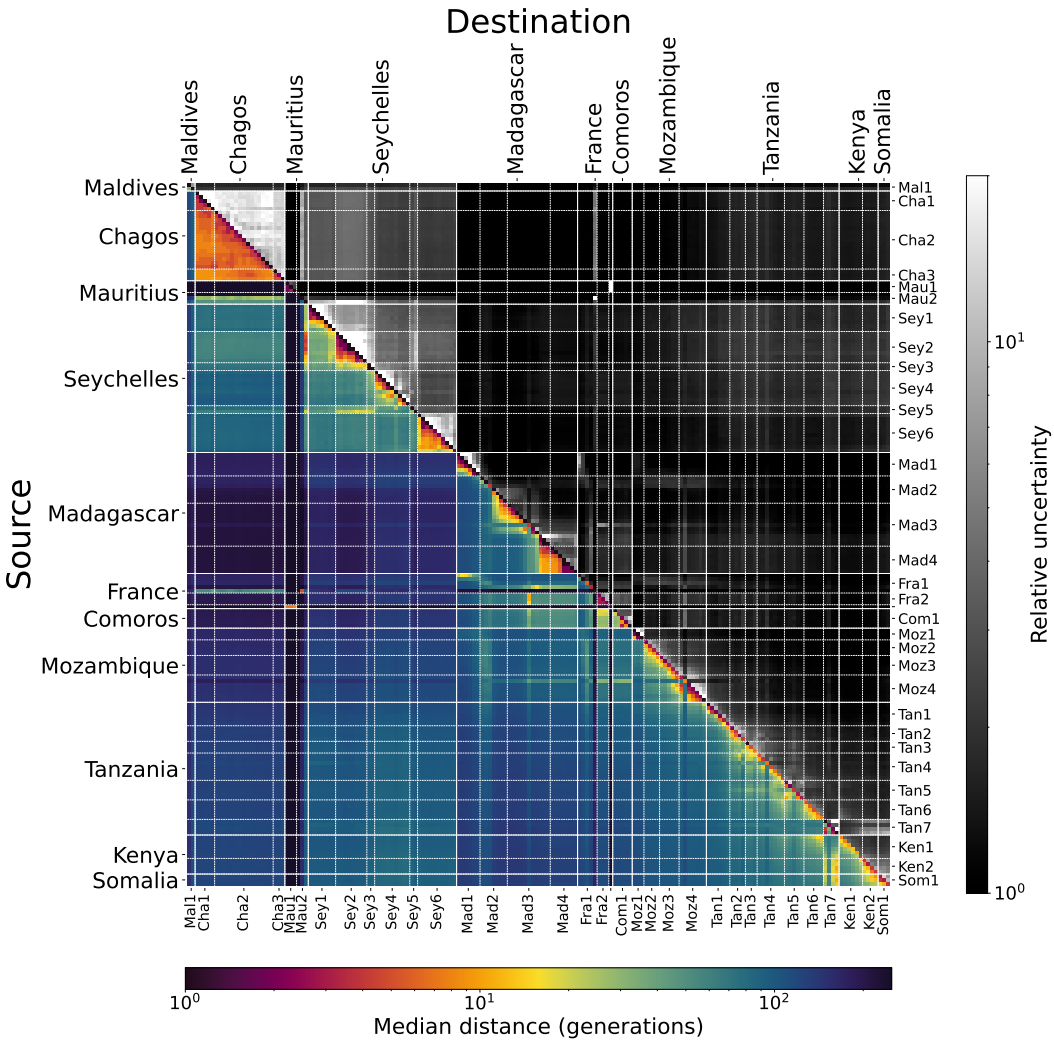

Fig. 3 *Lower triangle*: Median distance between pairs of sites in generations or steps based on CMIC (G_{ij}) across the 1000-member ensemble. *Upper triangle*: 95% confidence interval across the ensemble, divided by the median. Subregion codes as in fig. 2.

and three small island groups in the path of the South Equatorial Current (the Agaléga Islands, St Brandon, and Tromelin, fig. 1), all of which physically share ancestral populations within 10-100 dispersal steps. This underlines the potential importance of Seychelles in maintaining gene flow across the Indian Ocean by acting as a stepping-stone for dispersal. We do, however, note that the connectivity between the Chagos

Archipelago and the rest of the southwest Indian Ocean is rather sensitive to larval mortality and competency dynamics (see supplementary materials, section 2).

A small subset of reefs are considerably more isolated in terms of implicit connectivity, namely (the island of) Mauritius, Rodrigues, and Réunion. These reefs are separated by over 200 steps of dispersal from practically all other reef sites in the southwest Indian Ocean. This is not obvious from the single-step explicit connectivity matrix, since we expect that these reefs all send considerable numbers of larvae to Madagascar. This dispersal is strongly unidirectional, which may explain why the implicit connectivity (shared ancestry) is so low.

In contrast to single-step explicit connectivity (section 3.1), variability in multi-step implicit connectivity reduces with distance (fig. 3, upper triangle). For instance, although our simulations predict that pairs of reefs within the Chagos Archipelago are implicitly separated by around 10 steps of dispersal, this can vary by more than an order of magnitude depending on when exactly a spawning event takes place. In contrast, the larger number of steps of dispersal required to connect remote pairs of reefs smooths out variability, so the relative uncertainty in implicit connectivity between distant sites may, in fact, be lower than for nearby sites. This is a positive finding for large-scale biogeographic or population genetic studies, as we may therefore expect greater agreement between model predictions and observations over larger spatial scales (as compared to more localised studies).

3.3 Clustering

Infomap identifies a number of clusters of reefs that consistently retain larval flow despite variability due to dynamic ocean currents (fig. 4), which we call *meta-clusters*.

Some meta-clusters are particularly distinct, attributable to geographic isolation and/or weaker currents (such as the Outer Islands of Seychelles and the Chagos Archipelago). Other reefs appear to plot across more of a continuum, such as

Madagascar and the broader Mozambique Channel region. Computing the Euclidean distance between reef groups in principal component space (supplementary materials, fig. S5) therefore represents a distinct similarity metric to the implicit connectivity, representing how consistently reefs are assigned to clusters that retain larval flow.

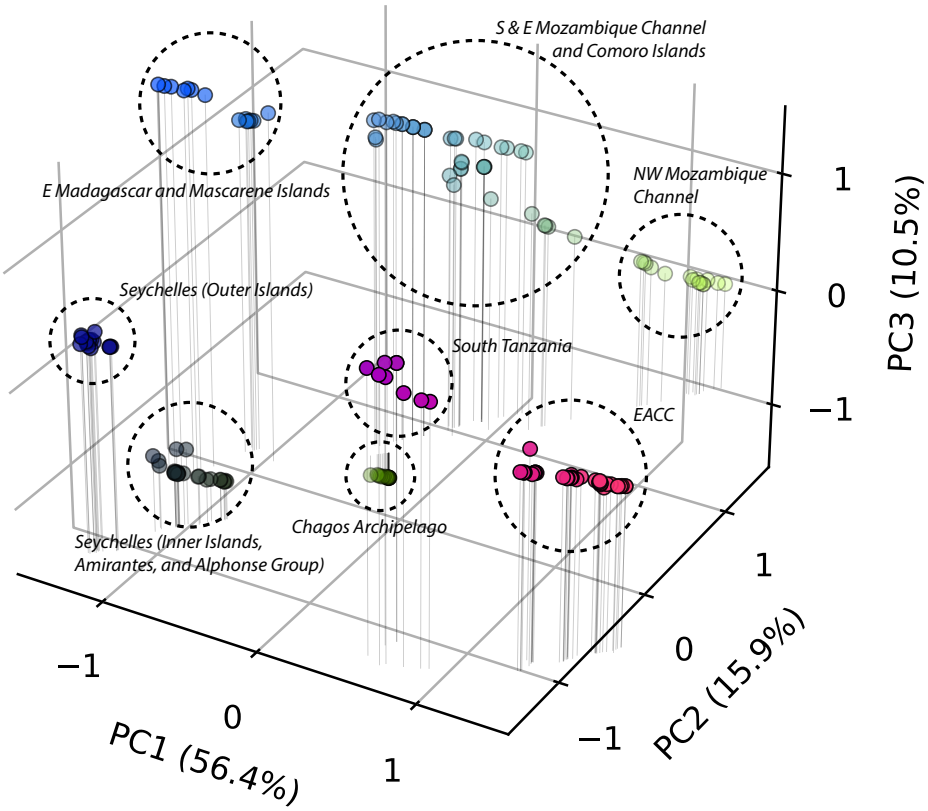

Fig. 4 The 180 reef groups plotted according to their first three principal components. The normalised values of PC1, PC2, and PC3 respectively also determine the red, green, and blue values of each group. The meta-clusters identified by dashed lines are based on K-Means clustering with 8 clusters, see supplementary materials, figs. S7-8 for an equivalent plot with discrete colouring by $k = 3$ and $k = 8$ K-Means clusters. Note that the principal components are normalised in this figure for clarity, but the true Euclidean distance between groups is plotted in the supplementary materials, fig. S5.

By assigning the values of the three principal components to red (PC1), blue (PC2), and green (PC3) channels respectively, we can plot meta-clusters geographically (fig. 5). We note that some caution is needed when interpreting this figure; the three principal components are not equally important, and RGB colour space is not perceptually uniform (Thyng et al, 2016). Nevertheless, fig. 5 represents an intuitive way to visualise the opacity of dispersal barriers (represented by sharp colour and brightness changes), and their position relative to geographic and oceanographic features.

4 Discussion

4.1 Physical barriers to gene flow

Divisions between meta-clusters (consistent barriers to dispersal) tend to clearly coincide with persistent oceanographic and geographic barriers. For instance, the strong westward flow of the Northeast Madagascar Current limits the potential for north-south larval exchange between the Outer Islands of Seychelles and the Mozambique Channel region, despite their geographic proximity. The westward flow of the South Equatorial Current similarly prevents larval dispersal between Seychelles and the Mascarene Islands, although the geographic isolation is certainly also important.

The bifurcations of the South Equatorial Current into the Northeast and Southeast Madagascar Currents, and the Northeast Madagascar Current into the East African Coastal Current and net-southward flow within the Mozambique Channel (fig. 1) result in consistent dispersal barriers in our simulations (also identified in previous simulations by Crochelet et al (2016); Gamoyo et al (2019)). Less obviously, a minor barrier appears in our meta-clustering analysis between south and north Tanzania, around Mafia Island (fig. 4). Mafia Island deflects the path of the East African Coastal Current, potentially sheltering reefs in its wake from upstream larvae (supplementary materials, fig. S6) and thereby generating a (leaky) break in connectivity along the

coast of Tanzania, which is also visible as a slight discontinuity in the time-mean explicit connectivity matrix (fig. 2).

Some physical dispersal barriers only appear using the multi-generational connectivity metrics that consider higher-order network structure. In our meta-clustering analysis, the Comoro Islands tend to cluster with north Madagascar rather than Mozambique. Although barotropic eddies generated in the wake of north Madagascar (Collins et al, 2014) provide a dispersal pathway from the Comoro Islands to Madagascar, larvae are nevertheless more likely to reach reefs in Mozambique, particularly the northern coast and Quirimbas Archipelago (fig. 2). However, over many steps of dispersal, a random walk is more likely to remain within the Comoros-Madagascar system than the Comoros-Mozambique system (which is also apparent in the CMIC, fig. 3), suggesting that the barrier to gene flow between Comoros and Mozambique may be stronger in the long term.

Similarly, although larvae generated from the Aldabra Group in Seychelles are considerably more likely to reach East Africa than the Inner Islands of Seychelles (due to the Northeast Madagascar Current), our meta-clustering analysis suggests that gene flow may tend to be retained within the Seychelles system (i.e. we may expect greater similarities between corals of Aldabra and the other Outer Islands of Seychelles, than with corals in East Africa). This may be due to multi-generational gene flow from the Inner Islands of Seychelles to the Aldabra Group via the Amirante Islands (fig. 2), which may overwhelm the larval 'leakage' from the Aldabra Group.

The three principal components identified by the meta-clustering analysis (fig. 4) individually have relatively clear physical interpretations (supplementary materials, fig. S10-12). The dominant principal component (PC1) is high in reefs influenced by the East African Coastal Current, and low elsewhere. The East African Coastal Current is therefore arguably one of the most important hydrographic features in the southwest Indian Ocean for coral reef connectivity, as the strength of the mean flow

facilitates consistent, strong reef connectivity along its path. PC2 is highest within the Mozambique Channel and Chagos Archipelago. This principal component therefore represents the important role of eddies and boundary currents within the Mozambique Channel in facilitating coral reef connectivity, as well as the role of the South Equatorial Current in transporting larvae from the Chagos Archipelago towards the Mozambique Channel region. Finally, PC3 is elevated east of Madagascar, across the Comoro Islands, and along the path of the East African Coastal Current, representing connectivity between the South Equatorial Current and the East African Coastal Current. It is not surprising that these last two principal components represent the importance of linkages between the South Equatorial Current, and the downstream East African Coastal Current and flow within the Mozambique Channel. Surface waters in the East African Coastal Current are largely sourced from the South Equatorial Current (Swallow et al, 1991), and variability in Mozambique Channel transport is closely tied to variability in the South Equatorial Current (Ridderinkhof et al, 2010; Backeberg and Reason, 2010). Indeed, 'switching' in downstream connectivity from the South Equatorial Current to East Africa versus the Mozambique Channel were two major modes of low-frequency reef connectivity variability identified by Vogt-Vincent et al (in press), using the same hydrodynamic model as the present study.

4.2 The role of dispersal in shaping biogeography and population structure

Although local adaptation can result in fine-scale phenotypic and genetic differentiation below the scale of dispersal (e.g. Sanford and Kelly, 2011; Hays et al, 2021), larval dispersal nevertheless plays an important role in setting population structure in the marine environment (e.g. Carpenter et al, 2011; Pinsky et al, 2017; Legrand et al, 2022). Comparison of the meta-clusters derived from our analyses with marine ecoregions identified by Spalding et al (2007) and Obura (2012) demonstrates that there

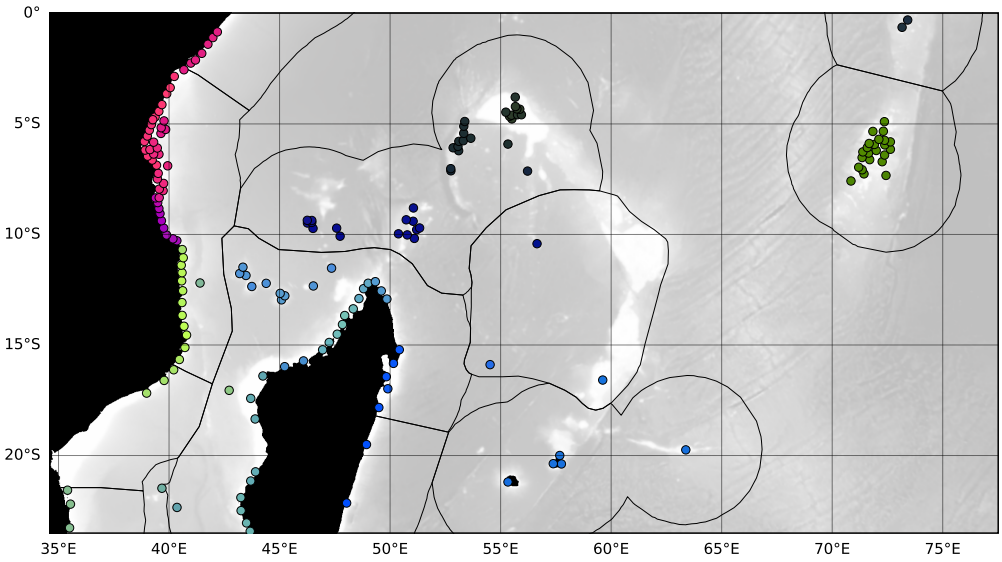

Fig. 5 Reef groups plotted geographically, coloured according to their position in principal component space (fig. 4). Black lines represent the boundaries of general biogeographical ecoregions (Spalding et al, 2007), and bathymetry (GEBCO Compilation Group, 2022) is plotted for reference in the background. See supplementary materials, figs. S7-8 for equivalent plots with discrete colouring by $k = 3$ and $k = 8$ K-means clusters.

is considerable agreement between clusters of reefs that consistently retain coral larvae, and regional biogeography across a range of taxa, including reef-building corals (fig. 5). In particular, these ecoregions reflect the role of the Northeast Madagascar Current as a dispersal barrier, the strength of connectivity within Seychelles, the clustering of the Comoro Islands with Madagascar, strong gene flow along the path of the East African Coastal Current, and the existence of significant genetic connectivity between the Chagos Archipelago and the rest of the southwest Indian Ocean (Obura (2012) specifically).

Obura (2012) proposed a 'Northern Mozambique Channel' ecoregion (characterised by high biodiversity and similar coral fauna), and noted that this ecoregion also shared considerable similarity with corals found in the Chagos Archipelago. With 3 clusters (the optimal number identified by the K-Means algorithm), a very similar grouping appears, containing the entire Mozambique Channel region and the Chagos

Archipelago (supplementary materials, fig. S7). This grouping is not identical to the ecoregion suggested by Obura (2012) (for instance, the northern boundary is at the border between Mozambique and Tanzania, rather than at Mafia Island), and the Chagos Archipelago is located slightly closer to Seychelles in PC space than the Northern Mozambique Channel. Nevertheless, this represents strong evidence that the observed faunal similarities between the Chagos Archipelago and Mozambique Channel identified by Obura (2012) are grounded in the geography of larval dispersal. However, although Obura (2012) suggested that the South Equatorial Countercurrent (fig. 1) could play a role in connecting the Chagos Archipelago with the Northern Mozambique Channel ecoregion, our simulations suggest that this dispersal pathway is negligible (fig. 2). Instead, any direct physical connectivity between the Chagos Archipelago and the Mozambique Channel is likely unidirectional and westward, through the South Equatorial Current.

Our analyses group the entire Mozambique Channel region together at low numbers of clusters (supplementary materials, fig. S7), indicative of frequent larval dispersal across the basin, further supported by population genetics from a broadcasting coral (van der Ven et al, 2022). However, with finer granularity, it is clear that a (permeable) dispersal barrier exists across the Mozambique Channel (fig. 5), placed by our analysis to the west of the Comoro Islands, agreeing well with the location of an ecoregion boundary proposed by Spalding et al (2007). van der Ven et al (2021) identified greater genetic differentiation across this barrier in the northern Mozambique Channel for a brooding coral, indicating that this dispersal barrier may be particularly important for corals with a lower pelagic larval duration (although stronger connectivity was maintained between Mozambique and southwest Madagascar).

In contrast to our predictions, neither Spalding et al (2007) nor Obura (2012) identified an ecoregion boundary at the border between Mozambique and Tanzania ($\sim$ 10°S). There is also no strong support for a barrier here from coral population genetics

(van der Ven et al, 2021, 2022), although a barrier was identified at a similar location in previous modelling study (Gamoyo et al, 2019). Instead, Obura (2012) placed an aforementioned ecoregion boundary at Mafia island ($\sim 7.5°$S). This is consistent with the potential role, as identified by our simulations, of flow diversion around Mafia Island acting as a barrier to larval dispersal, and is potentially supported (albeit equivocally) by some genetic studies (van der Ven et al, 2016, 2021). On the other hand, no such barrier was identified by Spalding et al (2007), or other population genetic analyses (e.g. Souter and Grahn, 2008; van der Ven et al, 2022). Spalding et al (2007) instead identified an ecoregion boundary in northern Kenya. There is some evidence for a dispersal barrier here in our simulations; although it is not clearly distinguished from the rest of the East African Coastal Current region for *Platygyra daedalea*, it does emerge as a barrier for a coral species with a shorter larval duration (supplementary materials, section 2, fig. S9).

In general, however, the prediction of strong coral connectivity along the path of the East African Coastal Current is strongly supported by coral population genetics (Souter and Grahn, 2008; Souter et al, 2009; van der Ven et al, 2016, 2021, 2022), although there is also evidence for local-scale genetic differentiation. For instance, Souter et al (2009) found significant differentiation between corals sampled in north-east and west Zanzibar, and most other samples in the region. van der Ven et al (2016) also identified a distinct cluster within the Pemba and Zanzibar channels. A possible explanation for the isolation of corals in northeast Zanzibar is the trapping of larvae along the coast due to the deflection of the EACC as it passes the southern tip of the island (Vogt-Vincent et al, in press). Due to comparatively sluggish flow within the Zanzibar Channel, most larvae generated at sites in west Zanzibar remain within the Zanzibar Channel rather than entering the EACC, again resulting in self-recruitment (also found by Mayorga-Adame et al (2017)). However, this cannot explain why a separate, nearby site in west Zanzibar showed little differentiation from other reefs in

the region (Souter et al, 2009). This is an important reminder that, although large scale biogeography and population genetics may be strongly grounded in regional scale oceanography, reef scale hydrodynamics which are not captured by our simulations may play an (in some cases, more) important role at a local scale. Despite the comparatively high resolution of our simulations compared to previous studies in the region, we are still, in practice, limited to inferring connectivity at scales of tens of kilometres and above, which therefore does not resolve connectivity (including vertical connectivity) within reef systems (e.g. Thomas et al, 2022; Takeyasu et al, 2023).

To the east, both Spalding et al (2007) and Obura (2012) placed a latitudinal ecoregion boundary between the Mascarene Islands (Mauritius, Rodrigues and Réunion) in the south; and St Brandon, Tromelin and the Agaléga Islands in the north. Indeed, due to the predominantly zonal currents in this region (the South Equatorial Current), we do not expect strong larval dispersal between these groups of islands. However, due to the seasonal position of the South Equatorial Current and the considerable geographic isolation, our results suggest that the primary latitudinal dispersal barrier is around 15 °S (north of St Brandon and Tromelin), rather than further to the south as suggested by Spalding et al (2007) and Obura (2012). Obura (2012) further assigned the Farquhar Group (Seychelles) to the ecoregion containing St Brandon, Tromelin and the Agaléga Islands, but our simulations predict that the Farquhar Group is more strongly connected to the Aldabra Group, as the latter is directly downstream of the former, which is further supported by coral population genetics (Burt et al, 2022).

Due to the bifurcation of the South Equatorial Current and the local relative absence of coral reef, we predict a dispersal barrier in northeast Madagascar around 15 °S. This is about 3 ° and 1 ° north of the analogous ecoregion boundaries identified by Spalding et al (2007) and Obura (2012), respectively. A possible explanation is related to seasonal variability in the bifurcation latitude of the South Equatorial Current: we only consider the northwest monsoon in this analysis (in line with coral

spawning seasonality), but bifurcation shifts to the south during the southeast monsoon (Chen et al, 2014), which could affect the dispersal of other taxa, and hence the Spalding et al (2007) ecoregions. However, van der Ven et al (2022) identified strong genetic connectivity for *Acropora tenuis* across the northeast Madagascar barrier identified by our study (as well as the slightly more southerly location suggested by Obura (2012)), instead supporting a barrier more consistent with Spalding et al (2007) (supplementary materials, fig. S13). This could suggest that the spawning seasonality assumed by our simulations is inappropriate for *Acropora tenuis*, or that some other environmental factor allows strong genetic connectivity to be maintained across northeast Madagascar despite limited dispersal.

In general, the good agreement between physical dispersal barriers identified by our analysis, biogeographic ecoregions identified by Spalding et al (2007) and Obura (2012), and coral population structure confirms the important role of ocean currents in shaping biodiversity and genetic connectivity. That this agreement is not perfect does not suggest that the classifications of Spalding et al (2007) and Obura (2012) are 'wrong' (although Obura (2012) notes that widespread data gaps limit the ability to constrain ecoregion boundaries). Discrepancies between our model predictions and observations from regional biogeography and population genetics could be due to limitations of the larval dispersal model. For instance, whilst our simulations improve on previous work by incorporating more sophisticated competency and settlement dynamics, we do not consider controls on larval mortality such as nutrient availability and temperature (e.g. Figueiredo et al, 2022), larval motility (e.g. Szmant and Meadows, 2006), or fine scale hydrodynamics that dominate the coastal environment (Monismith, 2007). The coral reefs we consider in this study could also be influenced by larval sources outside the model domain (such as southernmost Madagascar), although these regions are generally either downstream, or relatively devoid of coral reefs.

Assuming our potential connectivity predictions are broadly robust, our findings highlight that some biogeographic barriers appear to be maintained despite the potential for strong gene flow (e.g. between the Farquhar Group and the rest of Seychelles), and that physical dispersal barriers do not consistently translate into biogeographic differentiation (e.g. the bifurcation of the Northeast Madagascar Current, or the slightly greater explicit and implicit connectivity between Seychelles and the Chagos Archipelago, compared to the Mozambique Channel region). These discrepancies could be driven by the environment (i.e. selection), or past changes in geography and oceanography (e.g. Obura, 2016). For instance, large parts of the Mascarene Plateau may have been exposed at the last glacial maximum, around 21,000 years ago (supplementary materials, fig. S14; Cacciapaglia et al (2021)). If surrounded by fringing reefs, for instance, we could hypothesise that the glacial Mascarene Plateau acted as a stepping stone to facilitate larval dispersal from the Chagos Archipelago to the Mozambique Channel.

5 Conclusions

Despite the presence of many remote islands, no coral reef in the tropical southwest Indian Ocean is truly isolated over evolutionary timescales, with practically all pairs of reefs physically connected within a few hundred generations.

Our larval dispersal simulations suggest that the Northeast Madagascar Current acts as a leaky dispersal barrier, separating Seychelles in the north from the Mozambique Channel in the south, before bifurcating at the east African coast and generating a further barrier to larval dispersal between Mozambique and Tanzania. The East African Coastal Current facilitates strong and consistent connectivity along the coasts of Tanzania and Kenya, with a secondary dispersal barrier generated in the wake of Mafia Island. The Chagos Archipelago, whilst geographically isolated, is in a position to receive significant numbers of larvae from the Inner Islands of Seychelles through

the ephemeral surface expression of the Southeast Equatorial Countercurrent, and broadcasts larvae to the Mozambique Channel through the South Equatorial Current.

Although the flow of larvae between distant populations is generally unlikely to be high enough to drive demographic change, it is certainly strong enough to establish long-distance genetic connectivity (e.g. Lowe and Allendorf, 2010), as confirmed by the genetic and biogeographic studies discussed in this paper. Our findings suggest that the large-scale coral population structure of the tropical southwest Indian Ocean can be explained reasonably well through physical larval dispersal, with ocean currents playing a significant role in setting biogeographic barriers and gene flow. However, passive larval dispersal alone is unsurprisingly insufficient to fully explain regional biogeography and population genetics. It is not yet clear to what extent these differences have emerged due to complex larval behaviour, local adaptation and other post-settlement processes, palaeogeography and/or palaeoceanography, or sampling limitations by genetic and biogeographic studies.

To our knowledge, no genetic studies have investigated the relative connectivity of corals between Seychelles, the Chagos Archipelago, the Mascarene Plateau and Islands, and the Mozambique Channel, so there is limited genetic data to contextualise our predictions of connectivity across the many remote islands of the southwest Indian Ocean. A large scale, methodologically consistent population genetics study across the region would first be needed, in order to carry out a quantitative comparison to more rigorously test our model predictions.

Nevertheless, this study represents an important step towards quantifying the connectivity of coral reefs across the southwest Indian Ocean, and we hope that our connectivity predictions, which are freely available in full (Vogt-Vincent et al, 2023), will be useful to those studying biogeography and population structure in the region, by providing quantitative physical context to their observations. Marine managers and governments looking to enhance national or regional coral reef system resilience

could also integrate these predictions (and the associated web app) into marine spatial planning efforts, to identify important source and sink reefs, and thereby prioritise conservation efforts.

6 Data availability

The connectivity matrices used in this study, as well as all figures and scripts required to reproduce figures from the main text and supplement, are archived and documented in a Zenodo repository (Vogt-Vincent et al, 2023). All hydrodynamic data used in this study are described in Vogt-Vincent and Johnson (2023) and are available at the CEDA Archive. SECoW was described in Vogt-Vincent et al (in press), with the code available in the associated datasets.

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8 Conflict of interest statement

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

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