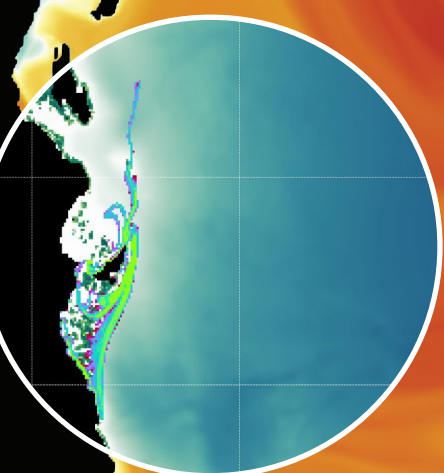
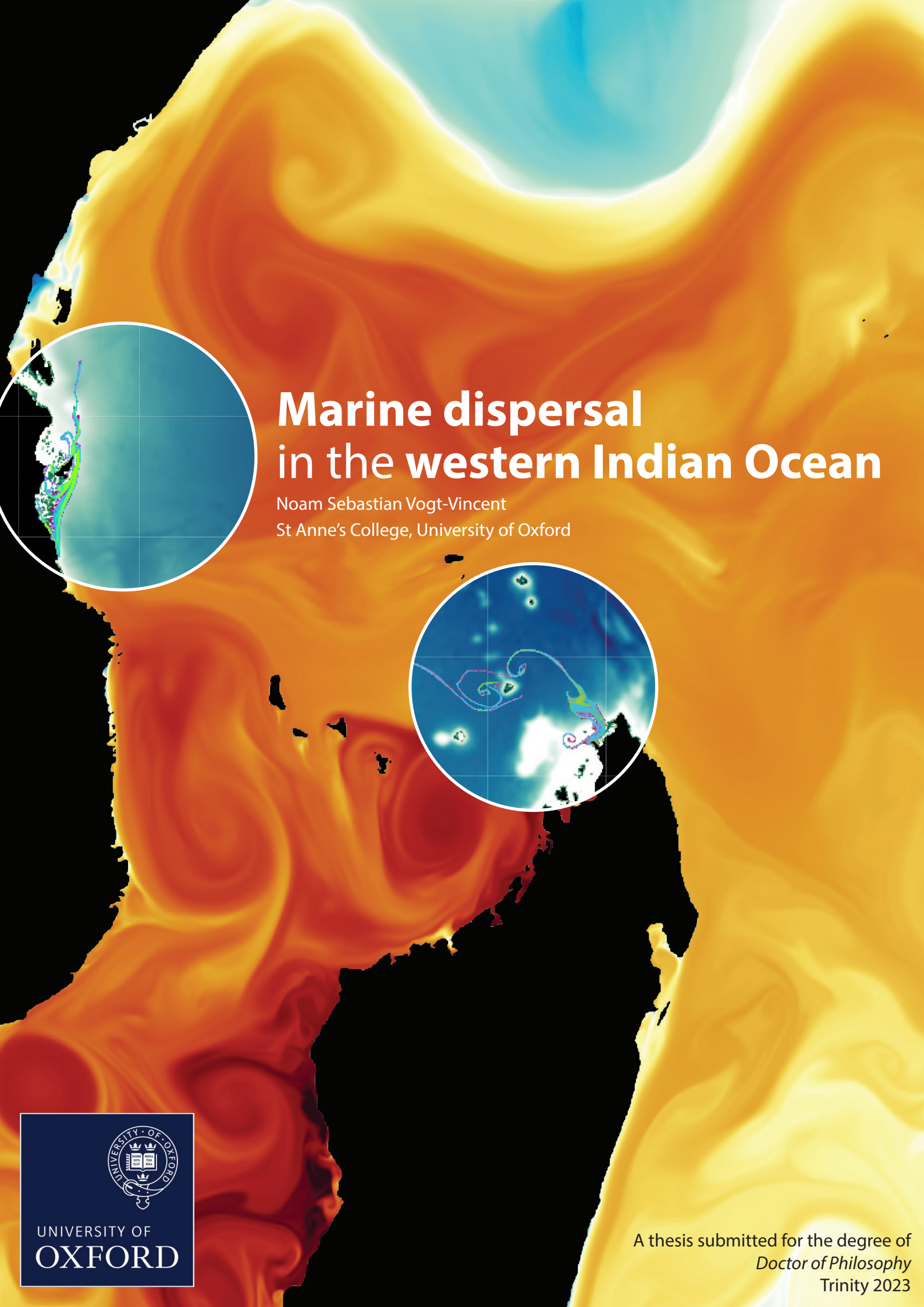
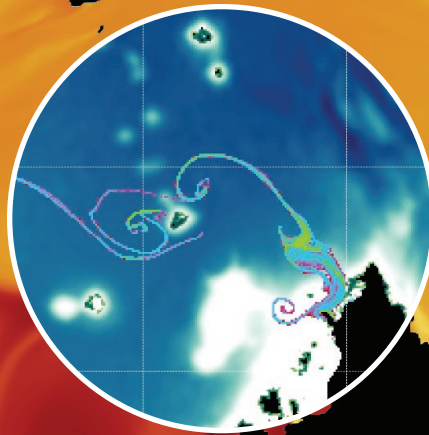




Marine dispersal in the western Indian Ocean

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Abstract

Marine plastic pollution and coral vulnerability may appear unrelated, but both problems rely on the dispersal of buoyant particles (plastic fragments and coral larvae) through ocean currents. Understanding their dispersal is vital for marine management and conservation, critical during a time of major environmental change. Through a series of Lagrangian studies, we investigate and contribute solutions to these twin problems, with a focus on the western Indian Ocean.

Using global Lagrangian simulations incorporating ocean currents, waves and winds, we find that much of the plastic debris beaching at remote islands in the western Indian Ocean likely drifted from the northern and eastern Indian Ocean. However, a substantial proportion at some islands may have been discarded from ships transiting the Indian Ocean and local fishing activity. Monsoonal winds play an important role in determining the seasonality of debris accumulation, facilitating targeted clean-up efforts.

We run a regional ocean simulation, generating almost three decades of validated surface current predictions for the tropical southwestern Indian Ocean at 2 km resolution. We couple this simulation with a larval dispersal model, predicting the potential connectivity between all shallow-water coral reefs in the region. The temporal variability of connectivity is dominated by high-frequency, stochastic variability introduced by ocean currents, limiting what we can usefully infer about short-term connectivity between remote reefs.

Ocean currents play an important role in explaining regional biogeography and population genetics, with well-connected clusters of reefs along the coasts of Kenya and Tanzania, and within the northern Mozambique Channel. The Chagos Archipelago, whilst geographically isolated, still exchanges significant numbers of larvae with the rest of the southwestern Indian Ocean. However, integrating modelled connectivity into an eco-evolutionary model suggests that the rate of environmental change, rather than connectivity, may dominate the response of coral reefs to warming over the 21st Century.

Authorship

I am very grateful to the following co-authors who contributed towards the research described in this manuscript. Helen Johnson in particular provided considerable guidance and advice on the thesis as a whole, and all constituent chapters.

Chapter 2 (*Noam S Vogt-Vincent, April J Burt, David M Kaplan, Satoshi Mitarai, Lindsay A Turnbull, and Helen L Johnson*)

LAT and HLJ conceived of the study. I planned the study, performed analyses, and wrote the manuscript (on which this chapter is based). DMK provided input on fisheries. All co-authors assisted in editing the manuscript, with AJB contributing significantly towards the conclusions. HLJ supervised the study throughout.

Chapter 3 (*Noam S Vogt-Vincent, Helen L Johnson*)

I conceived and planned the study, configured and ran the model, performed analyses, and wrote the manuscript (on which this chapter is based). Technical support was provided by ARCHER2 technicians. HLJ supervised the study throughout, and edited the manuscript.

Chapter 4 (*Noam S Vogt-Vincent, Satoshi Mitarai, Helen L Johnson*)

I conceived and planned the study, performed analyses, and wrote the manuscript (on which this chapter is based). SM provided input on analyses. All co-authors assisted in editing the manuscript. HLJ supervised the study throughout.

Chapter 5 (*Noam S Vogt-Vincent, April J Burt, Lisa C McManus, Lindsay A Turnbull, Helen L Johnson*)

I conceived and planned the study (excluding population genetics), performed analyses (excluding population genetics), and wrote the chapter. AJB, LAT and co-authors generated the Seychelles genetics data used in this chapter, and supported data interpretation. I developed Sea the Connectivity with Otis Brunner, and the application was primarily written by Julia Janicki. LCM supported the interpretation of the eco-evolutionary model. HLJ supervised the study throughout.

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List of Abbreviations

ALDFG		Abandoned, Lost or otherwise Discarded Fishing Gear
CMEMS		Copernicus Marine (Environment Monitoring) Service
CMIC		Cumulated Multistep Implicit Connectivity
dFAD		Drifting Fish Aggregating Device
DMI		(IOD) Dipole Mode Index
EACC		East Africa Coastal Current
ENSO		El Niño - Southern Oscillation
EOF		Empirical Orthogonal Function
GCM		General Circulation Model
GDP		Global Drifter Program
GLORYS		Global Ocean Reanalysis (used here as shorthand for the CMEMS GLORYS12 model)
IOD		Indian Ocean Dipole
NEMC		Northeast Madagascar Current
OGCM		Ocean General Circulation Model
PC		Principal Component
RK4		(Explicit) fourth-order Runge-Kutta scheme
SEC		(Indian Ocean) South Equatorial Current
SECC		(Indian Ocean) South Equatorial Countercurrent
SECoW		Simulating Ecosystem Connectivity with WINDS
SEMC		Southeast Madagascar Current
SSS		Sea Surface Salinity
SST		Sea Surface Temperature
(S)WIO		(South)west Indian Ocean
WAVERYS		Global Wave Reanalysis (used here as shorthand for the CMEMS WAVERYS model)
WINDS		Western Indian Ocean Simulation

1

Introduction

1.1 Motivation

The ocean is dynamic, connected across large distances through a network of ocean currents and eddies spanning a wide range of spatial and temporal scales. As well as water properties such as heat and solutes such as salt, discrete objects (which may be negatively, positively, or neutrally buoyant) can also be transported by the ocean.

This includes many types of objects with significant environmental and/or social importance. An example which has achieved considerable attention over the past decade is marine plastic pollution (MPP), which is now internationally recognised as a major environmental challenge facing the marine environment (UNEA, 2022). MPP enters the ocean from land (through direct input at the coast, overland flow, and rivers) as well as from sources at sea, principally from the fishing industry (Mihai et al., 2022). As long as MPP remains positively buoyant, it will accumulate at the surface of the ocean. This results in the formation of the famous ‘garbage patches’ at the centre of subtropical gyres due to convergent Ekman transport (e.g. Kubota et al., 2005; Maximenko et al., 2012), as well the accumulation of MPP in the coastal environment (e.g. Onink et al., 2021).

The high productivity and biodiversity along the coast results in these environments being particularly sensitive to the ecological (e.g. Bergmann et al., 2017; Hoare

et al., 2022; Nelms et al., 2016) and economic (Newman et al., 2015) costs of MPP. Identifying the source of accumulating MPP is one avenue towards the enforcement of treaties such as MARPOL Annex V (Marine Environment Protection Committee, 2017) or the upcoming United Nations treaty on plastic pollution (United Nations Environment Assembly, 2022), in accordance with the “polluter pays” principle (OECD, 1975). However, this is challenging, as MPP accumulating on beaches is often weathered and lacking in provenance indicators. Although GPS trackers can be attached to MPP (Duncan et al., 2020), it is neither practical nor ethical to deploy sufficiently large numbers of GPS trackers on ocean-bound MPP to quantify debris sources (rather than intercepting and disposing of the waste). Observation through satellites may work in certain cases (Biermann et al., 2020; Martínez-Vicente et al., 2019), but this remains impractical on a large scale, and *in situ* observations remain sparse in space and time (NCEI, 2022).

Also transported by surface currents are the larvae of marine organisms. Many marine invertebrates and fish undergo a larval stage, with a pelagic larval duration (PLD) that can, for certain species, reach months or longer (Connolly & Baird, 2010; Strathmann, 1985). Larval transport through advection in ocean currents can therefore result in effective dispersal over distances of hundreds of kilometres or more for larvae spending a significant length of time in the plankton (Shanks et al., 2003). If larval fluxes between populations are sufficiently large enough relative to population size, they may affect the population growth rate, defined as *demographic connectivity* (Lowe & Allendorf, 2010). Larval dispersal can also spread advantageous genotypes and, at higher migration rates, inhibit genetic differentiation between populations, establishing *genetic connectivity* (Lowe & Allendorf, 2010). As a result, the flow of larvae between spatially isolated populations may be critical in predicting population dynamics (e.g. Watson et al., 2012) and the capacity of populations to adapt to environmental change (e.g. McManus, Forrest, et al., 2021). This is crucial in an age where ecosystems such as coral reefs are potentially existentially threatened by climate change and other anthropogenic stressors (Cooley et al., 2022).

Similarly to MPP, however, predicting larval dispersal through observations alone is challenging. Otolith chemistry can in some cases be used to infer provenance for fish (Sturrock et al., 2012), but no analogous marker exists for animals such as corals, despite interesting recent developments of artificial markers which have been tested at the metre scale (Doropoulos & Roff, 2022). Coral eggs can be observed through aerial surveys as ‘slicks’, but these are difficult to track over large distances. This also relies on mass (synchronous) spawning, and most eggs within slicks are dead (Oliver & Willis, 1987). Whilst population genetics can be used to infer genetic connectivity, it is extremely expensive, generally has poor spatial resolution due to sampling limitations, and provides limited information about demographic connectivity (Lowe & Allendorf, 2010) and temporal variability in connectivity.

As a result, although the challenges of MPP transport and coral connectivity may not immediately appear related, both reduce to the problem of inferring (potentially long-distance) dispersal pathways of floating objects in the ocean. Tracking aggregates of (and certainly individual) plastic fragments and coral larvae is impractical on large scales, through both direct and indirect means. Instead, based on observations or predictions of ocean currents, it is possible to predict these dispersal pathways through computer simulations, replacing physical MPP and larvae with virtual particles (van Sebille et al., 2018).

The overarching purpose of this thesis is to robustly simulate the dispersal of MPP and coral larvae, with the intention of developing data products that will be useful and actionable for marine practitioners, as well as developing a physical understanding of the mechanisms behind dispersal pathways. We focus on the west Indian Ocean, with a particular emphasis on the southwest Indian Ocean (SWIO), a region which is historically under-studied (as can be seen, for instance, by looking at a map of drifter data coverage in figure 1.1), yet is disproportionately reliant on the health of the marine environment (Obura, 2017).

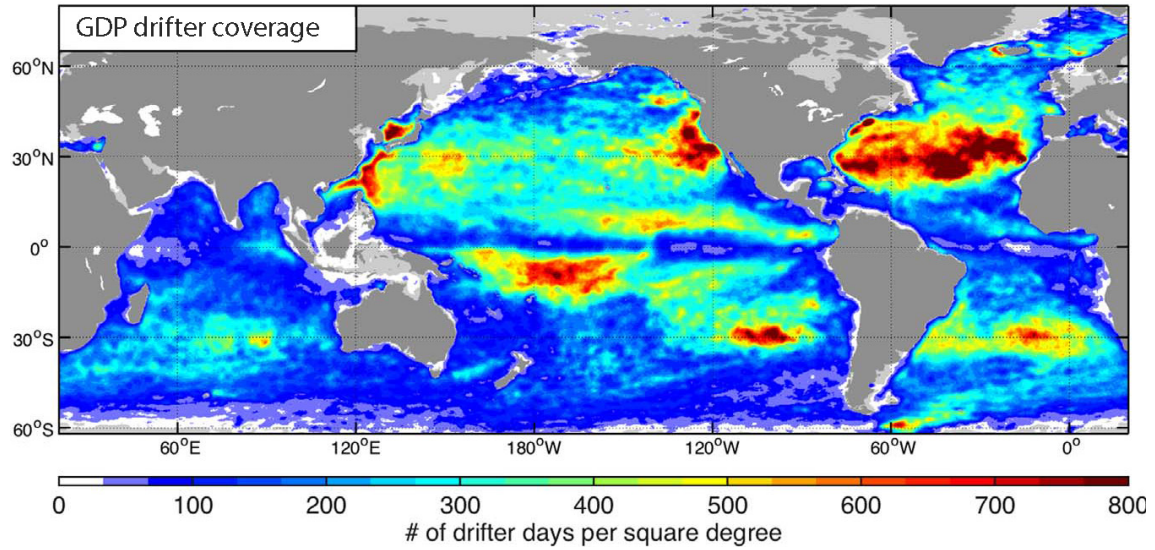


Figure 1.1: Data coverage for Global Drifter Program drifters (drogued and undrogued) from 1979 – 2015. Image adapted and used with permission from Laurindo et al. (2017).

1.2 Predicting marine dispersal

Many problems in oceanography, including those outlined in section 1.1, are in the following form:

Given a substance f with source function $S(\mathbf{x}, t)$, how does the distribution of f evolve with time?

where f may be MPP, coral larvae, or anything else of interest transported by ocean currents. Numerical approaches to finding how the distribution of f evolves with time can be broadly categorised as (i) *Eulerian*, or (ii) *Lagrangian*.

1.2.1 Eulerian and Lagrangian approaches

1.2.1.1 The Eulerian approach

Under the *Eulerian* approach, we represent the distribution of f with a scalar field $\phi(\mathbf{x}, t)$. ϕ is usually discretised in space and time and, in this case, no meaningful structure exists in ϕ below the discretisation resolution (although ϕ could be interpolated for convenience). This spatial discretisation is often fixed (and therefore the temporal evolution of ϕ is computed relative to a fixed reference frame) although time-varying grids are commonly used in numerical models (e.g.

Auclair et al., 2019). The interpretation of ϕ is clear when f is a water property such as temperature (in which case ϕ is just temperature), or a dissolved substance such as salt (in which case ϕ is the salinity). However, discrete objects can also be represented by a field ϕ . For instance, the distribution of phytoplankton could be reflected by ϕ representing chlorophyll-a concentration, or the distribution of MPP could be modelled by a field ϕ representing the number or mass of plastic fragments per unit area or volume. Importantly, any information about individual objects and their history is lost through this approach.

Take the example where f represents plastic fragments, and ϕ represents the number of plastic fragments per unit area of ocean, where $\mathbf{x} = (x_i, y_j)$, $\phi_{ijk} = \phi(x_i, y_j, t_k)$, $x_i = i\Delta x$, $y_j = j\Delta y$, $t = k\Delta t$, and $i, j, k \in \mathbb{Z}$. The number of plastic fragments in a grid cell is therefore $\phi_{ijk}\Delta x\Delta y$ (assuming flat geometry). We can interpret ϕ as a probability density function for fragment distribution, but we have no further information (such as provenance or age). Although additional tracers could be simulated to represent the average age or source latitude of fragments in a cell, which is useful for studies requiring only very limited provenance information, or attempting to model naturally occurring date tracers (MacGilchrist et al., 2017; Skinner & Bard, 2022), this rapidly becomes unfeasible when more information is needed about individual particles (such as the distribution of ages within a cell, exact location of origin, transport history, particle-specific behaviour, etc). The Eulerian approach is therefore most applicable for quantities where the concentration is the main property of interest.

Given an initial condition $\phi(\mathbf{x}, t_0)$, the distribution of f can be found at other points in time by integrating the advection-diffusion equation to solve for $\phi(t)$:

$$\frac{\partial \phi}{\partial t} + \mathbf{u} \cdot \nabla \phi - \kappa \nabla^2 \phi = S, \quad (1.1)$$

where κ represents the diffusivity of ϕ , $\mathbf{u}$ is the fluid flow field, and S represents sources and/or sinks. Note that the operator $\frac{\partial}{\partial t} + \mathbf{u} \cdot \nabla$ is commonly written as the Lagrangian derivative, $\frac{D}{Dt}$. For simplicity, we assume here that the diffusivity is constant and isotropic, whilst acknowledging that this is not true in general (Bachman

et al., 2020; van Sebille et al., 2018). If ϕ represents, for instance, the salinity of water, we might suppose κ represents the molecular diffusivity of salt in seawater, which is around $1.3 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$ (Talley, Pickard, & Emery, 2011). From equation (1.1), we find that the ratio of the advective versus diffusive terms scales with $\text{Pe} = UL/\kappa$ (the Peclet number), where U and L are again a characteristic horizontal current speed and length scale. For scales of interest to dispersal over more than a few metres, we find that $\text{Pe} \gg 1$, i.e. molecular diffusion is negligible relative to advection.

However, due to the limited resolution of most ocean current data (section 1.2.2), motion occurring at a sub grid-scale (e.g. associated with sub-mesoscale turbulence) is not typically fully resolved. Strain resulting from sub grid-scale motion results in filamentation of the true ϕ field, causing mechanical mixing (e.g. MacGilchrist et al., 2017; Welander, 1955). This mixing can be modelled as a diffusive process, with a diffusivity that scales with the grid resolution and the strain of the velocity field (Okubo, 1971; Smagorinsky, 1963). The resulting ‘eddy’ diffusivity is many orders of magnitude greater than the molecular diffusivity for most use cases in oceanography. As a result, when diffusivity is incorporated into Eulerian dispersal calculations, the parameter used is the eddy diffusivity rather than the molecular diffusivity. For instance, the $1/12^\circ$ resolution GLO12v4 Ocean General Circulation Model (OGCM), the core of the global ocean analysis and reanalysis systems run by the Copernicus Marine Environment Monitoring Service (CMEMS), applies a lateral diffusivity of $100 \text{ m}^2 \text{ s}^{-1}$ to salinity (Lellouche et al., 2022).

Equation (1.1) assumes that f has zero inertia (and therefore perfectly follows the fluid velocity) and has no additional forces acting on it. It is possible to augment equation (1.1) with the effects of forces such as buoyancy or a push from the wind, most commonly (and simplistically) by imposing an additional velocity representing the effects of said force. For example, the direct force of wind against the exposed portion of a buoyant object is often parameterised as ‘windage’, i.e. a velocity parallel to the surface (usually 10 m) wind vector and scaled by a fraction, the ‘windage coefficient’ (e.g. Maximenko et al., 2018). Buoyancy can also be incorporated as a vertical velocity component (e.g. Taylor, 2018). With the flow field $\mathbf{u}$, diffusivity

κ , source term S , initial state $\phi(t_0)$, and any additional components to the velocity specified, equation (1.1) can then be discretised in space and time, and integrated to solve for $\phi(t)$. If diffusion is neglected, it is also possible to integrate equation (1.1) backward in time to infer past distributions of f . It is fundamentally impossible to include diffusion in backward in time simulations, since diffusion leads to a loss of information. For instance, imagine injecting dye at a single point within a tank of water. Diffusion acts to homogenise the concentration of the dye in the tank so, once the dye is well-mixed, it is impossible to determine where the dye was injected.

1.2.1.2 The Lagrangian approach

Under the *Lagrangian* approach, we instead represent the distribution of f with a set of discrete particles, $\mathbf{X}_i(t)$ (van Sebille et al., 2018). The Lagrangian approach lends itself naturally towards the transport of discrete objects, but it is also commonly used to simulate continuous quantities, such as water masses (e.g. Blanke & Raynaud, 1997). A field $\phi(\mathbf{x}, t)$ may be derived from a particle set $\mathbf{X}_i(t)$ and vice versa (e.g. through Lagrangian Probability Density Functions, Mitarai et al. (2009)), but the Lagrangian approach is characterised by transport computation being carried out at the particle level.

One distinct advantage of the Lagrangian approach is that particles have ‘memory’ and can be associated with a set of attributes. For instance, if particles representing debris fragments are associated with a variable representing age, it is trivial to extract the age distribution of particles within a region of interest.

For most applications, it is not computationally feasible to simulate as many Lagrangian particles as exist in reality. For instance, van Sebille et al. (2015) estimated that there are $\mathcal{O}(10^{13})$ microplastic particles in the surface ocean, which is orders of magnitude greater than the number of particles simulated in most state-of-the-art Lagrangian simulations. Sensitivity analyses are therefore routinely carried out to test the number of particles required to reasonably represent quantities of interest (Simons et al., 2013), with each Lagrangian particle representing many ‘real’ objects that remain close in space.

Given an initial condition $\mathbf{X}_i(t_0)$, the distribution of f can be found at other points in time by integrating the following stochastic differential equation to solve for $\mathbf{X}_i(t)$ (van Sebille et al., 2018):

$$d\mathbf{X}_i = \mathbf{u} dt + \sqrt{2\kappa} d\mathbf{W}, \quad (1.2)$$

where $d\mathbf{W}$ is a normally distributed random variable with a mean of zero and a variance of dt , and we again take the special case that κ is constant and isotropic. As with the Eulerian case, this equation can be easily augmented to relax the assumption that particles are solely advected following the flow field, plus diffusion. Sources or sinks are not explicitly given in equation (1.2), but can be included by seeding or removing particles, or modifying an attribute associated with a particle. Backward in time (‘backtracking’) simulations are simple with equation (1.2) by reversing the sign of $\mathbf{u}$. Again, it is not possible to use diffusive parameterisations for sub-grid scale motion with backtracking simulations, although combined backward-forward simulations have been used to augment backtracking experiments with the effects of diffusion (Isobe et al., 2009).

1.2.2 Sources of ocean current data

Regardless of whether an Eulerian or Lagrangian approach is used, some form of ocean current data is required to predict changes in the distribution of f . A particular challenge is that, to sensibly integrate equation (1.1) or equation (1.2), data must span the entire domain of interest. For instance, a bottom-mounted Acoustic Doppler Current Profiler (ADCP) can provide ocean current data with excellent temporal and reasonable vertical resolution, but with a very small aerial footprint. If using measurements from an ADCP to predict the dispersal of f , the moment some f leaves the area where ocean currents can be reasonably approximated using the ADCP measurements, it is no longer possible to further forecast its dispersal. As a result, *in-situ* measurements alone cannot generally be used to predict marine dispersal (certainly not on large scales), although they can be useful in combination with other methods. Instead, most marine dispersal predictions use ocean current

data from (i) large sets of marine drifters, (ii) remote sensing, or (iii) numerical models (including reanalyses, which incorporate observational data).

1.2.2.1 Drifters

Substances behaving as passive, non-inertial, positively buoyant particles embedded within the flow field will be transported in the same way by $\mathbf{u}$ (neglecting other forces such as those associated with the wind). Fortunately, a large number of observations exist for the trajectories of buoys, in the form of the Global Drifter Program (GDP, Lumpkin & Centurioni, 2019). These buoys are positively buoyant and are deployed with a 15 m drogue to increase friction with the water, reducing the effects of drifter inertia and wind (although drogues may be lost). By gridding drifter positions and computing the probability per unit time M_{ij} of a drifter moving from cell i to cell j , a transition matrix $\mathbf{M} = \mathbf{M}_{ij}$ can be constructed (Maximenko et al., 2012). Assuming that any substance of interest is well mixed or equally distributed within each cell, the distribution of f can be discretised into the vector $\phi = \phi_i(t)$, resulting in the following differential equation:

$$\frac{d\phi}{dt} = \mathbf{M}\phi + S, \quad (1.3)$$

where $S = S_i(t)$ is a vector describing sources or sinks for the substance in cell i per unit time. Numerical methods can then be used to solve for ϕ , given an initial distribution $\phi(t_0)$. As discussed in section 1.2.1.1, this is an *Eulerian* approach to predicting marine dispersal (albeit derived from a Lagrangian dataset).

Equation (1.3) assumes that the statistical properties of the surface ocean circulation are stationary. In fact, the surface circulation of the ocean is not a statistically stationary process, as it can vary significantly following the seasonal cycle, interannual modes such as El Niño – Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) (e.g. Williams & Follows, 2011), and tidal cycles. The transport model described by equation (1.3) could be improved by permitting $\mathbf{M}_{ij}(t)$ to vary with time, e.g. following the seasons (van Sebille et al., 2012).

Whilst this transit matrix approach has many advantages, such as low computational cost and being entirely grounded in observations, there are some limitations.

First, sampling of the oceans by drifters is highly heterogeneous, with good sampling in the North Atlantic and western and eastern North Pacific, and poor sampling elsewhere, particularly in the Indian Ocean and Southern Ocean (Laurindo et al., 2017), degrading the spatial and temporal resolution achievable in these regions. Even in comparatively well-sampled regions, the transit matrix is still practically limited to climatology, with a spatial resolution of tens of kilometres at best (Laurindo et al., 2017; van Sebille et al., 2012). This approach is therefore mainly useful for establishing ϕ over large spatial and temporal scales. Second, drifters may be affected by external forces (such as the wind), particularly if drogues are lost (Poulain et al., 2009). The effects of external forces may be important to the dynamics of substances of interest (e.g. Domon et al., 2012), and resulting trajectories may therefore not be sensibly approximated by that of a GDP drifter. Third, if ϕ represents the distribution of discrete objects (e.g. the concentration of MPP or larvae), any object-specific information is lost, and it is therefore not straightforward to extract information about the history of individual objects, or other object-specific attributes. For some applications, these limitations are acceptable. The transit matrix approach reproduces the observed accumulation of MPP in subtropical gyres (Lebreton et al., 2018; Maximenko et al., 2012; van Sebille et al., 2012, 2015), and is well suited for accelerating the computation of passive tracer transport (Khatiwala et al., 2005).

1.2.2.2 Remote sensing

Rather than using drifters as a proxy for surface dispersal, it is possible to estimate the surface flow field $\mathbf{u}$ directly. Surface geostrophic flow $\mathbf{u}_g^s$ can be computed from pressure gradients across equipotential surfaces, inferred from gradients in the sea-surface height measured using satellite altimetry. The Ekman component of surface flow $\mathbf{u}_{Ek}^s$ can be computed from surface wind stress, usually based on output from atmospheric reanalyses (which may directly incorporate inferred surface stress from radar scatterometry). These components can then be combined to provide an estimate of the surface circulation of the ocean, grounded in observations (Morrow et al., 2023; Risien & Chelton, 2008). Note that, contrary to the geostrophic

component, the Ekman component may exhibit a significant depth dependence within the upper few metres of the ocean (Ekman, 1905).

The approximation $\mathbf{u} \approx \mathbf{u}_g^s + \mathbf{u}_{Ek}^s$ is only appropriate where the Rossby number $Ro = U/fL$ (the ratio between the inertial and Coriolis accelerations) is much less than 1, where U and L are respectively a characteristic horizontal current speed and length scale, and f is the Coriolis parameter. Over large spatial and temporal scales, this is indeed the case, and various near-real time (NRT) products exist based on surface geostrophic and Ekman currents (Rio et al., 2014). It may be possible to further improve the resolution and range of ageostrophic motions captured by satellite-inferred surface currents through the inclusion of sea-surface temperature data (Rio et al., 2016), which will soon be included in a NRT product (Eisner et al., 2023). The newly launched Surface Water and Ocean Topography (SWOT) mission will increase the spatial resolution of surface currents that can be computed through remote sensing (Chelton et al., 2019), although the limitations of geostrophy still apply.

Full surface currents can be obtained from coastal very high frequency (VHF) radar systems at sub-kilometre scale resolution (depending on the radar configuration), by measuring the Doppler shift of radio waves reflected from the surface (Prandle, 1987). However, VHF systems tend to have a range of tens of kilometres at most and are less likely to be installed in remote and/or economically disadvantaged areas, so are generally used for investigating near-coastal dispersal around the margins of the North Pacific, North Atlantic, and Mediterranean (e.g. Haza et al., 2010). Similar instruments have been proposed for future satellite missions, such as SeaSTAR (Gommenginger et al., 2023). Finally, sub-kilometre scale flow can also be computed from high-resolution optical satellite imagery through particle image velocimetry (Delandmeter et al., 2017; Marmorino, 2022), although this is not available at a regular temporal resolution, is dependent on high-energy shallow-water flow, and can also be blocked by clouds. This method is therefore not currently useful beyond local case-studies.

1.2.2.3 General circulation models

We could, instead, use a numerical model such as an ocean general circulation model (OGCM) to estimate $\mathbf{u}$. OGCMs integrate the primitive equations for fluid flow (with parameterisations to account for sub-grid scale processes), and often use simplifications to minimise computational expense, such as assuming hydrostatic balance and the Boussinesq approximation (e.g. Auclair et al., 2019). OGCMs do not impose the restriction $Ro \ll 1$, can be run at an arbitrarily high resolution (limited only by available resources), and also simulate the full three-dimensional flow field rather than just geostrophic surface flow.

OGCMs may be coupled (‘online’) to an atmospheric model as part of an atmosphere-ocean GCM (AOGCM), as well as other modules simulating the biosphere, cryosphere, and biogeochemistry as part of an Earth System Model (ESM). Online coupling allows the model to simulate interactions between components of the Earth system, but also increases the computational cost. ESMs are generally used for climate hindcasts and forecasts, such as the Climate Model Intercomparison Project (CMIP, Eyring et al., 2016) and Palaeoclimate Model Intercomparison Project (PMIP, Kageyama et al., 2018). In addition to the computational cost imposed by simulating more aspects of the Earth system, projects such as CMIP and PMIP aim to investigate environmental change over centennial timescales (and longer), further increasing the computational burden. For tractability, ESMs must therefore run at a relatively coarse resolution, typically $0.5^\circ - 1^\circ$ in the ocean for CMIP6 contributions (IPCC, 2021a). For the purpose of predicting the dispersal of buoyant material in the ocean, this is therefore not an improvement over the resolution obtained from satellite altimetry and scatterometry. However, for many marine dispersal applications, dispersal takes place over timescales of years at most, so the long integration times and comparatively slow interactions between components of the Earth system (aside from the atmosphere and, potentially, cryosphere) are of secondary importance.

In comparison, GCMs are operationally run on a global scale at a resolution of $1/4^\circ$ and better. For instance, the Integrated Forecasting System (IFS) of the European Centre for Medium-Range Weather Forecasts (ECMWF) couples a

1/4° configuration of the NEMO ocean model (Gurvan et al., 2022) with atmosphere, wave, and terrestrial components (ECMWF, 2021b, 2021c, 2021d). GCMs may be operationalised in a ‘free-running’ or ‘analysis’ configuration, in which they are initialised from a state that may incorporate observations, but are otherwise integrated without incorporating further observations (beyond boundary conditions which, in the case of a hindcast, may be directly or indirectly derived from observations). Alternatively, a GCM can be run in ‘reanalysis’ mode, which uses data assimilation to nudge the model state variables towards observations, such as satellite derived sea-surface height and sea-surface temperature, and *in-situ* observations of temperature and salinity (using increasingly sophisticated assimilation methods, e.g. ECMWF, 2021a). Not only do reanalyses help mitigate model biases (Lellouche et al., 2022), since the climate is a chaotic system, data assimilation can improve the ability of the GCM to correctly reproduce the *instantaneous* state of the ocean or atmosphere, as opposed to simply reproducing a statistically reasonable state which converges towards observations in the long-term time-mean (although this may be sufficient, depending on the application).

Reanalyses may be fully coupled AOGCMs (Laloyaux et al., 2018), AGCMs (Hersbach et al., 2020, although ERA5 is also coupled to land and ocean wave modules), or OGCMs (Cummings & Smedstad, 2013; Lellouche et al., 2022; Zuo et al., 2019). Due to the fundamental importance of the atmosphere in setting momentum, heat and freshwater inputs at the ocean surface, it is not possible to run a realistic OGCM configuration whilst completely disregarding the influence of the atmosphere (or *vice versa*). However, fluxes can be *prescribed* at the surface of the ocean. For instance, the 1/12° CMEMS GLORYS12 ocean reanalysis (Lellouche et al., 2022) now operationally uses atmospheric boundary conditions derived from the ~1/4° ERA5 atmospheric reanalysis (Hersbach et al., 2020).

The GCMs described above are run in a global configuration, i.e. with no lateral boundary conditions. These simulations are of significant general utility. In some cases, however, a user may be interested in resolving circulation at a higher resolution in a smaller region (chapter 3), or dynamically downscaling oceanographic forecasts

(Praveen et al., 2016; Van Hooideonk et al., 2015) or hindcasts (Vogt-Vincent & Mitarai, 2020; Yang et al., 2022). For these purposes, regional circulation models (RCMs) are used. RCMs may be run as a regional configuration of a general-purpose OGCM such as MITgcm (Jean-Michel Campin et al., 2023) and NEMO (Gurvan et al., 2022), or using a dedicated RCM such as ROMS (Shchepetkin & McWilliams, 2005), CROCO (which itself was derived from ROMS, Auclair et al., 2019), and FVCOM (Chen et al., 2003).

Unless the RCM is run for a basin with no open boundaries (such as a lake) or in an idealised configuration, forcing (including water temperature, salinity, velocity, and tides) is required at the lateral boundaries (Marchesiello et al., 2001). This forcing could come from observational climatologies such as the World Ocean Atlas (Boyer et al., 2018), a free-running model or reanalysis with a larger domain, or (in the case of tidal forcing) a tidal model (e.g. Egbert & Erofeeva, 2002). This is a type of ‘offline’ (or ‘one-way’) nesting, as opposed to ‘online’ (or ‘two-way’) nesting, where there is a two-way flow of information between higher and lower level nested domains (Debreu et al., 2012), which can be used to locally further enhance spatial resolution within a regional (or global) GCM. Although RCM simulations are often run in a ‘free-running’ configuration, some RCMs such as ROMS and NEMO can be run with data assimilation (Mogensen et al., 2012; Moore et al., 2011).

Which source of model-derived hydrodynamic data to use for a marine dispersal application depends on specific requirements. Applications involving transport on a global scale will obviously require a global model. Global OGCMs are very resource intensive to run, and for most applications involving contemporary marine dispersal, output from an existing global ocean reanalysis such as GLORYS12 (Lellouche et al., 2022) or GOFS (Cummings & Smedstad, 2013), or even - depending on the context - satellite-derived surface currents (section 1.2.2.2), may be appropriate. For applications involving dispersal on a regional scale, where transport nevertheless takes place over scales of hundreds of kilometres or greater, the horizontal resolution of reanalyses such as GLORYS12 and GOFS ($1/12^\circ$) is probably sufficient to resolve the processes dominating dispersal (Blanke et al., 2012; Putman & He, 2013).

As a result, a subset can simply be taken from the existing output of a global (O)GCM. For applications involving dispersal on a regional or local scale, where the dispersal distance is not significantly greater than the horizontal resolution of off-the-shelf global ocean reanalyses, output may already be available from an RCM. Examples include the CMEMS Ocean Physics Analysis for the North-West European Shelf, run in a 1.5 km configuration (Tonani et al., 2022), or CT-ROMS, a 5 km resolution hindcast for the Coral Triangle region in maritime SE Asia (Castruccio et al., 2013). One limitation is that model output is required at a relatively high temporal resolution (depending on the spatial resolution, e.g. Qin et al., 2014) to sensibly reproduce time-varying dispersal, which may not be available if the model was not run with dispersal applications in mind.

In the absence of available appropriate model output, a new hydrodynamical simulation may need to be run. In this case, the model configuration (i.e. the numerical model itself, grid, and forcing) will need to be designed as appropriate for the application (for instance following guidance in Polton et al. (2023)). Choices will also need to be made regarding the model output (i.e. which variables, and how frequently), since storage limitations mean it is unlikely to be practical or necessary to save the full state of the model at all time-steps.

1.3 Geography and surface circulation of the tropical southwest Indian Ocean

1.3.1 Geography

We define the tropical southwest Indian Ocean (hereon SWIO) as spanning the latitudinal range $23.5^{\circ}\text{S} - 0^{\circ}\text{N}$, from the coast of East Africa to the Chagos Archipelago (figure 1.2). Mozambique, Tanzania, Kenya, and Somalia border the SWIO in the west. Tanzania has three large islands (Mafia, Zanzibar, and Pemba) offshore, with Zanzibar and Pemba separated from the continent by the relatively shallow Zanzibar Channel, and much deeper Pemba Channel. Mozambique is associated with three major archipelagos: the Quirimbas Archipelago, a dense chain of coral islands along the northernmost coast of Mozambique; the Primeiras

and Segundas Archipelago, a long but sparser chain of coral islands; and the Bazaruto Archipelago in the south, also surrounded by coral reef (Lyons et al., 2022). Aside from continental Africa, the other major landmass in the SWIO is Madagascar, a large island separated from Mozambique by the Mozambique Channel. Madagascar is itself surrounded by a large number of smaller islands, most notably along its northwest coast.

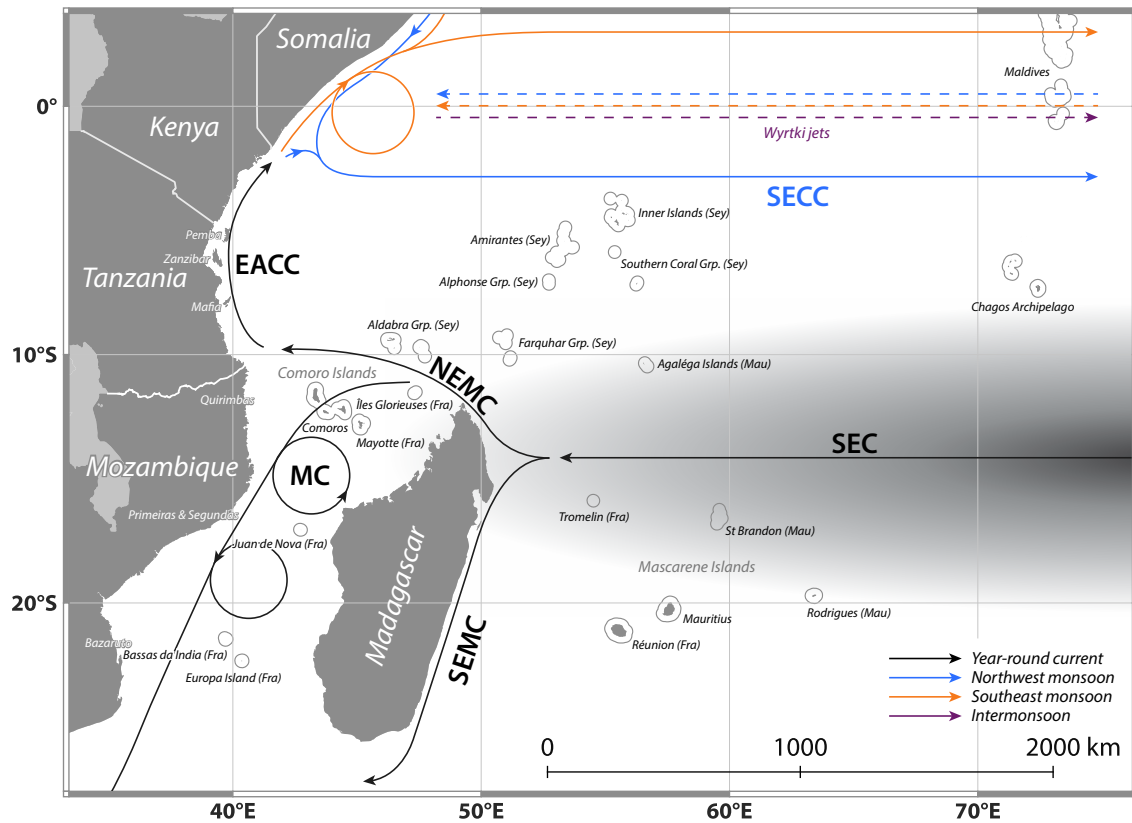


Figure 1.2: Map of the SWIO, with key countries, island groups, and basins highlighted. Small islands are highlighted with a halo for clarity. Arrows schematically represent the major surface currents in the Indian Ocean, interpreted from Laurindo et al. (2017) and Schott et al. (2009). Black arrows represent currents that broadly occupy the same location year-round, whereas blue, orange, and purple arrows respectively represent currents during the northwest monsoon, southeast monsoon, and intermonsoons. SEC: *South Equatorial Current*; SEMC: *Southeast Madagascar Current*; NEMC: *Northeast Madagascar Current*; MC: *Mozambique Channel (dominated by eddies)*; EACC: *East Africa Coastal Current*; SECC: *South Equatorial Countercurrent*. The shading around the SEC represents the general latitudinal extent of the current. Currents represented by dashed arrows are ephemeral and are associated with considerable interannual variability. Coastline vectors from Wessel and Smith (1996).

The Mozambique Channel is separated in the north from the rest of the Indian

Ocean by the Comoro Islands (figure 1.3), comprising four major islands, split between the country of Comoros (Ngazidja, Mwali, and Nzwani), and Mayotte, a department of France and almost entirely surrounded by a large lagoon and barrier reef. Also nearby is Îles Glorieuses, an atoll associated with the French Scattered Islands, and a number of submerged coral banks. There are three remote coral islands in the central and south Mozambique Channel: Juan de Nova, Bassas da India, and Europa Islands (all also administered as part of the Scattered Islands, figure 1.2).

North of Madagascar is the Seychelles Archipelago. Seychelles is split across a set of largely granitic *Inner Islands* on the shallow Seychelles Plateau in the north (the largest being Mahé and Praslin), and many remote, generally smaller coral islands, forming the *Outer Islands* (figure 1.3). The largest member of the Outer Islands by far is Aldabra Atoll (within the Aldabra Group), a raised reef surrounding an unusual tidal lagoon (Farrow & Brander, 1971; Stoddart et al., 1971) and a UNESCO World Heritage Site. To the east of the Aldabra Group is the Farquhar Group, with two large atolls and many submerged coral banks. Between the Seychelles Plateau and the Farquhar Group is the Amirantes Bank and associated Amirante Islands (or Amirantes), and nearby Desroches and the Alphonse Group. Finally, the Southern Coral Group is to the south of the Seychelles Plateau, with two major islands (Platte and Coëtivy).

Extending in an arc south from Seychelles is the elongate Mascarene Plateau, a system of shallow, submarine plateaus of volcanic origin (Mart, 1988). The Mascarene Islands are found at the southernmost end of the Mascarene Plateau system, with two major islands: Réunion (another department of France), and the main island of Mauritius. The coralline St. Brandon archipelago is the only significant exposed structure on the remainder of the Mascarene Plateau system, although there are several other volcanic and coral islands near the plateau, such as Rodrigues and the Agaléga Islands (Mauritius), and Tromelin (France).

The Chagos Archipelago is a major atoll system, often categorised as part of the central Indian Ocean (Souter et al., 2021), comprising the enormous Great Chagos Banks and several smaller atolls such as Diego Garcia. The Maldives are to the north

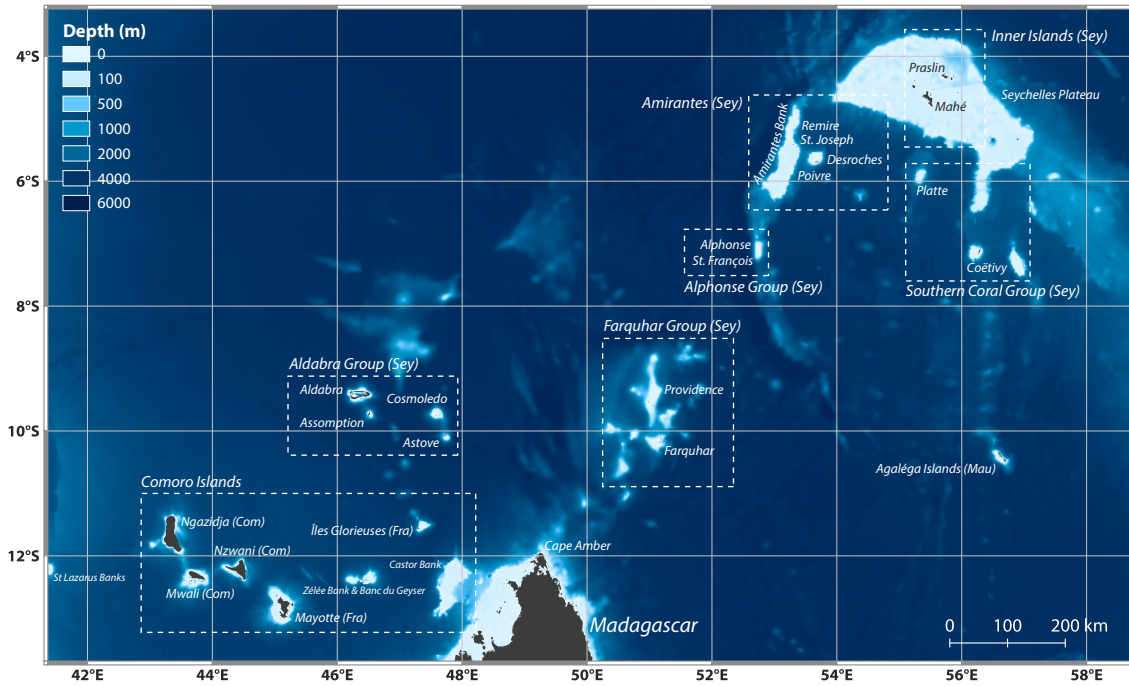


Figure 1.3: Bathymetric map of Seychelles and the Comoro Islands, with major islands, groups, and other bathymetric features labelled. Bathymetry from GEBCO 2022 (GEBCO Compilation Group, 2022) and coastlines from Wessel and Smith (1996). Due to the reliance on gravimetry-derived bathymetry (Tozer et al., 2019), some significant errors in bathymetry are apparent here, such as non-existent depressions with depths exceeding 1 km in the north and southeast Seychelles Plateau, and Aldabra lagoon.

of the Chagos Archipelago (and are associated with the same large-scale submarine structure, the Chagos-Laccadive Ridge), but only the southernmost Maldivian atolls of Addu and Fuvahmulah are south of the equator.

The formation of most islands in the SWIO is related to the breakup of Gondwana from the Jurassic onwards. Madagascar (then attached to continental fragments making up the present-day Seychelles Plateau and Indian subcontinent) began to rift from Gondwana in the Jurassic (Phethean et al., 2016), followed by the separation of Madagascar and then Seychelles from India during the late Cretaceous and Paleocene (Armitage et al., 2011; Collier et al., 2008; Scotese, 2001). This breakup was associated with massive flood volcanism, with an associated hotspot (which is presently under Réunion) forming much of the Mascarene Plateau and Chagos Bank, which are both consequently considerably younger than the continental Seychelles Plateau (Duncan & Hargraves, 1990). As reviewed by Obura (2016), the volcanic Mascarene Plateau

was likely once an island chain, and may have isolated the proto SWIO from the proto Indo-Pacific until the Miocene (~ 15 Ma). Modern-like patterns of connectivity with the wider Indo-Pacific may have been established from the Miocene, with the submergence of the Mascarene Plateau (Obura, 2016). The SWIO is also punctuated by a large number of volcanic seamounts. Some, associated with early volcanism, remain subaerially exposed to the present day as coral atolls due to rapid carbonate aggradation (e.g. Stoddart et al., 1971). Others, such as Réunion and Mauritius, are associated with geologically recent volcanism (Obura, 2016).

Many of the countries within the tropical SWIO are economically disadvantaged, with Somalia, Mozambique, and Madagascar amongst the ten poorest in the world by GDP per capita (World Bank, 2021). Combined with the high population growth rate in the region (Gerland et al., 2014), coastal communities in the SWIO are often highly dependent on marine resources but have limited capacity to mitigate environmental degradation, which is generally driven by wealthier countries (Obura, 2017). This also, in part, explains the general lack of oceanographic data in the region in comparison to the North Atlantic and North Pacific. We also note that there are several territorial disputes in the region, perhaps most notably concerning the Chagos Archipelago, which was associated with the British colony of Mauritius prior to decolonisation. The Chagos Archipelago continues to be administered by the United Kingdom as part of the British Indian Ocean Territory, despite the International Court of Justice ruling that the partitioning of the Chagos Archipelago from Mauritius was not lawful, and that the United Kingdom must return sovereignty to Mauritius “as rapidly as possible” (International Court of Justice, 2019).

1.3.2 Surface circulation

The surface circulation of the southwest tropical Indian Ocean is primarily wind-driven (like most of the Earth’s surface currents), but with the additional complexity of seasonally reversing monsoonal winds. During the austral summer (peaking around January), strong northeasterly winds blow over the northern Indian Ocean, switching to weak northerly-to-northwesterly winds over the tropical southern Indian

Ocean (figure 1.4). These patterns reverse in the austral winter monsoon (peaking around July), with strong southwesterly and southeasterly winds blowing over the northern and southern Indian Ocean, respectively. The monsoons are strongest over the northern half of the basin and are therefore most commonly known as the northeast and southwest monsoons (Schott & McCreary, 2001). However, due to the emphasis on the SWIO (and, in particular, Seychelles) in this thesis, we use the terms northwest and southeast monsoons, which are more common in this region (e.g. Burt et al., 2020; Cerutti et al., 2019; Koester et al., 2021).

Outside the equatorial regime, circulation in the tropical SWIO follows Sverdrup balance (Godfrey, 1989; Talley, Pickard, Emery, & Swift, 2011). The annual-mean wind stress curl is negative between the equator and around 15°S (corresponding to the bifurcation latitude of the South Equatorial Current, or SEC), and positive to the south of 15°S , resulting in southward and northward Sverdrup transport, respectively. This flow, plus a component from the Indonesian Throughflow, is transported to the western boundary through the SEC, which intensifies north of Madagascar as the Northeast Madagascar Current (NEMC). Flow within the equatorial gyre is returned on the western boundary through the northward East Africa Coastal Current (EACC, Mayorga-Adame et al. (2016) and Swallow et al. (1991)), whereas flow within the subtropical gyre is returned through the net-southward flow in the Mozambique Channel and the Southeast Madagascar Current (SEMC, Talley, Pickard, Emery, and Swift (2011)). Flow leaving the Mozambique Channel and SEMC enters the Agulhas Current, mostly recirculating within the subtropical gyre, but partially leaking into the Atlantic through eddies as ‘Agulhas Rings’ (De Ruijter et al., 1999).

SEC transport varies quite substantially on seasonal and interannual timescales, due to variability in local winds and wind-stress curl across the basin (Yamagami & Tozuka, 2015). This variability is largely transferred to the NEMC which, in contrast to early observations (Swallow et al., 1988), inherits significant seasonal and interannual variability in transport and current speed from the SEC (Backeberg & Reason, 2010; Yamagami & Tozuka, 2015). When the NEMC separates from the continental shelf of north Madagascar at Cape Amber, it forms a jet which can

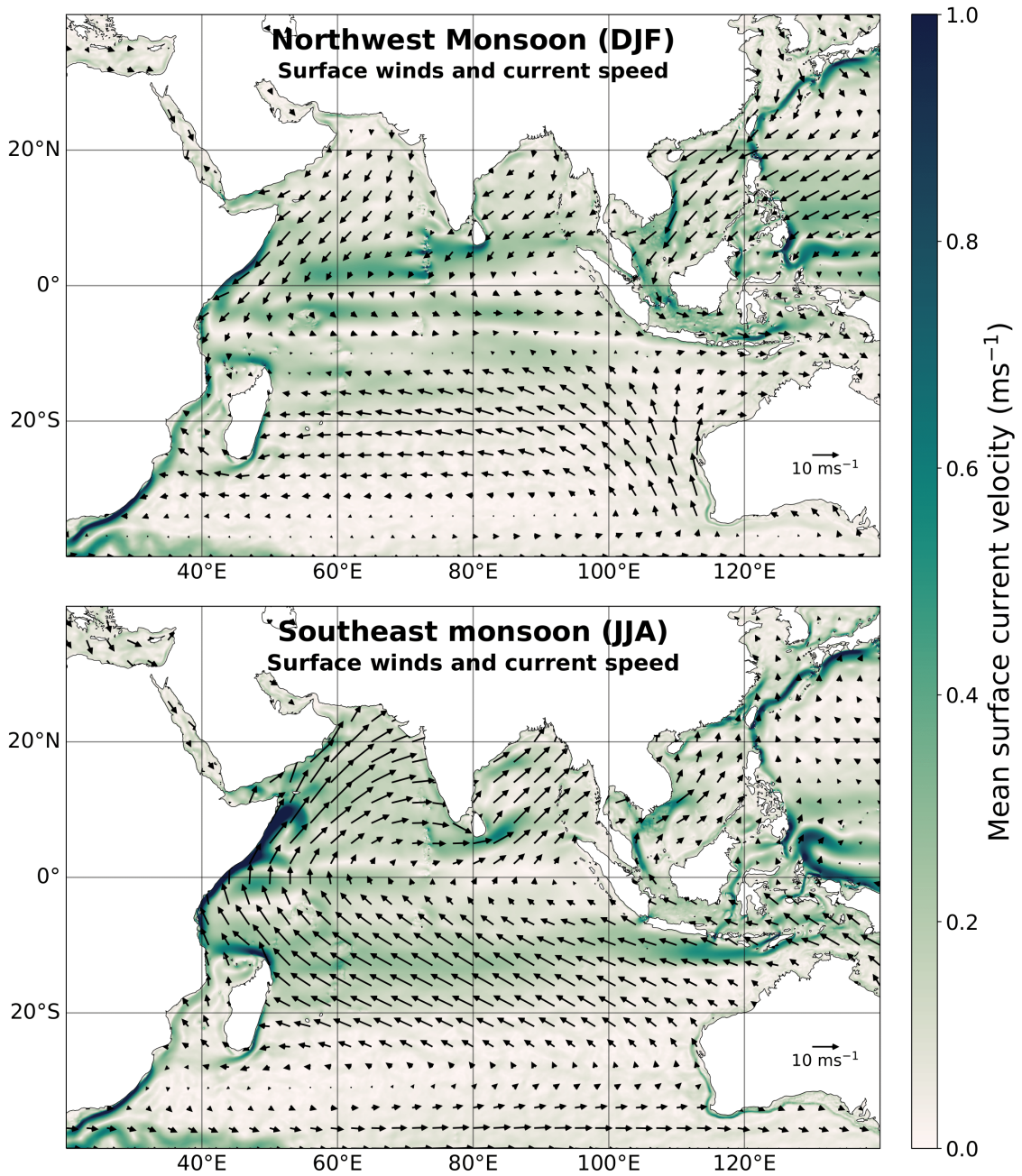


Figure 1.4: Mean surface current speed (colours, Lellouche et al. (2021)) and surface winds (arrows, Hersbach et al. (2020)) as used in our analyses in chapter 2 for the northwest monsoon (*top*) and southeast monsoon (*bottom*).

exceed 1.5 m s^{-1} (Voldsund et al., 2017), and generates anticyclonic eddies through barotropic instability, which decay only slowly and migrate southward through the Mozambique Channel (Backeberg & Reason, 2010; Collins et al., 2014). Cyclonic eddies are thought to be generated through baroclinic instability, mostly forming

along the margins of north Mozambique and northwest Madagascar. However, these eddies tend to remain and dissipate within the northern Mozambique Channel (Collin et al., 2014; Halo et al., 2014). Net southward transport within the Mozambique Channel is highly variable (occasionally even reversing), and it is not clear whether there is a robust seasonal cycle (Van Der Werf et al., 2010).

Most NEMC transport instead enters the EACC (Manyilizu et al., 2016; Schott & McCreary, 2001), a rapid, strongly surface-intensified western boundary current with a significant lack of large-scale, *in situ* oceanographic observations. Numerical models (Manyilizu et al., 2016; Mayorga-Adame et al., 2016) and drifters (Laurindo et al., 2017; Swallow et al., 1991) show that surface currents are intensified during the southeast monsoon, locally exceeding 2.0 m s^{-1} . During the southeast monsoon, the EACC generally crosses the equator, partly recirculating in the cross-equatorial ‘Southern Gyre’ (figure 1.2), and partly continuing northward along the coast of Somalia in the Somali Current (Schott et al., 1990; Schott & McCreary, 2001). The Somali Current reverses in the northwest monsoon, crossing the equator and meeting the weaker EACC between $0 - 5^\circ \text{S}$, with both then being deflected eastward (figure 1.2, Schott and McCreary (2001) and Swallow et al. (1991)).

Whilst varying in transport and latitudinal extent, zonal flow between $10 - 20^\circ \text{S}$ is generally dominated by the year-round westward flow of the SEC. In contrast, although the South Equatorial Countercurrent (SECC) returns flow eastwards from the EACC (and, in the southeast monsoon, from the Somali Current), zonal surface currents in the equatorial western Indian Ocean regularly reverse. The surface expression of the eastward SECC is strongest between the monsoons, where it is accompanied by strong surface-intensified jets known as ‘Wyrтки jets’ in response to equatorial westerly winds, intensifying towards the centre of the equatorial Indian Ocean (Sachidanandan et al., 2017; Wyrтки, 1973). Between Wyrтки jets (particularly towards the end of the northwest and southeast monsoons), surface currents can reverse entirely due to strong westward flow driven by equatorial easterly winds (figure 1.2). In addition to this biannual seasonality, there is considerable interannual variability in the intensity of Wyrтки jets, modulated by the Indian Ocean Dipole

(IOD). The IOD is a major mode of interannual climate variability in the Indian Ocean, characterised by the strengthening of easterly winds over the equatorial Indian Ocean during and following the southeast monsoon (peaking in October), leading to deepening of the thermocline and surface warming in the western Indian Ocean (Schott et al., 2009; Yu et al., 2005). Easterly wind anomalies associated with the IOD peak during a similar time to the austral spring Wyrтки jet, suppressing eastward surface currents (McPhaden et al., 2015; Sachidanandan et al., 2017), although significant zonal current anomalies can develop even outside IOD events, such as the development of strong westward currents during the austral autumn of 2006, when a Wyrтки jet would normally be expected (Horii et al., 2008).

1.4 Marine plastic pollution in the west Indian Ocean

Approximately 400 million tons of plastic are produced per year, a number which has grown steadily for over half a century, the majority of which is just discarded (Geyer et al., 2017). Estimating how much of this waste enters the ocean is challenging, as this requires knowledge of the geographic distribution of mismanaged waste, and the likelihood of this waste making its way into the ocean. This figure is therefore subject to considerable uncertainty. In the case of direct input from coastal populations, the input of MPP to the ocean has been estimated at 3.1 – 12.7 million tons per year (Jambeck et al., 2015; Lebreton & Andrady, 2019). The contribution of rivers (which can transport plastic waste from further inland) to MPP has been estimated at 0.8 – 2.7 million tons per year (Meijer et al., 2021). In both cases, the quoted uncertainty is likely a considerable underestimate of the true uncertainty associated with terrestrial fluxes of MPP into the ocean (e.g. Roebroek et al., 2022).

MPP can also be generated at sea, primarily by fisheries (as abandoned, lost, or otherwise discarded fishing gear, ALDFG). Unfortunately, there are even fewer estimates for ALDFG production rates. Observations of floating MPP in the North Pacific Subtropical Gyre found that at least 75% by mass was ALDFG (Lebreton et al., 2022), but this is not representative of MPP entering the ocean as a whole, as

MPP accumulating in subtropical gyres tends to be considerably older than average (Koelmans et al., 2017; Lebreton et al., 2019). Lebreton et al. (2018) estimated that 0.4-5.1 million tons per year of MPP is generated from fisheries and shipping, using figures from existing literature which were heavily extrapolated from sparse observations of beaching MPP, and patchy records of certain types of fishing gear loss. Kuczenski et al. (2022) estimated that 0.03-0.1 million tons per year of ALDFG was generated by three types of fishery, although this estimate does not include all sources of MPP production at sea.

In summary, although it is highly uncertain how much MPP actually enters the ocean, it is definitely a very large amount. This is reflected by the fact that MPP has been abundant (if spatially heterogeneous) in the open marine environment for well over a decade (Cózar et al., 2014), and microplastics in particular are ubiquitous throughout the water column (Choy et al., 2019; NCEI, 2022; Woodall et al., 2014). The impacts of macroplastic debris have been fairly well documented, causing harm to marine macrofauna (Gall & Thompson, 2015; Kühn & Van Franeker, 2020) and seabirds (Ryan, 2018), as well as economic damage, particularly to countries reliant on tourism (Newman et al., 2015; Thompson et al., 2009; Werner et al., 2016). What is less clear is the extent of the impact of microplastic ingestion and associated ecotoxicological effects (Galloway et al., 2017; Worm et al., 2017). Nevertheless, although the full extent is not yet clear, MPP certainly causes substantial harm to the marine environment¹.

The coastal environment is a major ‘sink’ for MPP (Onink et al., 2021) and, although accumulated MPP may be of local origin for some coastlines (e.g. Martinez-Ribes et al., 2007; Turrell, 2020a), this is certainly not the case for remote islands

¹As an important side note, whilst in no way intending to diminish the genuine and serious harms caused by MPP, there is a disconnect between widespread public perception of MPP as the primary threat to the marine environment, versus the overwhelming evidence that climate change and biodiversity loss, whilst linked to the MPP issue, are considerably more serious (Stafford & Jones, 2019). As a result, whilst recognising the genuine need to avoid unsustainable plastic use and enforce responsible waste disposal, it is important to put the MPP issue into context. An overemphasis on the MPP issue, perhaps due to the problem being highly visible and associated with solutions that give western consumers a sense of agency without necessitating systemic change, runs the risk of more critical threats such as climate change being sidelined, or potentially even exacerbated (e.g. Bisinella et al., 2018).

with minimal or no population, where most MPP has been transported over great distances by ocean currents, winds, and waves (van Sebille et al., 2020). These islands, many of which belong to small island developing states, are faced with the deeply inequitable situation of bearing the costs of removing waste they were not responsible for generating, contrary to the “polluter pays” principle (OECD, 1975). There are many small island developing states in the western Indian Ocean (figure 1.2) and, whilst marine plastic pollution is under-studied in this region relative to, for instance, the North Atlantic and western Pacific, MPP accumulation has been documented in many of these remote island groups. Seychelles is one such small island developing state, spread across over 100 islands north of Madagascar, from the isolated Aldabra Group in the southwest, to the Inner Islands on the Seychelles Plateau in the northeast. MPP monitoring programmes have found large quantities of debris accumulating across the latitudinal and longitudinal range spanned by Seychelles, such as at Aldabra Atoll (Burt et al., 2020), Alphonse Island (Duhec et al., 2015), Cousine Island (Dunlop et al., 2020), and many others (Macmillan et al., 2022). MPP is primarily of terrestrial origin at some of these sites (e.g. Alphonse Island, Duhec et al. (2015)) whereas ALDFG of marine origin dominates at others (e.g. Aldabra Atoll, Burt et al. (2020)).

Attribution of MPP accumulating at these remote islands would be a positive step towards accountability and prevention, but this is challenging. Several studies have inferred the sources of beached MPP based on intact labels on bottles (e.g. Burt et al., 2020; Duhec et al., 2015), but this method has historically been limited to small sample sizes, is biased against MPP lacking intact labels due to degradation and/or biofouling, and cannot give representative provenance information for all types of MPP, as transport pathways vary greatly with MPP geometry and composition (Maximenko et al., 2018).

Faced with this important data gap, in chapter 2, we combine global-scale numerical models of MPP transport with observations from the existing literature to predict the sources of MPP for remote islands in Seychelles, and the wider west Indian Ocean. In addition to source attribution, we also estimate the seasonality of

MPP accumulation to inform planning of future beach clean-ups on remote islands, which are expensive and logistically challenging (Burt et al., 2020), and infer the physical mechanisms behind these geographic and temporal patterns. This chapter was published in Marine Pollution Bulletin (Vogt-Vincent, Burt, et al., 2023).

1.5 Coral reef connectivity

Corals are a broad group of cnidarians (the same phylum as jellyfish). Stony corals of order *Scleractinia*, responsible for reef formation in the present day tropics, secrete an aragonite skeleton called ‘corallites’. If calcification rates are high enough (and supported by other cementing calcifiers such as crustose coralline algae), reefs can develop. Soft corals are also found in tropical coral reefs, but they do not form robust carbonate structures like stony corals. Most shallow-water tropical corals are both autotrophs and heterotrophs, in that they obtain photosynthetic products (carbohydrates) from autotrophic dinoflagellates called zooxanthellae, but can also capture zooplankton and organic particles through stinging tentacles and mucus (Houlbrèque & Ferrier-Pagès, 2009). Corals can also be found outside the subtropics and in deep water, but have lower calcification rates (generally forming coral communities rather than reefs) and rely on heterotrophy; we focus on shallow water tropical corals in this thesis. Individual corals are known as *polyps*, but can reproduce by asexual reproduction to generate large colonies of genetically identical individuals through *budding*. Asexual reproduction at a colonial level can occur through physical fragmentation of a coral colony, and individual polyps can also leave a colony through *polyp bail-out*. However, generally speaking, asexual reproduction is a localised process and is not a significant mechanism for long-distance dispersal.

Sexual reproduction in corals follows two divergent strategies. The first, known as *brooding*, occurs when fertilisation of the egg occurs internally, with coral larvae (also known as *planulae*) only being released once developmentally mature enough to settle. In contrast, the more common *broadcast spawning* strategy involves the mass release of positively buoyant eggs and sperm, and fertilisation (and subsequent development of the larvae or planulae) occurs within the water column (Harrison, 2010). As a

result, larvae generated through broadcast spawning spend a minimum period of time in the water column before they are mature enough (*competent*) to settle (the pre-competency period), and then have a window of time during which they can settle (the competency period, figure 1.5) before loss of competency and/or death. In many studies, the competency period is described as a ‘pelagic larval duration’ (PLD), but the competency period is actually highly variable amongst larvae and is therefore best described as a distribution (Connolly & Baird, 2010). Once a larva settles on an appropriate substrate, it finally has the opportunity to metamorphose into a polyp and potentially initiate a new coral colony (Harrison, 2010). Importantly, particularly in the case of broadcast spawning corals, larvae can disperse over significant distances, establishing connectivity between spatially disconnected coral reefs.

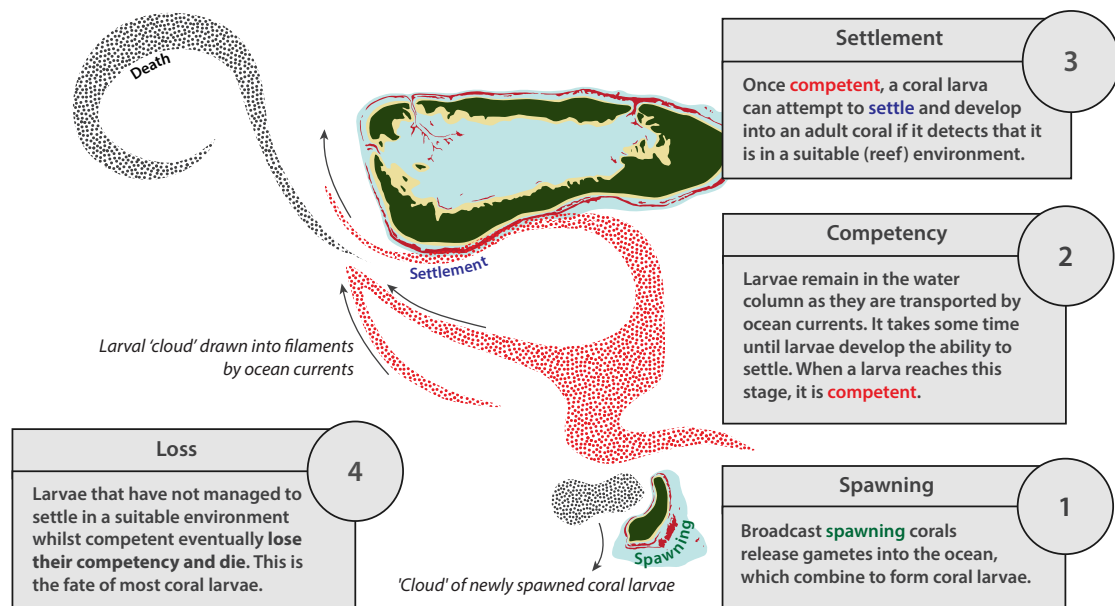


Figure 1.5: Schematic illustration of the process of larval dispersal for broadcast spawning corals, using Aldabra and Assomption (Seychelles) as an example. Reef cover data is based on Lyons et al., 2022.

The coral reefs of the tropical SWIO and Chagos Archipelago represent almost 7% of the global total but are relatively poorly studied, with only around 3% of observations coming from the region (Souter et al., 2021). Nevertheless, these reefs are extremely important for the generally economically disadvantaged countries within the SWIO, supporting the livelihoods of tens of millions and representing a

total asset value of around \$18 billion (Obura, 2017). In addition to (and supporting) their importance for society, the corals of the SWIO are the most diverse on the planet outside the Coral Triangle (Kusumoto et al., 2020; Obura, 2012; Veron et al., 2015), and therefore represent immense ecological value.

As well as pressures such as coastal development, water pollution, and over-fishing, tropical coral reefs are increasingly threatened by the warming of the ocean. Heat stress has already resulted in significant loss of coral cover and biodiversity, a fall in carbonate production rates and structural complexity, increased vulnerability to disease, and a shift towards macroalgae-dominated ecosystems (Cooley et al., 2022; Obura, Gudka, Samoilys, et al., 2021), although coral cover has so far demonstrated some capacity to recover from past severe bleaching events in the SWIO (Obura, Gudka, Porter, et al., 2021). It is practically certain that this situation will worsen considerably in the near future, with widespread decline expected by 2050 even under the most optimistic climate projections, despite uncertainty in coral adaptive capacity (Cornwall et al., 2023; Couce et al., 2023; Dixon et al., 2022; Frieler et al., 2013; Mason et al., 2023). In the face of this enormous, global environmental challenge, there is interest in identifying resilient, diverse, and well-connected coral reefs which may be able to act as reservoirs of biodiversity and support other reefs through the export of larvae (e.g. Almany et al., 2009; Balbar & Metaxas, 2019; Beyer et al., 2018; Cacciapaglia & van Woesik, 2015; Holstein et al., 2016; Schill et al., 2015).

It is unlikely that these ‘coral reef refugia’ can buffer the full diversity of present-day tropical reefs, but they may nevertheless facilitate long-term recovery for corals and coral reef fauna (Kavousi & Keppel, 2018; Pellissier et al., 2014; Smith et al., 2014). Connectivity may itself infer resilience to a coral reef. For instance, although most coral reefs are expected to collapse under realistic climate trajectories in the absence of adaptation (e.g. Dixon et al., 2022; Holstein et al., 2022; Van Hooidonk et al., 2016), it is (in theory) possible that large numbers of incoming larvae could partially compensate for elevated mortality rates (Suzuki & Economo, 2021), supporting coral cover despite poor adaptation to the environment. This is supported by ecological simulations predicting that coral reefs acting as larval sinks

are likely to experience less decline in coral cover (McManus, Forrest, et al., 2021). Coral reefs acting as sinks for reefs in different thermal environments may also receive genotypes adapted to warmer or cooler temperatures, improving or harming capacity for rapid evolution to adapt to warmer temperatures (Kleypas et al., 2016; Matz et al., 2020; McManus, Forrest, et al., 2021; McManus, Tekwa, et al., 2021).

As a result, a comprehensive understanding of coral reef connectivity in the SWIO would be useful for marine practitioners, to identify conservation priorities which may be disproportionately important for maintaining regional reef resilience, and reefs that may be more vulnerable to environmental change. However, although we have a coarse understanding of reef connectivity in the region from regional coral biogeography (Obura, 2012), coral population genetics (e.g. Keshavmurthy et al., 2013; van der Ven et al., 2022), and global (Wood et al., 2014) and regional (Crochelet et al., 2016; Gamoyo et al., 2019; Mayorga-Adame et al., 2017) larval dispersal simulations, no high-resolution, publicly available connectivity dataset exists spanning the entire SWIO.

Due to the lack of existing model output that reasonably represents hydrodynamics in the region at a resolution of 10 km or below, in chapter 3 we first run and validate a 2 km resolution ocean RCM for 28 model years to simulate surface currents across the SWIO, capturing variability ranging from tidal to interannual. This chapter was published in *Geoscientific Model Development* (Vogt-Vincent & Johnson, 2023b). Since previous results from theoretical ecology emphasise the importance of temporal connectivity variability for population dynamics (Watson et al., 2012), in chapter 4 we investigate the geographic variation in coral reef connectivity variability across the SWIO, and identify physical oceanographic drivers. This chapter is in revision for *Limnology & Oceanography*. Finally, using this understanding of the role of variability in setting coral reef connectivity in the SWIO, in chapter 5 we investigate to what extent the flow of larvae between reefs can explain regional coral biogeography and population genetics, and identify which reefs may be particularly resilient to environmental change, and support the resilience of the reef network.

1.6 Thesis overview

In this thesis, we set out to generate insight into (and contribute towards solutions to) the twin problems of MPP and coral reef vulnerability in the SWIO, physically linked through the process of marine dispersal. Our approach is led by numerical modelling, primarily rigorous and carefully thought-out Lagrangian simulations and diagnostics, and we aim to answer the following key questions:

1. What are the key sources of MPP for remote islands in the WIO, and how does this vary with the physical properties of debris? (chapter 2)
2. What sets the temporal variability of MPP beaching rates at these remote islands, and can we make recommendations for when clean-ups should be organised? (chapter 2)
3. How variable in time is coral larval dispersal in the SWIO, what sets this variability, and how important is it for understanding coral reef potential connectivity? (chapter 3 and chapter 4)
4. What sets long-term geographic patterns of potential connectivity in the SWIO, and to what extent does this explain coral biogeography and population genetics? (chapter 3 and chapter 5)
5. What does potential connectivity tell us about which coral reefs are most vulnerable to environmental change, and which reefs should be prioritised for conservation? (chapter 5)

1.7 Data availability

The data products generated as part of this thesis have been made available in publicly accessible repositories where possible (table 1.1).

Chapter	Dataset	Description
2	2.1	Raw trajectory data (Vogt-Vincent & Johnson, 2022a) http://doi.org/10.5285/fc001b104fe6458e92ab6a0be314e68e
	2.2	MPP matrices (Vogt-Vincent & Johnson, 2022b) https://doi.org/10.5287/bodleian:DEdqwXZQw
	2.3	Scripts and figures (Vogt-Vincent, 2022) https://doi.org/10.5281/zenodo.7427528w
3	3.1	WINDS-C (Vogt-Vincent & Johnson, 2022c) http://doi.org/10.5285/b2b9bfe408f14ea7a79d9ff7aee0d0b8
	3.2	WINDS-M (Vogt-Vincent & Johnson, 2022d) http://doi.org/10.5285/BF6F0CFBD09E47498572F21081376702
	3.3	Scripts and figures (Vogt-Vincent, 2023a) https://doi.org/10.5281/zenodo.7548260
4	4.1	Raw trajectory data (Vogt-Vincent & Johnson, 2023a) https://doi.org/10.5285/2727525bf80c4798b7319116a0c15353
	4.2	Scripts (Vogt-Vincent, Johnson, & Mitarai, 2023) https://doi.org/10.5281/zenodo.7825516
5	5.1	Scripts and figures (Vogt-Vincent, 2023c) https://doi.org/10.5281/zenodo.8104599
	5.2	Sea the Connectivity (Janicki et al., 2023) https://doi.org/10.5281/zenodo.8075898
Appendix	A.1	Animations (Vogt-Vincent, 2023b) https://doi.org/10.5281/zenodo.8104801

Table 1.1: List of datasets produced as part of this thesis.

2

Sources of marine plastic pollution for Seychelles and other remote islands in the western Indian Ocean

2.1 Introduction

As described in section 1.4, marine plastic pollution (MPP) is a significant threat to the marine environment and human society. This is particularly the case for remote islands in the western Indian Ocean (WIO, figure 2.1), which are unlikely to be responsible for much of the debris accumulating on their shores (e.g. Burt et al., 2020) yet are particularly vulnerable to the impacts of this MPP (Obura, 2017).

In addition to the sparse observations of debris accumulating at these remote islands, numerical models can be used to predict the source of beaching MPP by representing debris as Lagrangian particles or Eulerian tracers. These simulations can be run forward-in-time, i.e. assuming knowledge of some input distribution of MPP and predicting where it is transported (e.g. Chassignet et al., 2021; Kaandorp et al., 2020; van der Mheen et al., 2020), or backward-in-time, i.e. simulating trajectories that lead to a site of interest and inferring debris sources based on where MPP passed through in the past (e.g. Duhec et al., 2015; Stelfox et al., 2020). In the context of MPP attribution for remote islands, backward-in-time simulations are more efficient

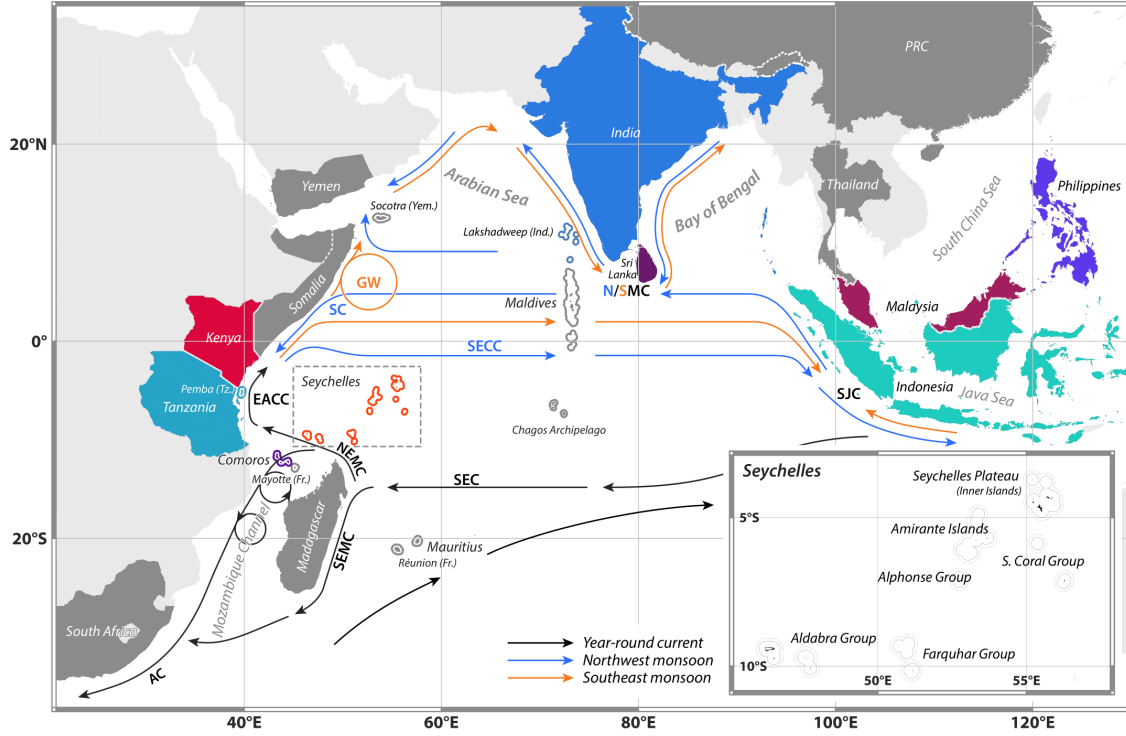


Figure 2.1: Map of the Indian Ocean, with key countries, island groups, and basins highlighted. The remote islands discussed in this study are drawn with a halo for clarity. The colours are the same as those used in figure 2.3. Arrows represent the major surface currents in the Indian Ocean, adapted from Schott et al. (2009). Black arrows represent currents that broadly occupy the same location year-round, whereas blue and orange arrows respectively represent currents during the northwest and southeast monsoon. See also figure 1.2. *Inset:* The major island groups within Seychelles.

as they must only compute the small subset of trajectories that end at the site of interest, reducing computational cost. However, there are significant limitations associated with the backward-in-time approach. For instance, it is not possible to implement parameterisations for subgrid-scale diffusivity (although see Isobe et al. (2009)). Even more significantly, since simulated backward trajectories comprise an unknown subset of all possible trajectories, there are fundamental limitations on the quantitative constraints that can be obtained on the sources of MPP. Most studies using backward-in-time simulations are limited to qualitative predictions of debris sources based on assumptions of a fixed drift time (e.g. Duhec et al., 2015). van Duinen et al. (2022) used a Bayesian framework to quantify sources of MPP for a beach in the Netherlands, but this approach still relies on assumptions on how long debris were adrift before beaching. For remote islands where potential sources

of MPP are many and distal, it is challenging to justify any *a priori* assumption for a drift time distribution. An innovative approach was used by Stelfox et al. (2020), who predicted the source fisheries for ghost gear accumulating in the Maldives based on backward-in-time simulations and constraints on drift time from biofouling. Unfortunately, these constraints are likely MPP-type and site specific, and no such estimates exist in general for most remote islands.

In the absence of constraints on drift time, forward-in-time simulations are required to provide quantitative, physically justifiable estimates for sources of MPP. To date, plastic debris sources have been quantified for the Seychelles as part of a regional (van der Mheen et al., 2020) and a global (Chassignet et al., 2021) study. However, neither study registered a significant number of particles arriving at Seychelles, and they were therefore unable to make robust conclusions about sources of debris for remote islands. Both were large-scale studies focusing on major MPP transport pathways, but this nevertheless highlights an important data gap, and a particular technical challenge for assessing sources of MPP for small and remote locations.

As a result, whilst there are indications from bottle labels, no quantitative estimates exist for the relative importance of sources of MPP for Seychelles, along with other remote island groups in the WIO. Good constraints exist on source regions for one specific type of fishing gear, drifting Fish Aggregating Devices (dFADs), accumulating on Seychelles' beaches (Imzilen et al., 2021; Macmillan et al., 2022), but this has not been generalised to all marine-based sources of MPP. The primary purpose of this study is to provide environmental practitioners working with remote WIO islands with a first quantitative estimate for MPP sources, and to make available a product that can be adapted to future improved constraints on MPP physics. We use large-scale Lagrangian forward simulations, forced by ocean currents, waves, and winds, generalisable to arbitrary sinking and beaching rates, to answer the following questions:

- Which countries are the most likely terrestrial sources of MPP accumulating in Seychelles (and other WIO islands), and how sensitive are these estimates to debris properties such as sinking rate and windage?
- If plastic debris is generated at sea (from fisheries, ships, etc.), from which regions is there most risk of debris beaching at Seychelles, and can we therefore predict high-risk fisheries and shipping channels?
- What are the physical drivers of MPP accumulation at Seychelles, and are variations in accumulation rates (seasonal and interannual) predictable, allowing for more targeted clean-up efforts?

All datasets generated by this study, as well as associated documentation, results that are not discussed in detail in the main text, and code to repeat analyses under different parameters has been made available (table 1.1).

2.2 Methods

2.2.1 Particle tracking

To simulate the transport of MPP, we carry out Lagrangian particle tracking using OceanParcels (Delandmeter & van Sebille, 2019; Lange & van Sebille, 2017). Particles are tracked for 10 years or until the end of 2019, with trajectories integrated using a fourth-order Runge-Kutta scheme and a time-step of 1 hour. Over large scales, buoyant MPP is transported by surface currents, Stokes drift, and in the case of debris protruding above the sea surface, windage (van Sebille et al., 2020). All three processes are important in describing its dispersal (e.g. Duhec et al., 2015; Maximenko et al., 2018). We assume the force experienced by particles from the wind is parallel and proportional to surface winds, but note that this is a simplification compared to the real forces experienced by buoyant debris (Domon et al., 2012).

We advect particles of terrestrial origin with 5 forcing scenarios: just surface currents (C0), surface currents + Stokes drift (CS0), and surface currents + Stokes drift + 1-3% windage (CS1-3). Particles of marine origin are advected using the

same sets of forcing, plus 4% and 5% windage (CS4-5). We use the $1/12^\circ$ CMEMS Global Ocean Physics Analysis GLORYS12 (Lellouche et al., 2021) for daily surface currents, $1/5^\circ$ Global Wave Reanalysis WAVERYS (Law-Chune, 2021) for three-hourly Stokes drift, and $1/4^\circ$ three-hourly surface winds from ERA5 (Hersbach et al., 2020) (all 1993-2019).

There is a land-sea mask mismatch between ocean current output from GLORYS and Stokes drift output from WAVERYS, as they are computed on different grids. To bypass this issue, we adopted the regular interpolated $1/12^\circ$ CMEMS GLORYS land-sea mask as the ‘true coast’, and used the `setmisstodis` operator in CDO (Schulzweida, 2021) to gap-fill Stokes drift in coastal regions (to avoid Stokes drift abruptly vanishing near the coast). We regridded ERA5 surface winds to the WAVERYS grid, and combined the resulting datasets to reduce the number of interpolations required by Parcels. For scenarios with more than set of forcings (i.e. CS0-5), these were added using an OceanParcels `SummedField` object.

Surface current speed and surface wind vectors for the northwest and southeast monsoons are shown in figure 1.4. We apply a homogeneous lateral diffusivity of $10 \text{ m}^2 \text{ s}^{-1}$ to particles to represent the diffusive effects of sub-grid scale surface currents, based on a typical value of the horizontal Smagorinsky diffusivity in the equatorial Indian Ocean diagnosed from GLORYS12 (Smagorinsky (1963)) and in line with previous studies (Kaandorp et al., 2020; Okubo, 1971).

We implemented beaching through post-processing (section 2.2.2), so it is important that particles do not explicitly ‘beach’ during particle tracking. Explicit beaching could occur due to the nonzero winds and Stokes drift at the coast, as well as from the use of a uniform diffusivity, and the fact that particle velocities approach zero as they approach the coast when using linear interpolation on an A-grid (the CMEMS GLORYS data are provided on an interpolated A-grid). To avoid this, we used the `freeslip` interpolation method in OceanParcels, emulating free slip boundary conditions during particle tracking. A small fraction of particles still ‘beached’ due to stochastic diffusion and numerical error, so to entirely eliminate explicit beaching,

we applied a velocity normal to the ‘coast’ once they approached within 0.5 grid cells of the coastline, with the strength ramping up with proximity to the coast.

2.2.2 Particle sinking and beaching

MPP is lost from the ocean surface through processes including beaching and sinking. These processes are complex and driven by small-scale physical and biological processes (Critchell & Lambrechts, 2016; van Sebille et al., 2020), and must therefore be parameterised in large-scale numerical models. Many models parameterise sinking as decay in the mass of MPP represented by a particle (e.g. Chassignet et al., 2021; Kaandorp et al., 2020). Although more sophisticated implementations exist (e.g. Turrell, 2020b), beaching is often parameterised by explicitly removing particles based on criteria, such as particles entering a land cell due to Stokes drift, wind and/or numerical error (e.g. Cardoso & Caldeira, 2021; Zhang et al., 2020), particle stagnation (e.g. Bosi et al., 2021; Seo & Park, 2020), or as a stochastic process associated with some probability (e.g. Onink et al., 2021; van der Mheen et al., 2020).

An advantage with modelling beaching as a stochastic process is the ability to incorporate complex behaviour such as resuspension (Liubartseva et al., 2018; Onink et al., 2021) and, as understanding of the physics of beaching improves, stochastic parameterisations will become an increasingly valuable tool. However, as these parameterisations remove Lagrangian particles from circulation (even if only temporarily), this can significantly reduce the number of particles representing floating MPP in the model. This is a problem when attempting to quantify the sources of debris for small and remote islands: these islands are very small ‘targets’ and beaching events may be missed due to an insufficient number of particles, as was the case for Seychelles in the studies of van der Mheen et al. (2020) and Chassignet et al. (2021).

Instead, we assume that there is (i) a constant rate of MPP removal through sinking, μ_s , and (ii) a constant rate of MPP removal through beaching, μ_b^* , when a particle is within a $1/12^\circ$ coastal grid cell, and implement sinking and beaching offline through post-processing of the trajectory data. These two parameters are highly uncertain, particularly μ_s . Fazey and Ryan (2016) estimated sinking timescales for

small polyethylene (LDPE and HDPE) fragments and, whilst the statistical model used in their study is not identical to our sinking parameterisation, they estimated sinking timescales on the order of 17–66 days. Kaandorp et al. (2020) predicted a slightly higher sinking timescale of $1/\mu_s = 81$ days based on an inverse model incorporating observations of floating MPP in the Mediterranean Sea. Koelmans et al. (2017) predicted an effective removal timescale of plastic debris from the ocean surface (through fragmentation into microplastics) on the order of months, based on mass-balance arguments and observations of floating debris. However, Lebreton et al. (2019) argued that observations of the age distribution of MPP in the North Pacific subtropical gyre are inconsistent with rapid sinking rates, instead suggesting that observations are more consistent with low sinking rates and rapid scavenging of debris at coastlines through beaching. Since these parameters are so uncertain, it is very useful to be able to modify these parameters through post-processing, rather than having to rerun expensive particle tracking analyses.

We store ‘beaching events’, defined as the mass of MPP beaching from a particle whilst that particle is continuously within coastal grid cells of a beaching site. In this study, we store results for 27 beaching sites, of which 18 are islands within Seychelles. For the terrestrial-sourced MPP experiments only, we included an additional 9 sites from the wider WIO (Comoros, Mayotte, Lakshadweep, Maldives, Mauritius, Réunion, Pemba, Socotra, and the Chagos Archipelago). A grid file with the labelled grid cells for all sites can be found in dataset 2.3 (table 1.1). For brevity, we focus on Seychelles in this chapter, specifically islands on the Seychelles Plateau (the Inner Islands), and the Aldabra Group as representative of the Outer Islands. We focus on these two island groups as the population of Seychelles almost entirely resides within the Inner Islands, while Aldabra is a World Heritage Site and the site of a major observational MPP study (Burt et al., 2020). Together, these groups span the geographical range of Seychelles. Analyses and figures for other island groups that could not be included in this chapter can be produced using the associated datasets.

The rate of change of mass M_i represented by a particular particle j influenced by a constant sinking rate μ_s and a beaching rate μ_b is given by:

$$\begin{aligned}\frac{dM_j}{dt} &= -(\mu_s + \mu_b(t)) M_j \\ M_j(0) &= M_j^0,\end{aligned}\tag{2.1}$$

where the beaching rate $\mu_b(t) = \mu_b^*$ when a particle is within a coastal grid cell, and 0 otherwise. The solution to this differential equation is:

$$\begin{aligned}M_j(t) &= M_j^0 \cdot \exp(-\mu_s t - \phi(t)) \\ \phi(t) &= \int_0^t \mu_b(\tau) d\tau.\end{aligned}$$

If we define a ‘beaching event’ as the time spent by a particle in a coastal cell, then the mass m_{jk} beached by particle j during beaching event k , $t_k^0 \leq t \leq t_k^0 + \Delta t_k$, is given by:

$$\begin{aligned}m_{jk} &= \int_{t_k^0}^{t_k^0 + \Delta t_k} \mu_b^* M_j(\tau) d\tau \\ &= \mu_b^* M_j^0 \int_{t_k^0}^{t_k^0 + \Delta t_k} \exp(-\mu_s \tau - \phi(\tau)) d\tau.\end{aligned}\tag{2.2}$$

It would be possible to calculate m_{jk} offline by saving the position (x, y, t) of each particle at regular time intervals, approximating $\phi(t)$ by evaluating the coastal status at each particle position, and solving equation (2.2) numerically. However, there are over 2×10^{11} particles across all our simulations and capturing every beaching event would require a sampling period of $\frac{\approx 8000 \text{ m}}{\approx 1 \text{ ms}^{-1}} \approx 2 \text{ h}$ (where 8000 m is the grid size, and 1 ms^{-1} is a typical maximum surface current speed), or around 44,000 samples over a 10-year integration. By storing (x, y) as 16-bit cell indices and assuming a constant time step between samples, one complete trajectory could be stored in 176 kB (uncompressed). For all particles, this would result in a storage requirement of over 30 PB. Even allowing for compression and permitting a coarser sampling frequency, this would still result in an unmanageable storage requirement.

Alternatively, equation (2.2) could be solved online (i.e. during particle tracking), greatly reducing storage requirements, as only m_{jk} and the associated beaching site

would have to be stored (for instance, as a 16-bit float and 8-bit integer respectively) for each beaching event. Assuming an average of ~ 10 beaching events per particle, this would reduce the raw storage requirement by almost 4 orders of magnitude to around 6 TB (and likely lower with compression). Unfortunately, solving this equation online means that μ_s and μ_b must be defined at run-time, so particle tracking would have to be rerun for every (μ_s, μ_b^*) configuration of interest. Given the computational cost involved in simulating the trajectories of order 10^{11} particles, this is undesirable.

However, there is a piecewise analytical solution to equation (2.2). Within a particular beaching event k , $t_k^0 \leq t \leq t_k^0 + \Delta t_k$:

$$\begin{aligned}\phi_k^0(t) &= \int_0^t \mu_b(\tau) d\tau \\ &= \phi_k^0 + \mu_b^*(t - t_k^0),\end{aligned}$$

where ϕ_k is ϕ during beaching event k , and $\phi_k^0 = \phi(t_k^0)$. Therefore:

$$\begin{aligned}m_{jk} &= \mu_b^* M_j^0 \int_{t_k^0}^{t_k^0 + \Delta t_k} \exp\left(-\mu_s \tau - \phi_k^0 - \mu_b^* (\tau - \tau_k^0)\right) d\tau \\ &= -\frac{\mu_b^* M_j^0}{\mu_s + \mu_b^*} \left[\exp\left(-\mu_s \tau - \phi_k^0 - \mu_b^* (\tau - \tau_k^0)\right) \right]_{t_k^0}^{t_k^0 + \Delta t_k} \\ &= \frac{\mu_b^*}{\mu_s + \mu_b^*} \left(M_j(t_k^0) - M_j(t_k^0 + \Delta t_k) \right).\end{aligned}\tag{2.3}$$

Equation (2.3) shows that, as long as we store the variables t_k^0 , Δt_k , ϕ_k^0 , and the sink cell index j for every beaching event k , we can perfectly reconstruct all m_{jk} . In our model configuration, these four variables can be stored as one 64-bit integer. By using this method, it is possible to recompute m_{jk} for different beaching and sinking rates (at very low computational cost relative to rerunning the particle tracking), whilst also minimising storage requirements. We have run these simulations using an OceanParcels kernel that tracks these four variables and saves them at the end of every beaching event. Compressed, our simulations have a total storage requirement of c. 1 TB, which is very manageable on inexpensive modern hardware.

2.2.3 MPP sources

We classify plastic debris into terrestrial sources (MPP that entered the ocean from coastlines) and marine sources (MPP that entered the ocean at sea, primarily from ships). Due to the relatively poor constraints on the input distribution and magnitude of marine sources, we use different approaches to consider terrestrial and marine sources.

2.2.3.1 Terrestrial sources

MPP can enter the ocean through rivers (transported from inland), as well as through direct coastal input from coastal populations through stormwater, sewage, or poor waste disposal (Mihai et al., 2022). For riverine MPP input, we use the modelled midpoint annual estimates from Meijer et al. (2021), gridding the emissions from each river mouth to the nearest coastal cell on the 1/12° GLORYS12 grid (section 2.2.1). For direct coastal input, we base our estimates on modelled annual mismanaged plastic waste generation estimates from Lebreton and Andrady (2019). We degrade the resolution of this product to the GLORYS12 resolution, and then calculate emissions to the ocean by assuming that a fraction $f_i = f_c \cdot \exp\left[-\left(\frac{d_i}{L}\right)^2\right]$ of the mismanaged waste produced in a grid cell i enters the nearest coastal cell, where f_c is the maximum likelihood of mismanaged waste entering the ocean, d_i is the distance of cell i from the coast, and L is a length scale over which direct coastal input to the ocean is significant. This parameterisation is based on the assumption that waste is less likely to enter the ocean the further from the coast it is generated. Many previous studies have used the alternative assumption, inherited from Jambeck et al. (2015), that a fixed fraction of mismanaged waste generated within 50 km of the coast enters the ocean. Both of these parameterisations are somewhat arbitrary, but we believe that our assumptions are more appropriate.

We set $L = 15$ km as a conservative value to reflect the length scale of a typical coastal city, and to reduce the risk of ‘double counting’ debris entering rivers from coastal cities (counted as riverine debris in Meijer et al. (2021)). The parameter f_c is the main control on the ratio r of MPP generation from coastal versus riverine

sources. In the absence of good constraints on this parameter, we take $f_c = 0.25$, corresponding to a total flux of plastic debris from coastal and riverine sources of 3.1 Mt y^{-1} and 1.0 Mt y^{-1} respectively ($r = 3.1$, between $r = 1.9$ in Kaandorp et al. (2020) and $r = 4.9$ in Lebreton et al. (2018)). The parameter f_c can, however, be modified during post-processing and, if it becomes better constrained in the future, it is straightforward to regenerate our results for another value of f_c , or even an entirely different MPP input distribution, using the associated datasets (table 1.1).

To minimise the cost of simulations, we only consider coastal cells for countries that could reasonably act as a source of MPP for islands in the WIO, identified from a preliminary backward particle tracking experiment (appendix A.1). Many coastal cells are associated with a very small flux of MPP, so we remove the 7773 (of 20742) coastal cells with the smallest contributions, leaving 99.99% of riverine plastic, and 99.9% of coastal plastic. An overview of the terrestrial sources of MPP used in our experiments is shown in figure 2.2.

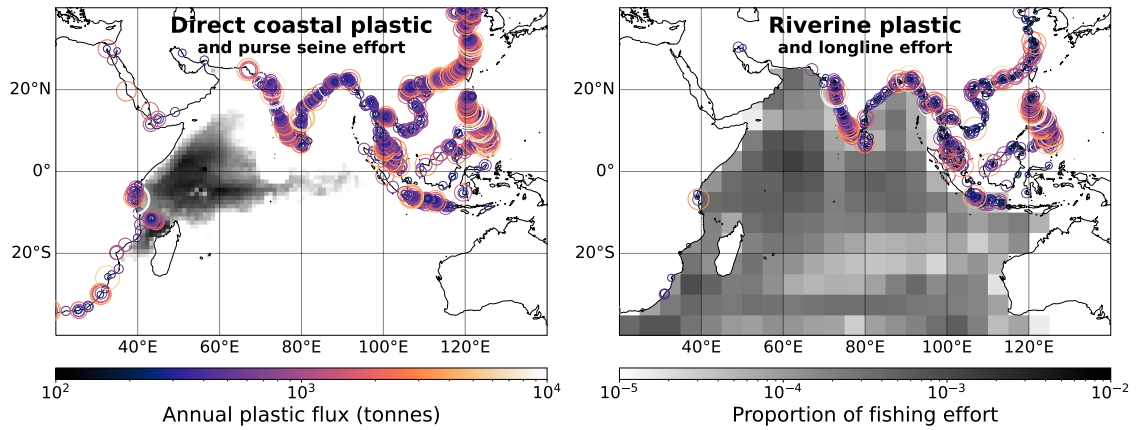


Figure 2.2: *Left:* Terrestrial sources of MPP from direct coastal input (as described in section 2.2.3.1, coloured and scaled by the annual plastic flux per grid cell), and proportion of purse seine fishing effort in the Indian Ocean (fishing hours, as described in section 2.2.3.2). *Right:* Terrestrial sources of MPP from riverine input, and proportion of longline fishing effort in the Indian Ocean (hooks).

2.2.3.2 Marine sources

Ship tracking data from the automatic identification system (AIS), broadcast by large ships, has been used as a proxy for fishing effort and therefore ALDFG production in

previous studies (e.g. Kaandorp et al., 2020). However, AIS coverage is poor in the Indian Ocean (Richardson, 2022). Instead, we use publicly available Indian Ocean Tuna Commission (IOTC) effort data for purse-seines and longlines (provided on 1° and 5° grids respectively), which is well-studied and has been used extensively as an indicator of fishing activity, particularly in the case of purse-seines (Imzilen et al., 2022; Kaplan et al., 2014). Effort is quantified as fishing time (purse-seines) and hooks (longlines). We consider longline fisheries from Japan, Taiwan, and Korea only, as data from these countries is the most reliable in terms of spatial distribution (Kaplan et al., 2014, Emmanuel Chassot (*personal communication*)). Since purse-seine and longline vessels lose gear at different rates (Kuczenski et al., 2022) with potentially different behaviour in the water, we do not aggregate effort from these two fisheries, and instead consider them separately.

MPP may also be discarded or lost at sea from commercial and recreational shipping traffic, which was suggested as a potentially significant source of plastic pollution for Alphonse, Seychelles by Duhec et al. (2015). This debris source is challenging to quantify, but we use AIS-based estimates of shipping traffic intensity from Cerdeiro et al. (2020) as an indication of where major shipping lanes in the Indian Ocean are (figure 2.5).

2.2.4 Seeding strategy

2.2.4.1 Terrestrial sources

For each coastal cell i on the GLORYS12 grid, we split the annual flux of MPP of terrestrial origin T_i (as described in section 2.2.3.1) across 4 equally spaced releases per month, for a total of 48 identical releases per year. Releasing a uniform number of particles per coastal cell would be computationally inefficient, as the mass represented by each particle would vary over 5 orders of magnitude. However, scaling particle number linearly with MPP flux would result in extremely low numbers of particles representing weak debris sources, which may still be locally important. As a compromise, we divide the MPP associated with each release across n_i particles, such that the initial mass associated with a particular particle j released at cell i

is $M_j^0 = T_i/48n_i$. We set $n_i = \lceil c_1 \cdot \log_{10} [F_i] - c_2 \rceil^2$, where $c_1 = 16$ and $c_2 = 18.4$ are arbitrary parameters chosen to distribute particles reasonably whilst keeping computation tractable, and $\lceil \dots \rceil$ is the ceiling function. We release 13.7 million terrestrial particles per release event, for a total of 656 million per model year.

2.2.4.2 Marine sources

In each marine cell on the GLORYS21V1 grid between 20°E-130°E and 40°S-30°N (excluding the Mediterranean) we generate 36 particles per release. We release particles at four equally spaced intervals per month, with 26.5 million particles per release event and a total of 1.27 billion particles per model year.

2.2.5 Quantifying beaching debris

2.2.5.1 Terrestrial sources

Since each particle representing terrestrial MPP has an explicit initial mass associated with it (section 2.2.4.1), there is also a mass associated with each beaching event. We therefore compute a list of beaching events (i, j, m_b, t_b) for each set of parameters, where i is the beaching site, j is the country of origin, m_b is the mass beached (kg), and t_b is the beaching month. We then bin m_b as a terrestrial-sourced MPP flux matrix $F_T^{ij}(t_b)$ for each set of parameters, giving the total mass beaching at i from j in month t_b .

2.2.5.2 Marine sources

We firstly compute a list of beaching events (i, x, y, m_b, t_s, t_b) for each set of parameters, where i is the beaching site, (x, y) is the input location, m_b is the ‘mass’ beached, t_s is the input month, and t_b is the beaching month. Importantly, we compute m_b as a *fraction* of MPP generated at (x, y, t_s) . From this list, we then define a marine-sourced MPP flux matrix $F_M^i(x, y, t_s, t_b)$, giving the mass (fraction) of MPP beaching at i and month t_b , given that it entered the ocean at (x, y) and time t_s . We further compute the marine-sourced MPP source flux $F_{Ms}^i(x, y, t_s) = \sum^{t_b} F_M^i$ and marine-sourced MPP beaching flux $F_{Mb}^i(x, y, t_b) = \sum^{t_s} F_M^i$. Note that $F_{Ms}^i(x, y, t_s)$ is equivalent to the likelihood of MPP entering the ocean at (x, y, t_s) *ever* beaching at i , and we call

this quantity the *risk*. We also compute monthly climatological versions of all these matrices (subscript c) by summing over all years, e.g. $F_{Mc}^i(x, y, t_s^*, t_b^*), t_s^*, t_b^* = 1 \dots 12$.

Assuming MPP input by fishery j is proportional to fishing effort $E_j(x, y, t_s^*)$, the relative flux $f_j^i(x, y)$ of fishery j MPP that *ever* beaches at site i is given by $f_{ij}(x, y) = \sum_{t_s=1}^{12} (E_j(x, y, t_s^*) \cdot F_{Msc}^i(x, y, t_s^*))$. We can normalise this relative flux by the total flux from all sources, to give the *realised risk* $R_j^i(x, y)$ to site j from fishery i at location (x, y) , $R_j^i(x, y) = \frac{f_{ij}(x, y)}{\sum_{x,y} f_{ij}(x, y)}$, which is the likelihood that MPP from fishery j beaching at site i entered the ocean at (x, y) . Along similar lines, we also compute a monthly climatology $B_j^i(t_b^*)$ for beaching rates from fishery j at site i , $B_j^i(t_b^*) = \sum_{x,y} \left(\sum_{t_s=1}^{12} (E_j(x, y, t_s^*) \cdot F_{Mc}^i(x, y, t_s^*, t_b^*)) \right)$.

2.2.5.3 Seasonality

To test whether seasonality exists in a time-series $f(t)$, we define the operator $\mathcal{F}[f(t)]$, which returns a sine wave with the phase and wavelength of the annual component of $f(t)$ (based on its Fourier spectrum). We determine that there is a significant seasonal component to $f(t)$ if $\text{corr}(\mathcal{F}[f(t)], f(t))$ is significant ($p < 0.01$, taking into account autocorrelation within both time-series (Bretherton et al., 1999)).

2.2.6 MPP Classes

In our model, the behaviour of MPP in the ocean is set by the three parameters μ_s (sinking rate), μ_b^* (beaching rate), and the forcing scenario (C0 or CS0-5). No one set of parameters will describe all MPP, and constraints on all three are poor. We simplistically explore the sensitivity of model results to this parameter-space in section 2.3.3.1, but to provide concrete examples, we define four representative MPP classes in table 2.1. Animation 2.1 (table 1.1) shows an example of dispersal for Class C debris.

To derive these classifications, we use guidance on windage coefficients from Duhec et al. (2015) and Domon et al. (2012), sinking rates from Fazey and Ryan (2016), and beaching rates from our own analysis (appendix A.2) and Kaandorp et al. (2020). However, we stress that windage coefficients and sinking rates for

	$1/\mu_b$ (d)	$1/\mu_s$ (d)	Scenario	Buoyancy	Exposure	Examples
Class A	30	30	CS0	Low	Negligible	mm-scale plastic fragments, nurdles
Class B	30	90	CS1	Med	Low	Bottle caps, small domestic items
Class C	30	360	CS3	High	Med	Beach sandals, bottles, foam sheets, buoyant nets
Class D	30	1800	CS5	Very high	High	ALDFG with buoys, robust empty bottles

Table 2.1: Representative classes of MPP used in this study, defined by beaching rate $1/\mu_b$ (days), sinking rate $1/\mu_s$ (days), physical scenario, buoyancy, exposure to the winds, and possible real-life examples of the representative class. All MPP classes have positive buoyancy.

different types of MPP remain poorly constrained, and the classes we have defined are suggestions only. Practitioners can recompute predictions for parameters of their own interest using the associated datasets.

2.2.7 Comparison with observations

Burt et al. (2020) estimated the total mass of MPP that accumulated on Aldabra Atoll (Seychelles), as well as countries of origin for a small sample of PET bottles. Quantitative source analyses have also been carried out for Alphonse, Coëtivy, Astove and Platte (Duhec et al., 2015; The Ocean Project Seychelles, 2019). Finally, Macmillan et al. (2022) analysed patterns of (satellite-tracked) drifting Fish Aggregating Device (dFAD) beaching events across Seychelles.

Our analyses provide an estimate of the mean annual (terrestrial) MPP beaching rates $\bar{B}$ at various sites assuming a constant rate of MPP input into the oceans (based on emissions in 2015 (Lebreton & Andrady, 2019; Meijer et al., 2021)), by averaging the accumulation rate from 1995-2014 (allowing for a 2-year ‘spin-up’). However, the mass of MPP entering the ocean has increased significantly through time (Geyer et al., 2017), so direct comparison with the total accumulated mass estimated by Burt et al. (2020) is not possible. Here, we outline two suggestions

to convert the total mass M_{Ald} of terrestrial MPP on Aldabra (approximately 87.3 tonnes (Burt et al., 2020)) into an average beaching rate based on 2015 emissions, $\bar{B}$, which can be directly compared to our analyses.

2.2.7.1 Method 1: Assume the rate of MPP beaching is proportional to the rate at which plastic is discarded

Geyer et al., 2017 estimated the mass of plastic waste D_i discarded per year i from 1950 to 2015. By assuming that the fraction of discarded waste that enters the ocean remains constant, the ratio R_{Geyer} of the total mass of waste that has entered the ocean to the mass of waste entering the ocean in 2015 is:

$$R_{\text{Geyer}} = \frac{\sum_{i=1950}^{2015} D_i}{D_{2015}} = 30.5.$$

Therefore:

$$\bar{B}_{\text{Geyer}} = \frac{M_{\text{Ald}}}{R_{\text{Geyer}}} = 2.9 \text{ tonnes y}^{-1}.$$

2.2.7.2 Method 2: Assume the rate of MPP beaching at Aldabra is proportional to the number of items observed beaching per year at Cousine Island, Seychelles

Dunlop et al., 2020 summarised the results of almost two decades of MPP monitoring at Cousine Island, Seychelles, providing estimates of accumulation rates (in terms of items per metre per day) for 10 years between 2003 and 2019. If we assume that interannual variability in MPP accumulation at Cousine Island (not explicitly included as a sink in this study, but closest to Praslin) mirrors that at Aldabra, we can estimate R_{Dunlop} based on the observations in Dunlop et al., 2020. If we define A_i as the accumulation rate for year i at Cousine Island, where A_i is set to the observed annual accumulation rate for years with data, and linearly interpolate between the nearest years otherwise, then we can compute R_{Dunlop} as:

$$R_{\text{Dunlop}}^{\text{low}} = \frac{\sum_{i=2003}^{2015} A_i}{A_{2015}} = 16.5,$$

$$R_{\text{Dunlop}}^{\text{high}} = \frac{\sum_{i=1950}^{2015} A_i}{A_{2015}} = 20.3,$$

where we assume $A_{i<2003} = 0$ for $R_{\text{Dunlop}}^{\text{low}}$, and $A_{1950} = 0$ (based on Geyer et al., 2017 for $R_{\text{Dunlop}}^{\text{high}}$ (treating $A_{1950} = 0$ as another data point and linearly interpolating between 1950 and the first actual observation in 2003)). Therefore:

$$\bar{B}_{\text{Geyer}}^{\text{low}} = \frac{M_{\text{Ald}}}{R_{\text{Dunlop}}^{\text{low}}} = 5.3 \text{ tonnes y}^{-1},$$

$$\bar{B}_{\text{Geyer}}^{\text{high}} = \frac{M_{\text{Ald}}}{R_{\text{Dunlop}}^{\text{high}}} = 4.3 \text{ tonnes y}^{-1}.$$

As a result, our first-order estimates suggest that the annual beaching rate of terrestrial MPP at Aldabra should be around 2.9-5.3 tonnes per year, possibly on the lower end as our results in Section 2.3.2 suggest that interannual variability is considerably different between Aldabra and Praslin (and by extension, nearby Cousine).

2.3 Results and discussion

2.3.1 Sources of MPP for remote islands in the WIO

2.3.1.1 Debris of terrestrial origin

There is significant variation in the predicted source countries for MPP beaching at the 27 sites investigated in this study (figure 2.3). These figures can be interpreted as the predicted likelihood of a fragment of MPP originating from the source country and beaching at the target island (group), given that it has properties reflecting Class A, B, or C debris as defined above.

For Class A debris (figure 2.3(a)), East Africa (predominantly Tanzania) is expected to be the largest source of MPP for most of the Outer Islands of Seychelles, although Comoros is the dominant source for Aldabra and Assomption. For the Inner Islands on the Seychelles Plateau, most Class A debris is expected to come from within Seychelles, with the remainder sourced from East Africa. For sites in the central-northern Indian Ocean (Maldives and Lakshadweep), India and/or Sri Lanka are expected to be the principal sources of MPP. Only the Chagos Archipelago is predicted to source most of its Class A MPP from Indonesia.

For Class B debris (figure 2.3(b)), a combination of longer residence time at the ocean surface (3 months) and easterly winds allows Indonesia to begin to dominate

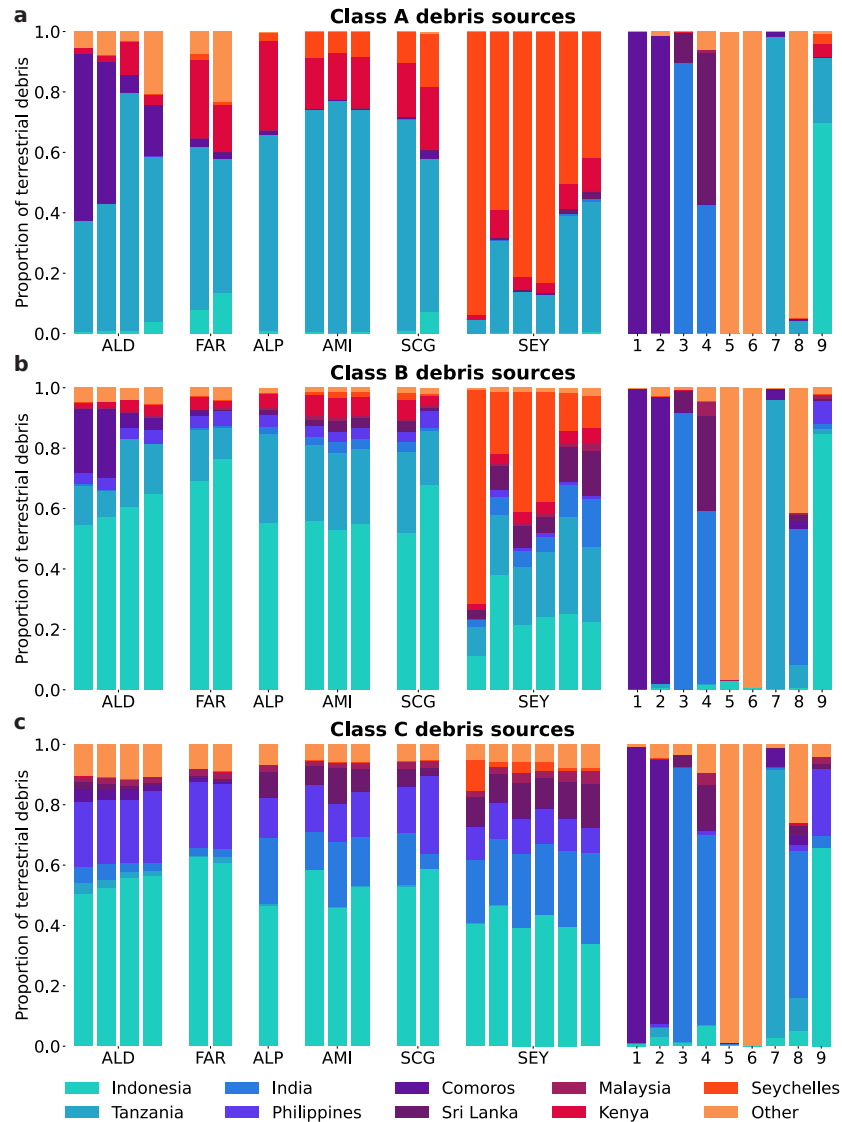


Figure 2.3: Sources of beaching (terrestrial) MPP from all MPP releases 1993-2014 for (a) Class A, (b) Class B, and (c) Class C MPP. Sites from left to right: **Aldabra Group** (Aldabra, Assumption, Cosmoledo, Astove), **Farquhar Group** (Providence, Farquhar), **Alphonse Group** (Alphonse), **Amirante Islands** (Poivre, St Joseph, Desroches), **Southern Coral Group** (Platte, Coëtivy), **Seychelles Plateau** (Mahé, Fregate, Silhouette, Praslin, Denis, Bird); Comoros (1), Mayotte (2), Lakshadweep, India (3), Maldives (4), Mauritius (5), Réunion, France (6), Pemba, Tanzania (7), Socotra, Yemen (8), Chagos Archipelago (9). Nine source countries have been chosen; all other sources are grouped under ‘other’. For sites with significant proportions of Class A MPP from ‘other’ countries, the largest ‘other’ sources are as follows: Astove (Madagascar); Farquhar (Madagascar); Mauritius (Mauritius); Réunion (Réunion); Socotra (Yemen). For Class B MPP: Mauritius (Mauritius); Réunion (Réunion); Socotra (Yemen). For Class C MPP: Mauritius (South Africa and Mauritius); Réunion (Réunion and South Africa); Socotra (Yemen and Pakistan).

the MPP budget for much of the WIO. Our analyses predict that Indonesia is responsible for over 50% of all Class B debris for all Outer Islands of Seychelles (and remains the dominant source for the Chagos Archipelago). Seychelles and Tanzania are still expected to be significant sources of MPP within the inner islands of Seychelles (particularly Mahé, the main population centre of Seychelles), but substantial proportions are also predicted to originate from Indonesia and, in the case of islands in the northernmost Seychelles Plateau (Denis and Bird islands), India and Sri Lanka. India and Sri Lanka are expected to still act as the main sources of MPP for the relatively nearby island groups of Lakshadweep and Maldives, but the lower sinking rate and contributions from winds and waves during the northwest monsoon also results in these countries becoming significant sources of Class B MPP for Socotra, dominated by local sources from Yemen for Class A MPP.

Finally, Class C debris (figure 2.3(c)) beaching across Seychelles (and the Chagos Archipelago) is expected to originate almost entirely from the northern and eastern Indian Ocean. Indonesia is still expected to be the largest single source country, but a significant proportion is swept from the Philippines and, in the case of more northerly islands, India and Sri Lanka. Seychelles and East Africa are not significant sources of Class C debris for any sites in Seychelles. Our analyses also suggest that Mauritius and Réunion, dominated by local sources for less-buoyant classes of MPP, receive significant quantities of Class C debris from South Africa (57% and 36% respectively).

In general, the distribution of terrestrial sources is sensitive to the sinking rate, but relatively insensitive to the beaching rate (see section 2.3.3.1). The distribution of terrestrial sources is sensitive to both Stokes drift and windage, although the presence or absence of Stokes drift appears to be particularly important in partitioning sources between the eastern and WIO for the outer islands of Seychelles (not shown).

We can also extract the predicted drift time distribution for MPP accumulating at our study sites (shown for Aldabra in figure 2.4). Unsurprisingly, the more buoyant MPP classes have a broader range of drifting times, where drifting times are stratified by the oceanographic distance of source countries from Aldabra. For instance, for Class C debris accumulating at Aldabra, MPP arriving from Comoros and Tanzania

have generally only been at sea for 1–2 months, whereas MPP arriving from Indonesia has been at sea for at least 6 months, with a small proportion exceeding 2 years. However, the distribution of drift times is complex and multimodal. Although Lagrangian backtracking is considerably less computationally expensive than the approach used in this study, van Duinen et al. (2022) were required to make an *a priori* assumption for the drift time distribution of MPP accumulating at their site of interest. These drift time distributions for Aldabra highlight that assuming a uniform age distribution of beaching MPP is not an appropriate assumption for remote islands.

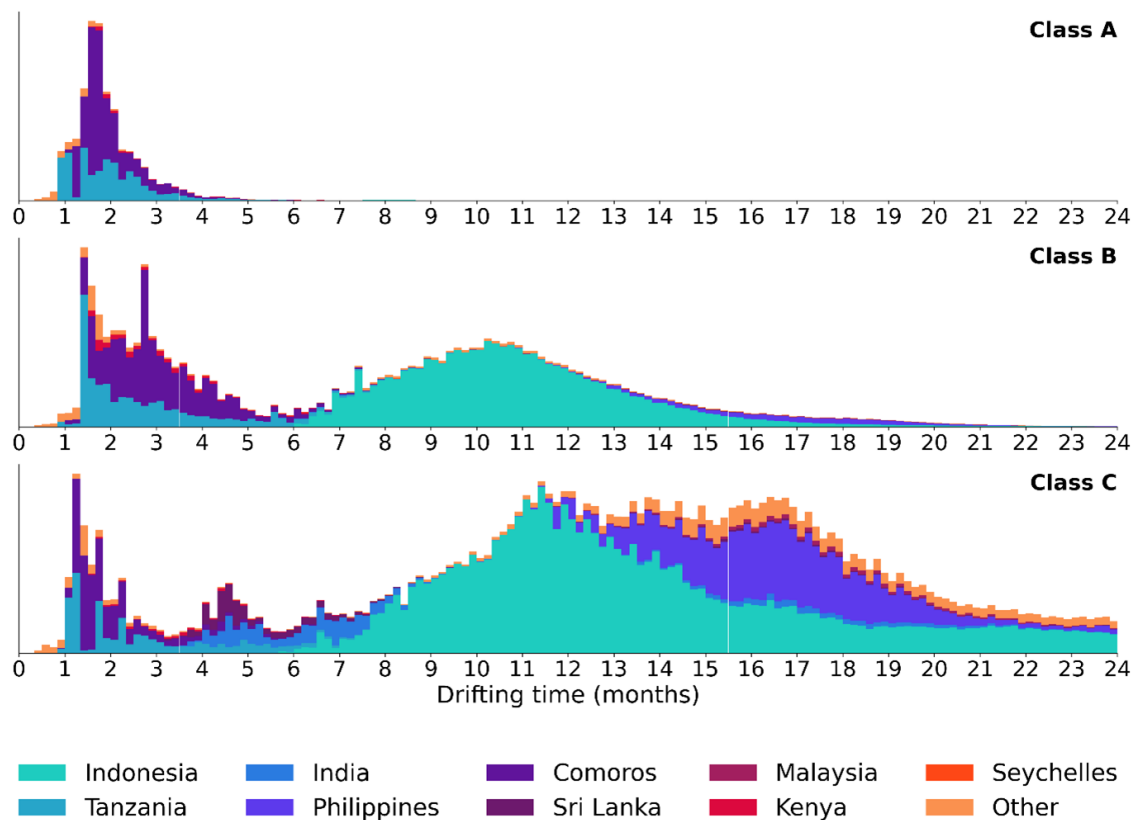


Figure 2.4: Drift time distribution of Class A, Class B, and Class C MPP accumulating at Aldabra (*y*-axis normalised for comparison).

As further discussed in section 2.3.2, there is significant temporal variability in accumulation rates at many of these remote sites, particularly for Class A debris. However, recomputing figure 2.3 for subsets of the full time-series suggests that our source attribution is robust for almost all sites.

2.3.1.2 Debris of marine origin

As with the terrestrial case, the probability of MPP lost or discarded at sea eventually beaching at Seychelles strongly depends on the physical properties of the debris, and where it entered the ocean. Figures 5(a) and (d) show the time-mean *risk* $\bar{F}_{Ms}(x, y)$ of debris to the Aldabra Group, i.e. the mean likelihood that MPP entering the ocean at (x, y) ever beaches at the Aldabra Group. Incoming Class A debris beaching at Aldabra (figure 2.5(a)) is sourced from a relatively narrow latitudinal band, due to primarily zonal currents around Aldabra. The Class A risk region for the Aldabra Group is almost entirely eastward of the island group, as these islands are in the path of a powerful westward-flowing ocean current (the North Madagascar Current). In contrast, the Class A risk map for the Seychelles Plateau is centred on the plateau due to the monsoonal reversal of prevailing zonal currents around the island group (Schott et al., 2009).

With a significantly longer residence time at the ocean surface, and greater propulsion due to windage, the risk maps for Class D debris (figure 2.5(d)) cover a much greater area than for Class A debris. For both the Aldabra Group and Seychelles Plateau, MPP from most of the tropical Indian Ocean has a non-negligible chance of beaching at one of these island groups. Although much MPP in the Indonesian archipelagic seas and further afield is removed through beaching within the narrow straits of the Indonesian Throughflow, the sheer quantity of mismanaged waste generated in Indonesia and the Philippines allows a significant quantity to leak into the Indian Ocean.

The right-hand side panels in figure 2.5 show predictions of the realised risk to the Aldabra Group of ALDFG associated with purse-seine and longline fisheries. In the case of purse-seine debris, due to the concentration of purse-seine fishing effort around the Seychelles, our analyses suggest that most MPP originates from the WIO. In contrast to purse-seine fisheries, effort associated with longline fisheries is more broadly distributed around the Indian Ocean. As a result, the footprint of the potential source region is much larger than for purse-seines. In the case of longline ALDFG behaving as Class D debris, MPP could reasonably be sourced from as far

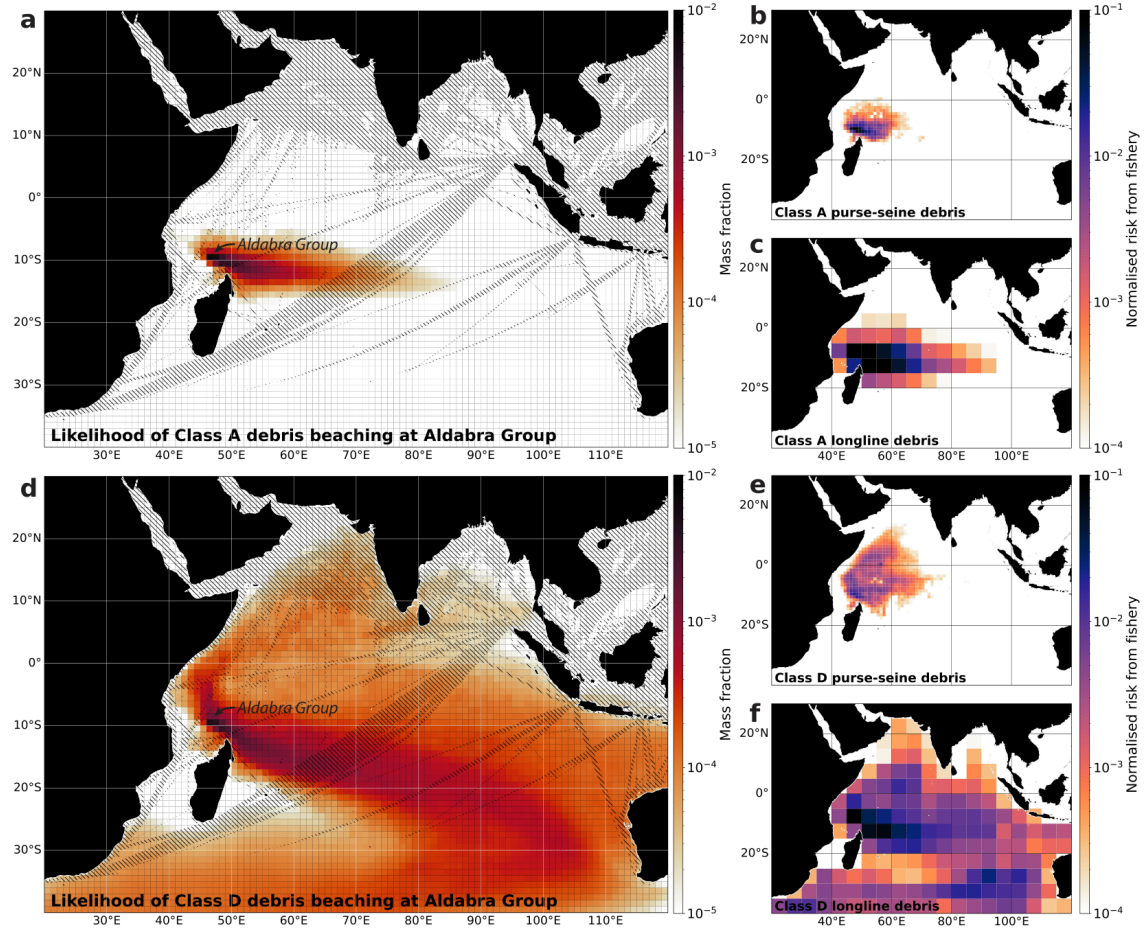


Figure 2.5: Time-mean risk $\bar{F}_{Ms}(x, y)$ for the Aldabra Group for (a) Class A debris and (d) Class D debris. Hatching shows shipping corridors with the most intense traffic from Jan 2015 to Feb 2021 (Cerdeiro et al., 2020). Realised risk $R_j^i(x, y)$ for (b-c) Class A debris and (e-f) Class D debris from (b,e) purse-seines and (c,f) longlines. Note the logarithmic scales in all panels.

afield as the southeastern Indian Ocean, west of Australia (figure 2.5(f)), largely due to the broader areal footprint of longline fisheries in the Indian Ocean. This suggests that a significant proportion of ALDFG beaching at Seychelles could originate from outside the Seychelles EEZ, particularly in the case of longline debris.

Finally, figure 2.5 also shows that there is significant overlap between major shipping lanes (shading in figure 2.5), and high risk regions for Seychelles. Even in the case of short-lived Class A debris, the major shipping lanes linking the Bay of Bengal and South China Sea to the Atlantic pass within the high risk zone for the Aldabra Group. For Class D debris, most of the major shipping lanes in the Indian Ocean pass through regions associated with a high risk of beaching for both

the Inner and Outer Islands of Seychelles, including Atlantic-bound connections from the Middle East and Java Sea, as well as those originating from the Bay of Bengal and South China Sea.

2.3.2 Variability and drivers of beaching MPP

Despite the monthly input of terrestrial debris remaining constant in our analyses, there is substantial temporal variability in beaching rate predicted for remote islands. Figure 2.6(a) shows the mass of Class A debris beaching at the Aldabra Group and Seychelles Plateau per month from 1995 (two years after the first MPP release) to 2014 (the last release year for terrestrial debris). Although the average accumulation rate for Class A debris at the Seychelles Plateau is substantially higher than for the Aldabra Group, the monthly accumulation rate at the Aldabra Group varies over 6 orders of magnitude. These patterns are a result of the different principal sources of Class A debris for each island group (figure 2.3(a)). In the case of the Seychelles Plateau, most Class A debris is sourced from within Seychelles, largely from Mahé (<100 km from most islands). The transport pathways from source to sink for Class A debris beaching within the Seychelles Plateau are therefore short (< 2 weeks), with less of an opportunity for seasonal variations in ocean currents or eddy variability to disrupt this pathway. In contrast, most Class A debris beaching at the Aldabra Group originates in Comoros and Tanzania, both of which are hundreds of kilometres away and are connected through low probability connections (figure 2.5(a)). As a result, the Aldabra Group sees almost no Class A debris beaching in most months, but if an eddy happens to direct a filament of Class A MPP towards Aldabra, a large amount of MPP may beach in a short period of time. This prediction is similar to patterns of ‘pulsed recruitment’ predicted for the long-distance larval dispersal of some marine organisms (e.g. Siegel et al., 2008).

In contrast, *both* the Aldabra Group and Seychelles Plateau see a similar level of variability in beaching rates for Class C debris (figure 2.6(b)). Most Class C debris beaching at both island groups originates from distal sources in Southeast Asia and, in the case of the Seychelles Plateau, South Asia. Class C debris arrives

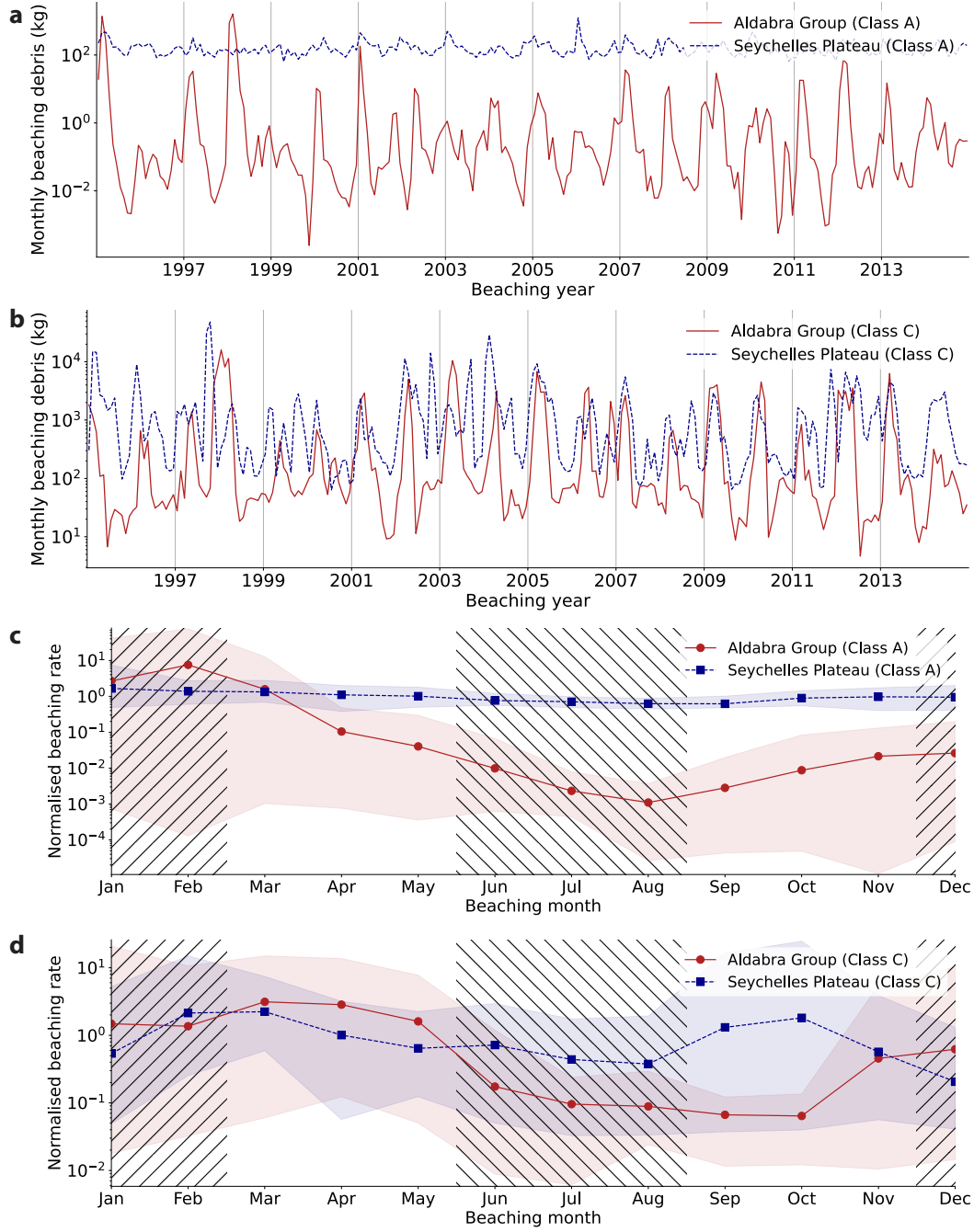


Figure 2.6: (a)-(b) Monthly beaching rate $F_T^{ij}(t_b)$ from 1995-2014 at the Aldabra Group and Seychelles Plateau assuming all terrestrial debris is (a) Class A and (b) Class C. (c)-(d) Monthly beaching rate averaged across 1995-2014 ($F_T^{ij}(t_b^*)$) at the Aldabra Group and Seychelles Plateau (normalised by the annual mean) for (c) Class A and (d) Class C debris. The hatching indicates the approximate timing of the northwest monsoon (~ December to February) and southeast monsoon (~ June to August). The shading represents the range in monthly beaching rates.

at both groups through long-distance transport pathways, and there is therefore ample opportunity for these transport pathways to be controlled by stochastic, eddy-induced variability. This can be clearly seen in animation 2.1 (table 1.1), which also reveals a ‘jittery’ component to debris transport due to the different spatial scales of atmospheric and oceanic forcing. The variability in accumulation rate at the Aldabra Group is lower for Class C debris than for Class A, possibly because the wider geographic distribution of sources and greater time available for mixing ‘smooths out’ the distribution of MPP in the ocean. Nevertheless, monthly beaching rates for both groups are predicted to vary across around three orders of magnitude, with most MPP arriving during short periods of high accumulation rate.

2.3.2.1 Seasonal variability from terrestrial sources

Given this enormous variability in beaching rate, it is useful to understand whether beaching rate varies entirely stochastically, or whether there is some predictability (which could help with the organising of beach clean-ups and other management activities). In particular, prevailing winds and many currents in the Indian Ocean change direction following the monsoons, which have previously been suggested to control the partitioning of MPP between the southern and northern Indian Ocean (van der Mheen et al., 2020). Figure 2.6(c)-(d) shows the monthly accumulation rate for Class A and C debris arriving at the Aldabra Group and Seychelles Plateau, averaged over 1995-2014. For Class A debris (figure 2.6(c)), almost all debris beaches at the Aldabra Group between January and March, i.e. the end of the northwest monsoon. Comoros is a major source of Class A debris for the Aldabra Group, but ordinarily, debris from Comoros is swept into the Mozambique Channel and away from Aldabra. Rapid debris transport from Comoros to Aldabra relies on a relatively uncommon pathway in which MPP is entrained into eddies in the northern Mozambique Channel and transported towards Madagascar, before entering the North Madagascar Current upstream of Aldabra, and subsequently beaching (animation 2.1, see table 1.1). This pathway is improbable during the southeast monsoon, as a strong North Madagascar Current (Backeberg & Reason, 2010) results in MPP rapidly

beaching along the east African coast. As a result, transport from Comoros to Aldabra is generally only feasible during the northwest monsoon and subsequent intermonsoon. In contrast, there is very little seasonal variability in Class A beaching rates across the Seychelles Plateau. There is some seasonality at individual islands, however. For instance, during the northwest monsoon, the South Equatorial Countercurrent shifts towards the south near the Seychelles Plateau (Schott et al., 2009), facilitating the eastward transport of MPP from the highly populated island of Mahé towards Praslin. Conversely, the South Equatorial Countercurrent shifts to the north during the southeast monsoon, and MPP is more likely to be transported westward from Mahé due to the northwestward Stokes drift over the Seychelles Plateau at this time. Indeed, the seasonal pattern for Class A MPP beaching at Silhouette Island, west of Mahé, is in exact antiphase to the pattern at Praslin (not shown).

In the case of Class C debris (figure 2.6(d)), the Aldabra Group again sees a strong seasonal cycle, with a clear minimum in beaching rate during the southeast monsoon, and a peak following the northwest monsoon. The seasonal cycle at the Seychelles Plateau is weaker than for the Aldabra Group, with two peaks broadly aligned with the intermonsoons, with the former driven by MPP arriving from South Asia, and the latter by MPP arriving from Southeast Asia. However, the second peak associated with MPP from Southeast Asia is driven by a small number of large beaching ‘pulses’, and it is not clear from figure 2.6 whether this seasonal cycle is robust. Alternatively, we can observe that, in most years, log-transformed beaching rates are dominated by a single clear sinusoidal peak at most sites we considered. By analysing (log) beaching rates in the frequency domain and extracting the phase of the component with a period of 1 year (see section 2.2.5.3), we can estimate during which season beaching rates *consistently* peak. This is summarised for Class C debris in table 2.2. These seasonal cycles are significant for almost all islands considered.

Table 2.2 suggests that the seasonality of beaching rates across Seychelles is actually in phase for Class C debris of terrestrial origin, with a significant peak predicted in March or April for almost all Seychellois islands (i.e. the end of the northwest monsoon and the subsequent intermonsoon). This peak shifts slightly

Beaching site	Seasonal cycle peak	Seasonality strength
Aldabra	March	35.1
Assomption	March	36.7
Cosmoledo	March	35.1
Astove	March	35.2
Providence	March	48.3
Farquhar	March	47.4
Alphonse	March	39.0
Poivre	April	13.6
St Joseph	March	10.9
Desroches	April	8.7
Platte	March	6.3
<i>Coëtivy</i>	<i>March</i>	<i>20.1</i>
Mahé	March	5.2
Fregate	April	6.3
Silhouette	April	10.5
Praslin	March	8.0
Denis	April	5.7
Bird	April	6.9
Comoros	December	1.9
Mayotte	January	18.7
Lakshadweep	February	92.4
Maldives	February	10.7
<i>Mauritius</i>	<i>August</i>	<i>1.9</i>
<i>Réunion</i>	<i>November</i>	<i>1.3</i>
Pemba	January	4.4
Socotra	March	12.7
Chagos Archipelago	September	7.9

Table 2.2: Class C debris beaching rate seasonal peak, and strength of the seasonal cycle (1995-2014), based on the annual component of the beaching rate spectrum. The strength of the seasonal cycle is the ratio of the mean beaching rate during the three months with the highest and lowest beaching rates. All time series correlated significantly with idealised cycle ($p < 0.01$) aside from sites in *italics*.

earlier in the year for less buoyant classes, but remains during the northwest monsoon for Class A and Class B debris beaching at most islands in Seychelles. The strength of this seasonality (quantified by the ratio of the beaching rate during the highest and lowest three months), however, is considerably larger for the Outer Islands of Seychelles, particularly for the Aldabra, Farquhar and Alphonse Groups.

2.3.2.2 Seasonal variability from marine sources

We gain further insight into the physical drivers of this seasonality by repeating this spectral analysis for marine-sourced debris $F_{Mb}^i(x, y, t_b)$ (section 2.2.5.2), i.e. the beaching rate at site i and time t_b given a uniform rate of MPP generation at (x, y) . This reveals whether MPP entering the ocean at a uniform rate is more likely to beach at i in certain parts of the year. Plotted in figure 2.7(a) is the correlation in time between the log of the marine-sourced MPP beaching flux, $\log(F_{Mb}^i)$, and the annual component, $\mathcal{F}(\log(F_{Mb}^i))$. Although our analyses suggest that Indonesia is the dominant source of Class C debris for Aldabra, figure 2.7(a) shows that MPP generated across most of the Indian Ocean is significantly ($p < 0.01$) more likely to beach at Aldabra in certain seasons. The phase of the seasonal cycle $\mathcal{F}(\log(F_{Mb}^i))$, given in figure 2.7(b), represents when in the year MPP is most likely to beach at the Aldabra Group, for a uniform rate of MPP production. Importantly, the entire region is perfectly in phase. This may be surprising, as the drift time to the Aldabra Group varies considerably across the Indian Ocean. If the seasonality of Class C debris beaching at the Aldabra Group depended on remote forcing (e.g. currents, winds and waves at the MPP source region, or along its transport path), we would expect considerable spatial heterogeneity in figure 2.7(b).

Instead, this figure demonstrates that the seasonality of Class C debris beaching at the Aldabra Group is dominated by *local* forcing, specifically the monsoonal variation in the winds. During the northwest monsoon, winds around Aldabra are relatively weak (figure 1.4) and westward zonal surface currents are proportionately more important. As a result, MPP arriving at Aldabra during the northwest monsoon is sourced, on sub-seasonal timescales, east of Aldabra, from the southern tropical

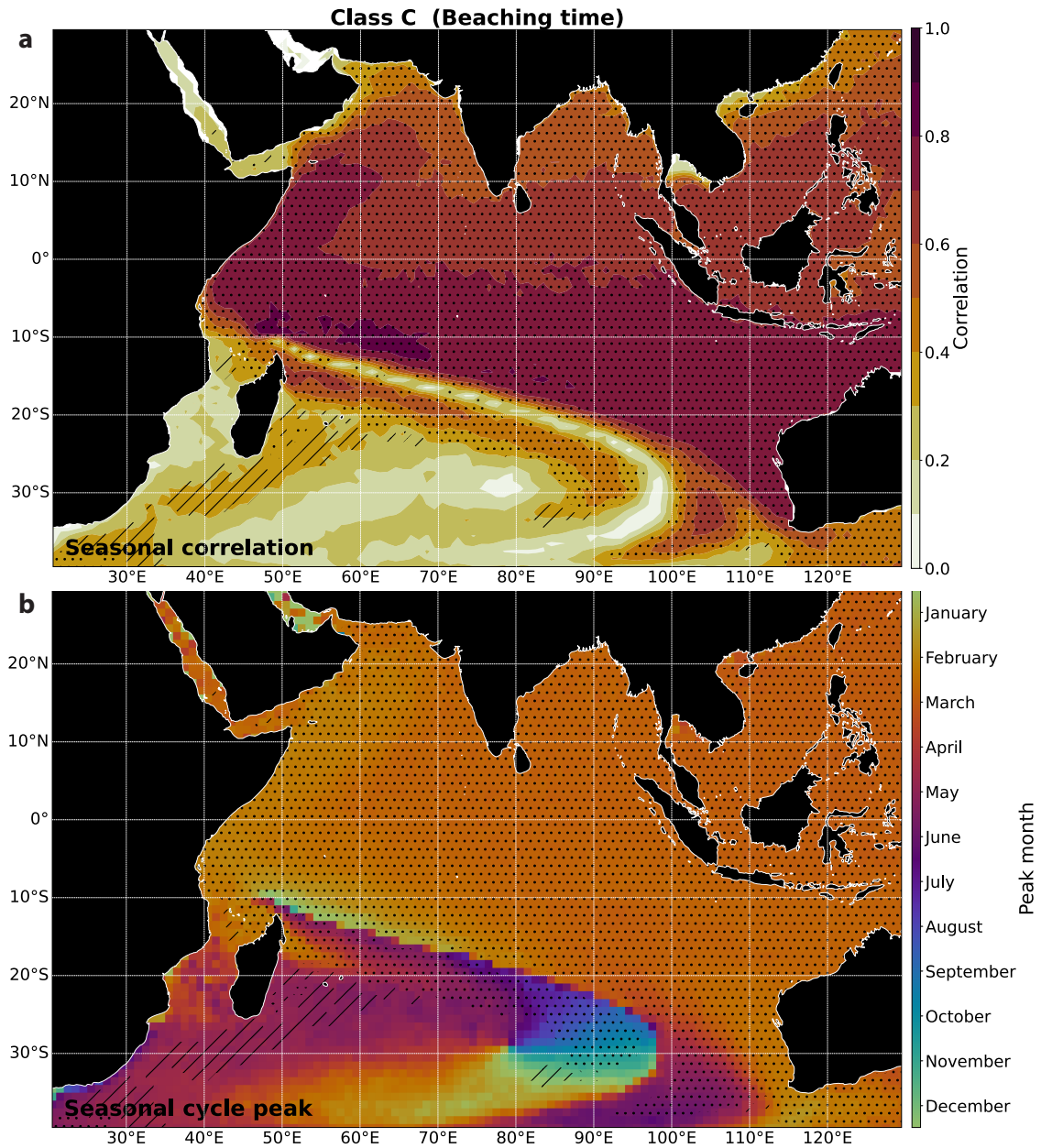


Figure 2.7: (a) Correlation between (log-transformed) time-series of MPP beaching at the Aldabra Group from each cell, and the idealised seasonal cycle extracted from the Fourier spectrum (section 2.2.5.3). Shading indicates that the time-series in a cell correlates with the seasonal cycle significantly, $p < 0.01$ (dotted) and $p < 0.05$ (hatched), taking into account autocorrelation within both the modelled and seasonal time-series (Bretherton et al., 1999). (b) Phase of the seasonal cycle extracted from the Fourier spectrum, in terms of the seasonal cycle peak.

Indian Ocean. Conversely, during the southeast monsoon, strong southeasterly winds blow over the Aldabra Group (figure 1.4) and the source region for Aldabra (on sub-seasonal timescales) shifts to the *southeast* of Aldabra, in the southern

subtropical Indian Ocean. Since winds over the southern Indian Ocean never have a strong northerly component (figure 1.4), there is *no efficient pathway* for Class C debris to reach the subtropical southern Indian Ocean from Indonesia (or other south(east) Asian sources), and therefore no route to Aldabra. As a result, it is improbable for Class C debris from the eastern or northern Indian Ocean to reach Aldabra during the southeast monsoon. This wind-driven mixing barrier can be clearly seen in figure 2.7(b) as the sharp phase discontinuity extending southeastwards from the Aldabra Group.

In this way, the monsoonal winds over the Aldabra Group act as an MPP ‘switch’ for highly buoyant debris, alternating the principal debris source between the SWIO (with minimal debris sources), and the remainder of the basin. The dominance of winds in determining the seasonality of beaching at the Aldabra Group remains valid for Class B debris, but not for Class A debris (figure A.4), where the seasonality instead appears to be dominated by the strength and position of the North Madagascar and South Equatorial Currents. The phase of the Class C seasonal cycle with respect to the Seychelles Plateau (figure A.5) is similar to the Aldabra Group, but due to the more northerly position of the Inner Islands, winds associated with the southeast monsoon do not have as extreme a blocking effect as with the Aldabra Group. Additionally, as hinted at by the greater spatial heterogeneity in figure A.5, remote forcing may play a greater role for MPP beaching at the Inner Islands.

At some remote islands, such as Aldabra, most beaching MPP is actually related to fishing activities rather than terrestrial input (Burt et al., 2020). As a result, the seasonal patterns identified for Aldabra may not necessarily be the same for fishing-related MPP as terrestrial MPP due to the very different input distributions. Monthly beaching rates for ALDFG are given by the quantity $B_j^i(t_b^*)$ (section 2.2.5.2), and are plotted in figure 2.8(a)-(b). This shows that, although peaks are not perfectly aligned with predictions for MPP of terrestrial origin, purse-seine and longline associated MPP beaching at the Aldabra Group will still likely peak during the northwest monsoon or subsequent intermonsoon, and fall to a minimum during the southeast monsoon. Therefore, although there may not be a clearly defined peak of MPP

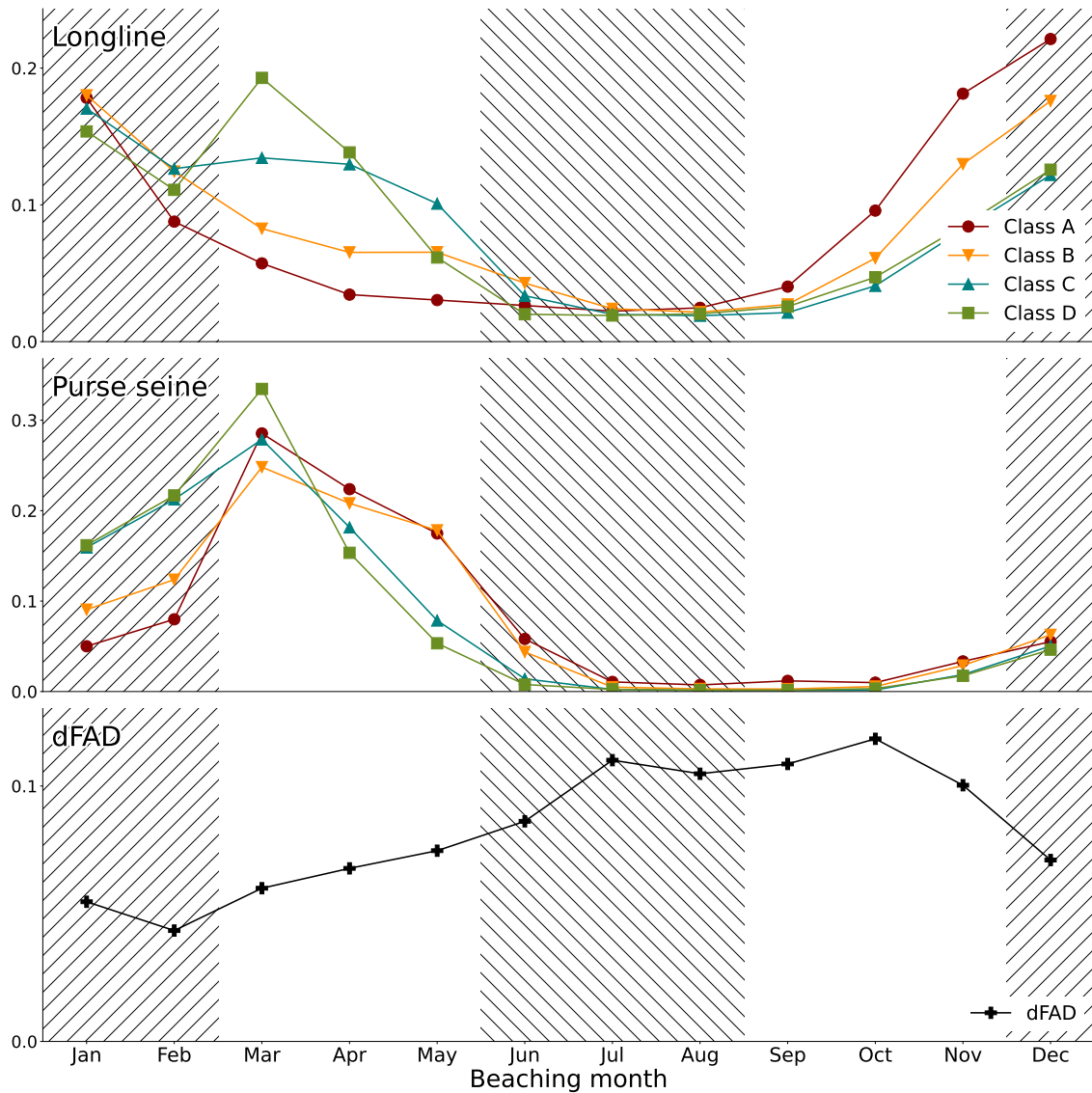


Figure 2.8: (a)-(b) Monthly beaching rate from 1995-2012 at the Aldabra Group for MPP related to (a) longlines and (b) purse-seines, for Class A-D debris. (c) Predicted monthly beaching rate of dFADs, assuming they are not affected by winds or Stokes drift, i.e. follow physical scenario **C0** (Imzilen, 2021).

accumulation at Aldabra in March as suggested by table 2.2, we would still expect MPP accumulation to be significantly enhanced during the northwest monsoon and subsequent intermonsoon, as compared to the southeast monsoon. For fishery-related MPP accumulating at sites across the Seychelles Plateau, our analyses suggest that the seasonal cycle would be similar to the Aldabra Group, but slightly broader and shifted later in the year. This may be due to the more central position of the Seychelles Plateau with respect to intensive fisheries in the WIO, as well as the

seasonality of fishing activities in the region, which is incorporated into these analyses.

It is also possible to investigate the seasonality of the marine-sourced MPP source flux or ‘risk’ ($F_{Ms}^i(x, y, t_s)$, see section 2.2.5.2), i.e. the likelihood that MPP entering the ocean at (x, y) during month t_s eventually beaches at site i . This analysis demonstrates that the risk to remote islands of MPP generation is greater at some parts of the year than others. For instance, our analysis suggests that Class C ALDFG generated by fishing activities throughout most of the Indian Ocean is most likely to beach at the Aldabra Group if it enters the ocean from August to December (figure A.6), indicating that these may be months during which fishing activity is most at risk of generating harmful ALDFG. However, in contrast to the beaching flux, the phase of the seasonal cycle associated with risk is more spatially heterogeneous, indicating that both local and remote forcing drives risk.

2.3.2.3 Interannual variability

Although our analyses suggest that temporal variability in beaching rates at remote islands in the WIO is dominated by seasonal variability from the monsoons, there is still considerable interannual variability (figure 2.6(a)-(b)). Northerly wind anomalies across the southern Indian Ocean are associated with IOD and ENSO events (Yu et al., 2005) and, as described in section 2.3.2.1, the meridional component of winds over the southern Indian Ocean associated with the monsoons appears to be driving the seasonal cycle in beaching rates across Seychelles. We may therefore expect IOD and ENSO phases to amplify the seasonal cycle for highly buoyant MPP beaching at Seychelles, increasing northwest monsoon beaching rates for MPP from Southeast Asia during positive phases, and further suppressing southeast monsoon beaching rates during negative phases.

To test this, we passed marine-sourced MPP beaching flux $F_{Mb}^i(x, y, t_b)$ through a low-pass filter with a cut-off frequency of 1.25 years, to remove intra-annual variability from the signal. We then carried out a lagged correlation of the filtered time-series against the Dipole Mode Index (DMI), an IOD index based on SST gradients across the equatorial Indian Ocean, and NINO3.4, an ENSO index based on mid-Pacific

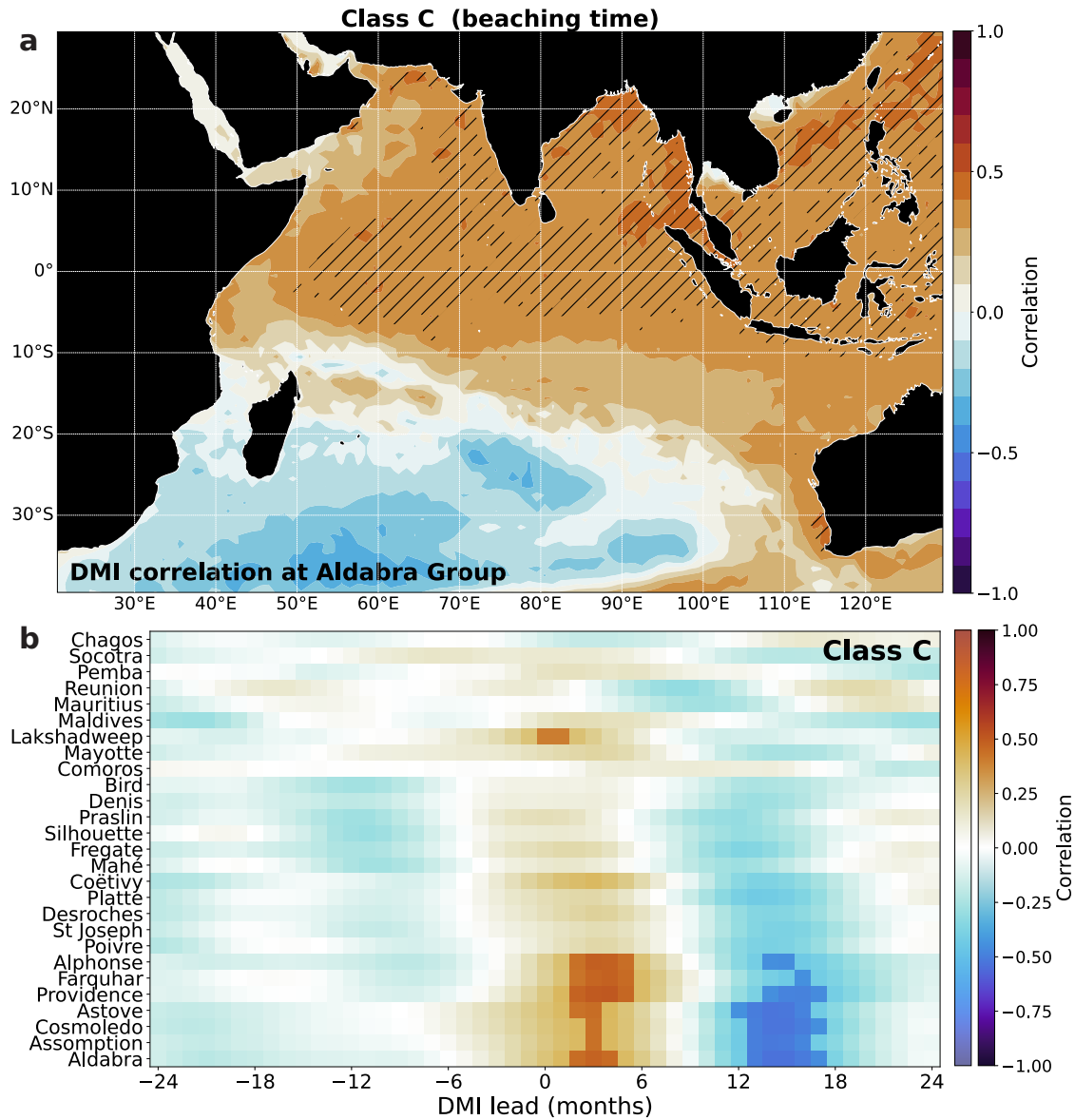


Figure 2.9: (a) Correlation between (log-transformed) time-series of MPP beaching at the Aldabra Group from each cell, and the IOD Dipole Mode Index (DMI). Hatching indicates that the time-series in a cell correlates with DMI ($p < 0.05$), taking into account autocorrelation within both the modelled and DMI time-series (Bretherton et al., 1999). (b) Correlation between the (log-transformed) time-series of MPP beaching at each site investigated in this study, and DMI, as a function of DMI lead time (months). Correlations significant to $p < 0.01$ are shown in bolder colours (the second colour bar).

SST. Figure 2.9(a) shows an analogue of figure 2.7(a) based on correlations of Class C debris beaching rates at the Aldabra Group with DMI. Although correlations are unsurprisingly lower than for the seasonal cycle, interannual variability in Class C beaching rates at Aldabra are correlated with DMI for source sites across much of

the north and northeastern Indian Ocean. Additionally, the spatial pattern of these correlations strongly resembles the pattern in figure 2.7(a) from the seasonal cycle, supporting the hypothesis that the IOD may amplify the seasonal cycle through modulation of meridional winds in the southern Indian Ocean. Figure 2.9(b) shows correlations between the total Class C debris beaching rate at all sites considered in this study, and DMI, as a function of DMI lead time. DMI correlates significantly with beaching rates at islands in the Aldabra, Farquhar, and Alphonse groups, which is expected as these are the same island groups that saw the most dramatic modulation by the seasonal cycle. DMI also correlates most strongly with beaching rates with a lead time of a few months, which supports the hypothesis that the IOD modulates the seasonal cycle as the monsoonal winds also lead peak Class C debris beaching rates (the seasonal cycle peaks in table 2.2 within Seychelles generally occur just after the northwest monsoon, during the subsequent intermonsoon).

Correlation with the NINO3.4 index returns higher correlation coefficients compared to DMI, which is consistent with the partial correlations with the surface wind field given in Yu et al. (2005), as ENSO appears to be associated with stronger meridional wind anomalies closer to Aldabra. However, due to the longer autocorrelation timescale within the NINO3.4 time-series, the correlation of the NINO3.4 index with beaching rates at our study sites was not significant ($p > 0.01$), and are therefore not shown.

2.3.3 Comparison with beached debris observations

2.3.3.1 MPP accumulation at Aldabra

There are few observational estimates for MPP beaching rates. Burt et al. (2020) carried out a five-week clean-up on Aldabra, Seychelles, and estimated that 513.4 tonnes of MPP had accumulated on the island, of which 87.3 tonnes was terrestrial in origin. Annual emissions of MPP into the ocean have increased over time, but our numerical model assumes constant annual MPP emissions at 2015 levels. Through simple assumptions (based on global plastic production rates, and accumulation rates on another island in Seychelles), we estimate that the 87.3 tonnes of terrestrial

MPP that has accumulated at Aldabra corresponds to an annual beaching rate of around 2.9-5.3 tonnes per year, assuming no losses (see section 2.2.7).

Calculating the average annual beaching rate at Aldabra across μ_b^* - μ_s parameter space (from 1999-2014 to allow a longer spin-up for lower values of μ_s) reveals (1) that the beaching rate at Aldabra is relatively insensitive to the parameter μ_b^* in the range $1/\mu_b^* \in [5, 60]$, and (2) that the inferred average bulk beaching flux at Aldabra is most consistent with $100\text{d} < 1/\mu_s < 400\text{d}$, depending on the windage coefficient (figure 2.10). This is not to suggest that all MPP has a sinking rate in this range (μ_s is a variable which depends on MPP composition, geometry, and biofouling rates), but it does indicate that most MPP, by mass, is likely to have a sinking rate on the order of months to a year. This is consistent with the findings of Fazey and Ryan (2016), Kaandorp et al. (2020), and Koelmans et al. (2017). As a result, Class A debris is unlikely to represent a significant fraction of MPP beaching at Aldabra by mass. Additionally, it is also unlikely that most MPP beaching at Aldabra has a sinking timescale of multiple years, since we would expect a significantly greater mass of terrestrial MPP to have accumulated on Aldabra if this were the case.

2.3.3.2 Temporal variability of drifting Fish Aggregating Devices across Seychelles

Drifting Fish Aggregating Devices (dFADs) are buoyant drifters used primarily by purse-seine fisheries to aggregate tuna. The majority of these dFADs are tracked remotely using satellite-transmitting GPS-equipped buoys and, as a result, dFADs are one of the few types of MPP that can be tracked directly from source to sink (Imzilen et al., 2021). Macmillan et al. (2022) identified over 3000 dFAD beaching events across Seychelles, and analysed beaching rates and seasonality. This provides a useful test-case for our trajectory analysis, but the physics of dFAD transport do not correspond well to any of our MPP classes A-C due to their long drogue. As a result, we define ‘dFADs’ as a new Class of MPP with $\mu_s = 1800\text{d}$ (dFADs are large, buoyant, and non-biodegradable), $\mu_b^* = 20\text{d}$ (based on observed beaching rates of dFADs, see appendix A.2), and physical scenario **C0** (surface currents only, Imzilen (2021)). We compute the predicted seasonal distribution of dFAD beachings

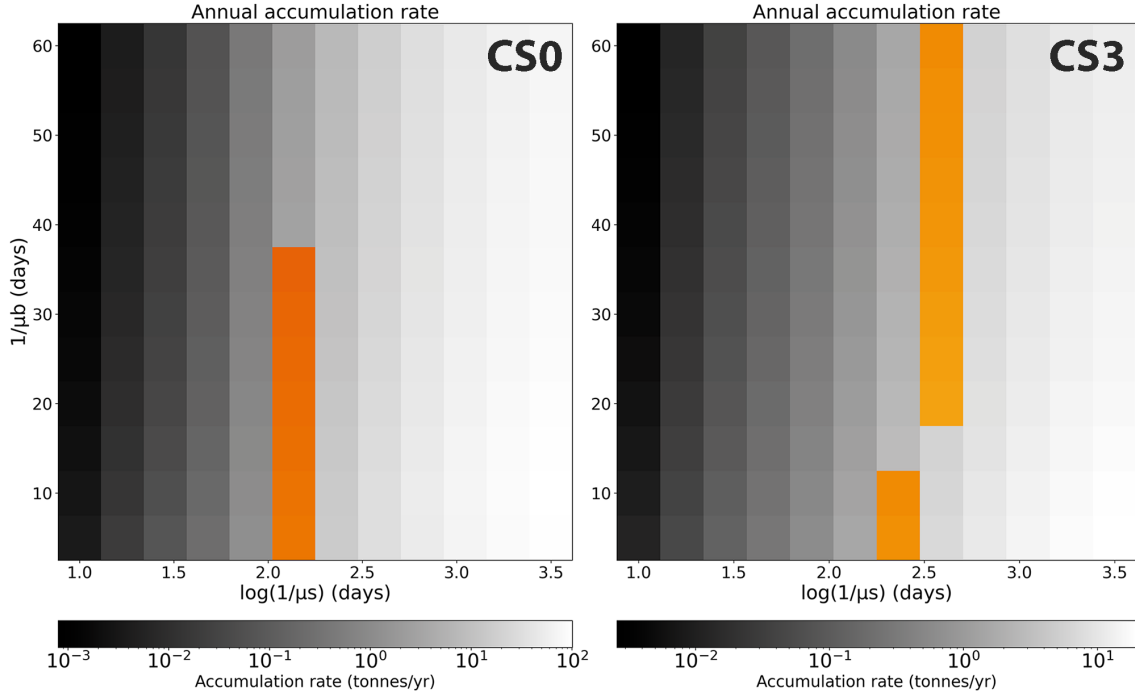


Figure 2.10: Mean annual beaching rate of MPP at Aldabra for physical scenarios CS0 and CS3, as a function of the sinking and beaching rates. The range of accumulation rates consistent with observations at Aldabra (see Section 2.3.3.1) is highlighted in orange.

based on the methodology described in section 2.3.2.2, taking into account the seasonality of dFAD deployments. Our simulations reproduce a relatively muted seasonal cycle of dFAD beachings at Aldabra (figure 2.8(c)) and a pronounced peak in dFAD beaching rates within the Seychelles Plateau during the intermonsoon following the northwest monsoon, both of which correspond well to observations (Isla MacMillan, *personal communication*).

2.3.3.3 Countries of origin for MPP beaching across Seychelles

Aldabra (Seychelles)

In addition to quantifying the total mass of MPP on Aldabra, Burt et al. (2020) identified the origin of 45 PET bottles. In table 2.3, we compare the predicted distribution of countries of origin for Class B and Class C debris beaching at Aldabra, to the distribution of countries of manufacture for intact PET bottles found at Aldabra.

Origin	Class B (%)	Class C (%)	Burt et al. (2020) (%)
China	<0.1	<0.1	46.7
Indonesia	54.5	50.6	13.3
Thailand	<0.1	0.5	8.9
India	0.5	5.3	6.7
Malaysia	0.5	1.6	6.7
Singapore	<0.1	<0.1	4.4
South Africa	<0.1	5.0	2.2
Comoros	20.7	4.4	-
Tanzania	13.1	3.7	-
Philippines	3.8	21.2	-
Madagascar	2.0	0.7	-
Sri Lanka	0.2	2.4	-
Timor-Leste	1.8	1.7	-
Kenya	1.7	0.3	-

Table 2.3: Distribution of countries of origin or manufacture from this study (based on Class B and C MPP) and the sample of 45 PET bottles with intact labels from Burt et al. (2020). Only countries associated with at least 1% of accumulated MPP (this study) or at least 1 bottle (Burt et al., 2020) are included.

For several countries of origin, there is agreement between the two datasets, particularly for Class C debris. Of the 5 largest sources of Class C debris predicted by the model, bottles were found on Aldabra from 3 (Indonesia, India, and South Africa). Indonesia was the largest source of Class C debris in our model, and was the second-largest country of manufacture in the sample from Aldabra. However, there are some significant differences. This in itself is not unexpected. The sample size (45) of PET bottles in Burt et al. (2020) is small, and the sample is likely biased against bottles with longer drift times, as only bottles with intact labels could have their country of manufacture identified. Additionally, the country of manufacture of a bottle is not necessarily the same as the country where a bottle entered the ocean. However, the particular countries associated with model-observation disagreement provide interesting insights into the sources of MPP for Aldabra.

The most obvious discrepancy between the two datasets is China. In our analysis, China was responsible for a negligible proportion of MPP of any class accumulating at Aldabra (<0.1%), but was responsible for the manufacture of almost half of all

bottles actually found on Aldabra. Although our MPP classes may be an imperfect representation of the physics driving PET bottle transport, no realistic combination of μ_b^* , μ_s , or physical scenario results in a significant flux of MPP from China to Aldabra. More likely is an explanation suggested by Duhec et al. (2015), that a large proportion of labelled items from Asia accumulating at beaches in Seychelles were thrown overboard or lost from shipping activities (commercial, leisure, and fishing) in the vicinity of Seychelles. Indeed, this is strongly supported by figure 2.5, which shows that Aldabra is directly downstream of the extremely busy shipping lanes linking SE Asia to the Atlantic. This same explanation could account for the number of bottles found on Aldabra from Thailand and Singapore, both of which were more than an order of magnitude more abundant in the clean-up than our predictions based on trajectory analysis. There is also significant fishing activity by vessels which may be avoiding tracking systems (Welch et al., 2022), so it is possible that these could also account for some of this MPP. Shipping aside, another possibility is that some waste entering the ocean from countries such as Indonesia was manufactured abroad. This could be due to the export of goods for sale and/or the export of waste. Indonesia is a major waste importer, but the main export partners are in Europe and the Americas (Greenpeace East Asia, 2019), so this cannot account for the discrepancies in table 2.3. We do not have data on the proportion of bottled drinks sold in Indonesia (or other identified source countries) which are imports, but imports would have to account for almost all PET bottles sold in these countries to explain the discrepancies in table 2.3. We therefore suggest that disposal at sea is the most likely explanation for the discrepancies we have found.

Disposal at sea cannot, however, explain the absence of bottles from the Philippines amongst PET bottles found at Aldabra relative to our predictions. We suggest the most likely explanation is that the value for μ_b^* diagnosed from drifters based on a global dataset is inappropriate for the complex archipelagic coastline and bathymetry around the Philippines, resulting in our analyses underestimating the local beaching rate for MPP of Philippine origin, and therefore overestimating the quantity of MPP entering the Indian Ocean. It is also possible that Lebreton and Andrady (2019)

overestimated the MPP generated by Philippines, as their estimate is several times larger than earlier estimates by Jambeck et al. (2015). The very long drift time from Philippines (figure 2.4) may also have resulted in most labels degrading.

Alphonse (Seychelles)

Duhec et al. (2015) carried out a six week MPP monitoring program at Alphonse during the southeast monsoon in 2013, and identified the country of origin for plastic and glass bottles (and caps) with intact labels. Duhec et al. (2015) found that 75% of labelled items originated from Southeast Asia (primarily Indonesia and Thailand, although two glass bottles were found from the Philippines), with 13% originating from East Asia (mainly China). In stark contrast to Aldabra, beach clean-ups are carried out regularly on Alphonse, and the survey described by Duhec et al. (2015) *only* included MPP that had beached within the six-week period (rather than MPP that had been accumulating for many years, as at Aldabra). Due to the prediction of a seasonal cycle in beaching rate, it is important to compare these observations at Alphonse to our predictions for the southeast monsoon season, rather than an annual mean. During June-July (the main months during which the survey at Alphonse took place), our analysis suggests that 76.4% of Class C debris beaching at Alphonse originated from Southeast Asia, primarily from Indonesia and the Philippines. As with Aldabra, our results do not predict that Thailand or China are significant sources of MPP, suggesting that most bottles of Thai or Chinese origin beaching at Alphonse likely entered the ocean at sea. Although South Asia is likely a significant source of Class C debris over the course of a year (figure 2.3), only 6.4% of Class C debris expected to beach at Alphonse in June and July originated from India or Sri Lanka. Instead, we expect most of this MPP to accumulate at Alphonse during the northwest monsoon and subsequent intermonsoon, explaining the absence amongst MPP analysed by Duhec et al. (2015), who also predicted this seasonality using backtracking simulations.

In any case, 6 weeks is an insufficient accumulation time to accurately represent MPP sources for remote islands in the WIO. On average, at least half a year of

accumulation is required to reasonably represent the source distribution of Class C debris at Alphonse but, even after a year of accumulation, the relative importance of major MPP sources remain statistically indistinguishable (figure 2.11). This suggests that future observational studies intending to assess sources of MPP for remote islands should either target beaches that are not regularly cleaned, or should monitor MPP accumulation over many years.

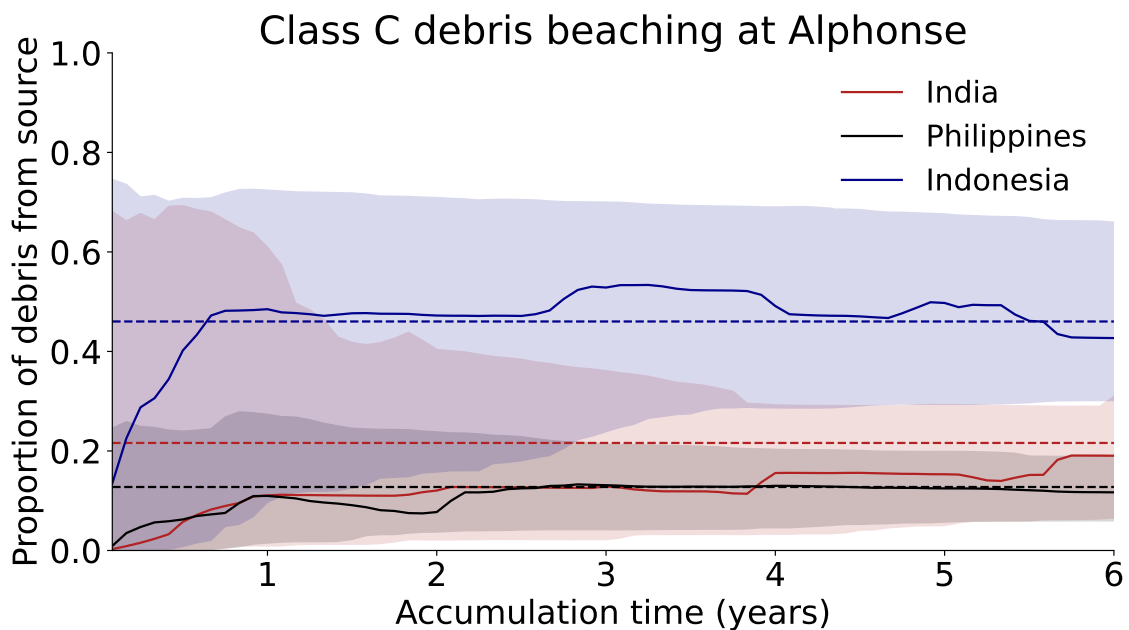


Figure 2.11: Proportion of MPP from three major source countries of Class C debris at Alphonse, as a function of accumulation time. In this analysis, we compute the cumulative proportion of Class C debris beaching at Alphonse from India, Philippines, and Indonesia, across 168 6-year periods between 1993-2014 (e.g. Jan 1993 – Dec 1998, Feb 1993 – Jan 1999, . . . , Jan 2009 – Dec 2014). The bold line shows the median proportion of MPP across the 168 6-year periods, and the shaded region spans the 5th-95th percentile. The horizontal dashed line shows the time-mean proportion of MPP across the 20-year period 1993-2014. The median estimates approach the ‘true’ time-mean value after about 6 months, but the range depending on the starting time of the accumulation period is very large. For instance, the 5th-95th percentile range for Class C debris from India and Indonesia only stop overlapping after around 4 years of accumulation, despite the time-mean flux of Class C debris from Indonesia being more than double that for India.

Outer Islands of Seychelles

Based on a sample of 189 labels found on four islands in Seychelles (Alphonse, Coëtivy, Astove, and Platte), The Ocean Project Seychelles (2019) found that 49%

of labels originated from SE Asia, and specifically noted that the most common countries of origin were Indonesia (26.5%), Mauritius (12%), and Malaysia (10.2%). This is broadly in line with the findings of the other MPP monitoring programmes in Seychelles, although one exception is the large proportion of MPP originating from Mauritius. Given that no other studies assessing sources of MPP in Seychelles noted a large proportion of MPP from Mauritius ($< 4\%$ at Alphonse (Duhec et al., 2015), and there has been no mention at Aldabra (Burt et al., 2020)), it is possible that these items from Mauritius instead originated from nearby ships.

2.4 Conclusions and implications for conservation

Environmental conservation NGOs have been burdened with the task of cleaning up vast quantities of MPP arriving on coastlines across Seychelles and other small island developing states. Observations have suggested that most of these states are not responsible for the bulk of MPP accumulating on their shores, but limited quantitative data are available on sources, hindering management of the issue through source interventions and pursuing the ‘polluter pays principle’. We have provided the first quantitative estimates for the sources of MPP (both terrestrial and marine in origin) across Seychelles, as well as other remote islands in the WIO.

We estimate that a large proportion of MPP beaching at Seychelles has drifted from Southeast Asia (principally Indonesia) and, in the case of the Inner Islands, South Asia (primarily India and Sri Lanka). Since MPP drifting from sources such as Indonesia will have been at sea for at least six months, this also increases the risk of invasive species and pathogen introductions through rafting from the eastern and northern Indian Ocean. These results emphasise the scale of the challenge facing small island developing states such as Seychelles, and underlines the need for multilateral discussions about waste management. Smaller and/or less buoyant MPP fragments may originate from East Africa (mainly Tanzania) and from within Seychelles itself, although these are unlikely to account for most beaching MPP by mass, particularly for the Outer Islands of Seychelles. Our results suggest that Seychelles as a whole is at very high risk from MPP that has been lost from shipping and fisheries in the Indian

Ocean, and that most MPP accumulating at Seychelles from Malaysia, Thailand and, in particular, China, is likely associated with these activities. This prediction could be used to initiate discussions with shipping companies and cruise operators to reduce these sources of marine pollution. We have also found that abandoned, lost or otherwise discarded fishing gear has a high probability of beaching within Seychelles, directly polluting island ecosystems. Beaching purse-seine fragments are likely associated with fishing activity around Seychelles, but longline fragments could feasibly drift from fisheries across the southern Indian Ocean. Greater enforcement by regional governments of MARPOL Annex V (Marine Environment Protection Committee, 2017), forbidding the discharge of fishing gear and other plastics at sea, would reduce these sources of pollution, particularly for Aldabra.

We have also found that there is likely to be significant predictability in MPP accumulation rates across Seychelles, primarily from a strong seasonal cycle dominated by the monsoons. For classes of MPP experiencing a significant push from the winds, our analysis suggests MPP from terrestrial sources and fisheries are most likely to beach at Seychelles (but most significantly the Aldabra, Farquhar, and Alphonse Groups) during the northwest monsoon and subsequent intermonsoon. Beach clean-ups should ideally take place after peak beaching (i.e. May to June for much of Seychelles) to reduce the likelihood of beached plastics breaking down into smaller unmanageable fragments and impacting ecosystems. Due to considerable seasonal and stochastic variability in beaching rates, future observational studies aiming to assess the provenance of MPP beaching at remote islands should either target beaches that are not subject to regular clean-ups, or monitor MPP accumulation over multiple years. We have also proposed a mechanism by which ENSO and the IOD may modulate this seasonal cycle, and have presented some evidence to suggest that beaching rates of high-windage MPP at the more southerly island groups within Seychelles may be greater during and following positive IOD phases. These predictions may be helpful for practitioners deciding when to carry out beach clean-up operations.

There is reasonable agreement between our predictions and the limited quantitative observations of MPP that are available from across Seychelles. Key discrepancies

with observations have highlighted the importance of shipping lanes as a source of MPP for remote WIO islands. Nevertheless, it is important to remember that our trajectory analysis relies on a large number of poorly constrained parameters. There is an urgent need for further studies on the rate of marine macro MPP fragmentation, biofouling, and sinking. Despite the number of MPP modelling studies incorporating windage into simulations and acknowledging the important role it plays in determining drift trajectories, there are limited publicly available estimates of appropriate windage coefficients for common classes of MPP. Additionally, the windage coefficient will likely change with time, as MPP loses buoyancy and/or fragments. We remind the reader that our MPP classes are just examples, rather than validated representatives of bulk MPP properties. Our analyses also lack some processes such as tides and defouling of MPP at depth, with unclear consequences for long-distance MPP transport (Cózar et al., 2014; Deschepper et al., 2019; Suanda et al., 2018). Finally, considerable uncertainty remains in the input function of MPP into the ocean. Nevertheless, a strength of this study is that our results can be easily recomputed for different combinations of sinking rate, beaching rate, and windage so, if improved constraints in the future demonstrate that our classification of MPP (into our four classes A-D) is inappropriate, it will be straightforward to recompute results with the dataset and scripts provided in the associated datasets (table 1.1).

Having investigated the problem of MPP dispersal around remote islands in the WIO, we now turn to the physically related problem of predicting coral reef connectivity. However, since the lifespan of a coral larva is typically considerably shorter than floating MPP (Connolly & Baird, 2010), this first requires higher resolution ocean current predictions than the 1/12° data used in this study. This is the subject of the next chapter.

3

Multidecadal and climatological surface current simulations for the southwestern Indian Ocean

3.1 Introduction

The western Indian Ocean is a relatively data-sparse region. Surface current data are required to simulate the dispersion of buoyant particles such as marine debris or coral larvae (van Sebille et al., 2018), and whilst global products exist that cover the SWIO, derived from satellite altimetry (e.g. Rio et al., 2014) and global ocean reanalyses (e.g. Lellouche et al., 2021), these products are at a coarse resolution relative to the scales of larval dispersal and do not resolve sub-mesoscale dynamics which are thought to be important for larval transport (e.g. Dauhajre et al., 2019; Grimaldi et al., 2022; Monismith et al., 2018). Some higher-resolution models have been run in the SWIO, but these simulations only spanned a limited subset of coral reefs within the region, and are not available on publicly-accessible repositories (Mayorga-Adame et al., 2016, 2017; Miramontes et al., 2019). Our objectives in this chapter were to (1) provide improved estimates of regional surface currents across the tropical SWIO, including at sub-mesoscale, and (2) for use in the coral connectivity studies that follow in chapter 4 and chapter 5. Bridging the gap between the fine-scale dynamics that

dominate in coastal seas, and large-scale ocean currents and mesoscale variability in the high seas, is a major challenge in modelling larval dispersal (Edmunds et al., 2018). Future developments in unstructured ocean models, and improvements in the availability of computational resources, will be invaluable in addressing these challenges. However, for this study, we used a $1/50^\circ$ (~ 2 km) configuration of a regional (structured) ocean model to simulate circulation in the SWIO, which we call the **W**estern **I**ndian Ocean **S**imulation (WINDS). Here, we provide a full description of WINDS and the two experiments we ran using the configuration, and validate WINDS as relevant for buoyant Lagrangian particle tracking applications.

3.2 Methods

3.2.1 Numerics

We ran WINDS using version 1.1 of the Coastal and Regional Ocean Community Model (Auclair et al., 2019), coupled with the XIOS2.5 I/O server for writing model output (<https://forge.ipsl.jussieu.fr/ioserver>). WINDS uses a nonlinear equation of state (Jackett & McDougall, 1995; Shchepetkin & McWilliams, 2003) with a 3rd-order upstream biased scheme for lateral momentum advection, a split-and-rotated 3rd-order upstream biased scheme for lateral tracer advection, a 4th-order compact scheme for vertical momentum advection, and a 4th-order centred scheme with harmonic averaging for vertical tracer advection. Lateral momentum mixing is achieved through a Laplacian Smagorinsky parameterisation (Smagorinsky, 1963), and a Generic Length Scale $k - \epsilon$ scheme is used for vertical mixing (Jones & Lauder, 1972). A bulk formulation is used for surface turbulent fluxes (COARE3p0) with current feedback (relative wind stress) enabled. The configuration uses radiative boundary conditions for forcing at the lateral boundaries (including non-tidal and tidal SSH, barotropic tidal currents and baroclinic non-tidal currents, and temperature and salinity). A 10-point cosine-shaped sponge layer is also used at the lateral boundaries for tracers and momentum. Bottom friction is implemented using quadratic friction with a log-layer drag coefficient, with $z_{0,b} = 0.02$ m, and $0.002 \leq C_d \leq 0.1$ (limits

chosen for numerical stability). We used a baroclinic time step of 90 s, with 60 barotropic steps per baroclinic step (Shchepetkin & McWilliams, 2005).

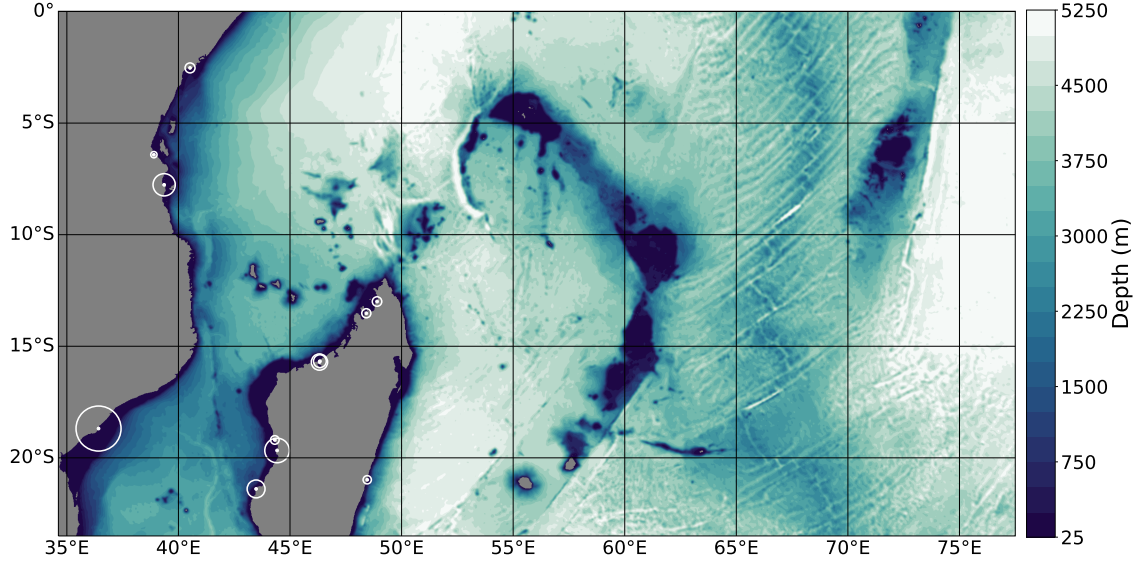


Figure 3.1: The entire WINDS domain, with contours representing the bathymetry used in WINDS. Circles represent the 12 rivers included in WINDS, scaled by the total annual discharge (Dai & Trenberth, 2002).

3.2.2 Model grid

We built the model grid using `CROCO_TOOLS` with longitudinal limits $34.62^\circ \text{ S} - 77.5^\circ \text{ E}$, latitudinal limits of $23.5^\circ \text{ S} - 0^\circ \text{ N}$, and a specified horizontal resolution of $1/50^\circ$ (figure 3.1). The western boundary of the domain is entirely land (East Africa). We chose this domain as it spans almost all coral reefs in the SWIO, as well as the Chagos Archipelago, allowing connectivity between the Chagos Archipelago and the rest of the SWIO to be investigated. A small number of coral reefs south of 23.5° S (in southernmost Madagascar and South Africa) are therefore excluded, but this was necessary to keep computational and storage requirements tractable. To maintain roughly even dimensions of grid cells across the domain, `CROCO_TOOLS` adjusts the meridional resolution of cells away from the equator, so the true meridional resolution of grid cells at the southern boundary of the WINDS domain is slightly finer, at around $1/55^\circ$. The horizontal resolution of WINDS is therefore approximately 2 km, but actually ranging from 2.04 km at the southern boundary, to 2.22 km at the equator.

CROCO uses a terrain-following (s-coordinate) grid in the vertical. We used 50 vertical layers in WINDS, using a vertical stretching scheme that improves the resolution at the surface and bottom boundary layers, defined by the parameters $\theta_s = 8$, $\theta_b = 2$, and $h_c = 100\text{m}$ (see the CROCO documentation for the technical explanation of these parameters). Since s-coordinates are terrain (and sea-surface) following, translating s-coordinates to depth depends on the local ocean depth and the sea-surface height. The minimum and maximum ocean depth permitted in WINDS is 25 m and 5250 m respectively. For water depth of 25 m and $\eta = 0$ m, the vertical resolution is 0.40 m at the surface, 0.67 m at the sea-floor, and the coarsest vertical resolution within the water column is 0.74 m. For water depth of 5250 m, the vertical resolution is 2.07 m at the surface, 280 m at the sea-floor, and the coarsest vertical resolution within the water column is 353 m. As a result, WINDS provides excellent vertical resolution within the upper water column, particularly in shelf seas where coral reefs are.

3.2.3 Bathymetry

We used GEBCO 2019 (GEBCO Compilation Group, 2019) as the basis for the bathymetry in WINDS. The nominal horizontal resolution of GEBCO 2019 is 15 arc-seconds (approximately 500 m) but, due to the lack of in-situ bathymetry measurements in the SWIO, most bathymetry in this region is satellite-derived, with a practical resolution of around 6 km (Tozer et al., 2019). Although these satellite-derived measurements are relatively well validated, there are problems in areas of extensive continental shelves and steep bathymetry (Tozer et al., 2019). These problems are quite dramatic in the SWIO. For instance, through comparison with Admiralty hydrographic navigation charts with in-situ soundings, we found local bathymetry errors in excess of 1 km around Aldabra Atoll, Seychelles, and a large number of erroneous ‘islands’ across Seychelles, which are in reality in significant water depth. Unfortunately, the only real solution to this lack of data is obtaining more in-situ bathymetric readings (e.g. see <https://seabed2030.org/>). However, to somewhat mitigate the most extreme errors in the SWIO, we carried

out two preprocessing steps of the GEBCO 2019 dataset. We firstly digitised all point-depth soundings from Admiralty Chart 718 (Islands North of Madagascar), including Aldabra, Assomption, Cosmoledo, Astove, and Îles Glorieuses, and then linearly gridded these data-points onto a regular 15 arc-second grid, carrying out necessary tidal adjustments, before linearly blending these grids with the rest of the GEBCO 2019 grid across a length-scale of 10-30 km. Secondly, to remove erroneous ‘islands’, we generated a land-sea mask at the GEBCO 2019 resolution from the highest resolution version of the GSHHG shoreline database (Wessel & Smith, 1996). We then set the depth of all false land cells (i.e. land according to GEBCO, ocean according to GSHHG) to 25 m. Although this minimum depth of 25 m is not realistic, it is a considerable improvement over a large number of fake islands, and a minimum depth of around 25 m is required for numerical stability at this resolution by CROCO anyway. As a final processing step, we carried out smoothing of bathymetry using CROCO_TOOLS, with a target $\nabla h/h \leq 0.25 \text{ m}^{-1}$, to improve model stability, and reduce pressure-gradient errors in regions of steep bathymetry. The bathymetry and associated grid parameters used in all WINDS simulations can be found in the `croco_grd.nc` file in the associated datasets, and is shown in figure 3.1.

3.2.4 Experiments: WINDS-C and WINDS-M

WINDS is forced at the surface through a bulk formulation based on ERA-5 (Hersbach et al., 2020), and at the lateral boundaries with the 1/12° GLORYS12 global ocean reanalysis (Lellouche et al., 2021) and tides (Egbert & Erofeeva, 2002). To investigate the importance of interannual variability in circulation in the SWIO, we ran two experiments within WINDS. The first, WINDS-C, is based on a monthly climatology computed from ERA-5 and GLORYS12 from 1993-2018. The second, WINDS-M, is based on hourly forcing from ERA-5 and daily forcing from GLORYS12 from 1993-2019, plus an additional year (2020) based on the associated 1/12° global ocean analysis (the reanalysis product for 2020 was not available at this point). It is important that WINDS-M spans multiple decades, to fully incorporate the effects of multidecadal variability in surface circulation, and therefore dispersal (Thompson

et al., 2018). WINDS-C was run after a 4-year spin-up, and WINDS-M was run from the end state of WINDS-C. WINDS-C and WINDS-M are otherwise identical.

3.2.5 Surface forcing

Surface forcing is parameterised using a bulk formulation based on the ERA-5 global atmosphere reanalysis (Hersbach et al., 2020) at hourly (WINDS-M) or monthly climatological (WINDS-C) temporal resolution, using the following fields, bilinearly interpolated to the WINDS grid: surface air temperature (`t2m`); sea-surface temperature (`sst`); sea-level pressure (`msl`); 10 m wind speed (`u10`, `v10`); surface wind stress (`metss`, `mntss`); specific humidity (`q`); relative humidity (`r`); precipitation rate (`mtpr`); shortwave radiation flux (`msnswrf`); longwave radiation flux (`msnlwrf`); and downwelling longwave radiation flux (`msdwlwrf`).

Since ERA-5 is computed on a different (coarser) grid to WINDS, there is a land-sea mask mismatch between ERA-5 and WINDS. To avoid terrestrial values erroneously being applied to ocean cells in WINDS, we masked land values from ERA-5 using the ERA-5 land-sea mask, and carried out a nearest-neighbour interpolation over the small number of coastal WINDS cells that are counted as land cells in ERA-5.

3.2.6 Lateral forcing

3.2.6.1 Ocean currents

WINDS is forced at the lateral boundaries with the 1/12° GLORYS12 global ocean reanalysis, using daily-mean (WINDS-M) or monthly-climatological (WINDS-C) depth-varying ocean current velocities, sea-surface height, temperature, and salinity. GLORYS12 was run using tides and, as a result, we do expect there to be aliased tidal signals remaining in the daily-mean sea-surface height fields. However, we computed that the amplitude of the strongest aliased tidal signals (both SSH and currents) should be at least 20× smaller than the true tidal signals, and frequency shifted to a period of 10–30 days. As a result, we do not expect that any remnant tidal signals in GLORYS12 will have any significant effect on tides in WINDS.

3.2.6.2 Tides

WINDS is forced at the lateral boundaries with 10 tidal constituents (barotropic tidal currents and surface height) from the TPX09-atlas (Egbert & Erofeeva, 2002): M_2 , S_2 , N_2 , K_2 , K_1 , O_1 , P_1 , Q_1 , Mf , and Mm .

3.2.7 Rivers

We have simplistically included 12 major rivers in WINDS: the Zambeze, Rufiji, Tsiribihina, Mangoky, Ikopa, Betsiboka, Tana, Mahavavy Nord, Sambirano, Manambolo, Mananjary, and Ruvu rivers. We assume that water in the river-mouth area has a constant temperature of 25°C and a salinity of 15PSU, with monthly climatological discharge set according to Dai and Trenberth (2002). These riverine fluxes enter the ocean through the nearest ocean cell to the river mouth, set through inspection from satellite imagery (Google Earth). The location and annual-mean discharge of these rivers is shown in figure 3.1.

3.3 Data Records

We have made three sets of output available from WINDS:

30 minute output frequency

Zonal surface velocity (`u_surf`); meridional surface velocity (`v_surf`)

1 day output frequency

Sea-surface temperature (`temp_surf`); sea-surface salinity (`salt_surf`); free-surface height (`zeta`); depth-averaged velocity (`u_bar`, `v_bar`); kinematic wind stress (`wstr`); surface momentum stress (`sustr`, `svstr`); surface freshwater flux, E-P (`swflx`); surface net heat flux (`shflx`); net shortwave radiation at surface (`radsw`); net longwave radiation at surface (`shflx_rlw`); latent heat flux at surface (`shflx_lat`); and sensible heat flux at surface (`shflx_sen`).

5 day output frequency

Velocity (**u**, **v**); temperature (**temp**); and salinity (**salt**).

We did not output the vertical velocity. This can be reconstructed at a 5 d frequency using the ocean depth, free-surface height, and zonal and meridional velocities.

3.4 Technical Validation

The following validation relates to WINDS surface properties only, as relevant for marine dispersal, since this was the primary use case WINDS-M and WINDS-C were run for. WINDS may, of course, be used for other purposes as well, but for these applications the model is provided *as is*. This validation focuses on WINDS-M, since WINDS-C is a control simulation which is not expected to fully reproduce observations as it is driven by low-frequency (monthly) climatological forcing.

3.4.1 Tides

Table 3.1 shows a comparison of WINDS tidal predictions with in-situ tidal gauges spanning the longitudinal and latitudinal range of WINDS, at Mombasa (Kenya), Aldabra (Outer Islands, Seychelles), Mahé (Inner Islands, Seychelles), Diego Garcia (Chagos Archipelago), and Mauritius and Rodrigues (Mauritius). This comparison demonstrates that WINDS can reproduce in-situ tidal predictions well, particularly at remote islands away from extensive continental shelves.

3.4.2 Surface currents

Figures 3.2 – 3.4 compare monthly climatological surface currents averaged across 1993–2020 from WINDS-M (left); surface currents from 1993–2020 from Copernicus GlobCurrent, combining altimetric geostrophic currents with modelled Ekman currents (centre, Rio et al. (2014)); and near-surface currents estimated from the Global Drifter Program (GDP) using drifter trajectories from 1979–2015 (right, Laurindo et al. (2017)). Both products used for comparison are entirely independent of WINDS. These figures demonstrate that WINDS successfully captures the location

Site/Constituent	Amplitude (cm, WINDS)	Amplitude (cm, observed)
Mombasa (Kenya)		
M_2	102.8	105.5
S_2	46.7	52.1
N_2	17.8	20.1
K_1	20.8	19.1
O_1	10.5	11.3
Aldabra (Seychelles)		
M_2	94.0	93.3
S_2	47.4	46.0
N_2	16.5	17.4
K_1	16.4	16.3
O_1	8.9	10.0
Mahé (Seychelles)		
M_2	41.8	40.7
S_2	19.6	18.1
N_2	8.4	8.7
K_1	18.6	18.7
O_1	9.1	10.7
Diego Garcia (Chagos)		
M_2	47.6	49.3
S_2	28.2	28.5
N_2	8.7	8.9
K_1	3.6	3.8
O_1	3.3	3.9
Rodrigues (Mauritius)		
M_2	41.3	40.0
S_2	22.8	25.5
N_2	8.1	-
K_1	5.9	5.0
O_1	3.3	-
Mauritius (Mauritius)		
M_2	25.6	26.0
S_2	14.2	15.8
N_2	5.2	-
K_1	6.0	6.1
O_1	2.5	-

Table 3.1: Observational sources: Pugh (1979) (Mombasa, Aldabra, and Mahé); Lowry et al. (2009) (Rodrigues and Mauritius); Dunne (2021) (Diego Garcia). A hyphen (-) indicates that no value was reported in the data source.

and velocity associated with major ocean currents in the SWIO such as the Southern Equatorial Current, Southern Equatorial Countercurrent, North Madagascar Current, East Madagascar Current, and East African Coastal Current e.g. Schott et al., 2009, as well as their seasonal variability. For instance, WINDS reproduces the observed strengthening of surface currents associated with the North Madagascar Current during the southeast monsoon (June-August), which can instantaneously reach 2 m s^{-1} , in accordance with in-situ observations (Swallow et al., 1988; Voldsund et al., 2017). The East African Coast Current (EACC) also correctly strengthens dramatically during the southeast monsoon, reaching speeds of up to (and sometimes exceeding) 2 m s^{-1} , in agreement with observations (Painter, 2020; Swallow et al., 1991). The strongest surface currents in the EACC are simulated by WINDS to be close to the equator, and can instantaneously reach 3 m s^{-1} . We are not aware of observational evidence supporting such strong surface currents within the EACC. There is a discrepancy between the strength of surface currents simulated by WINDS and predicted by GlobCurrent for the South Equatorial Countercurrent close to the equator (e.g. see figure 3.4, November). However, this is unsurprising as GlobCurrent uses geostrophic currents, which are not defined at the equator. Agreement between WINDS and GDP-derived surface velocities are much better in this region, with WINDS reproducing observations of zonal surface currents in excess of 1 m s^{-1} , particularly towards the east of the WINDS domain (Schott & McCreary, 2001; Shao-Jun et al., 2012).

To assess the ability of WINDS to reproduce surface current variability associated with eddies, figure 3.5 compares the eddy kinetic energy (EKE) in WINDS and Copernicus GlobCurrent (high-frequency surface currents are not available from the Global Drifter Program), as well as 8 moorings from the RAMA array (Beal et al., 2019; McPhaden et al., 2009). The spatial pattern in EKE is similar between WINDS and Copernicus GlobCurrent, with both products returning high EKE associated with mesoscale eddy activity in the Mozambique Channel, around Mauritius and Réunion, in the wake of the Mascarene Plateau, and near the equator. EKE is generally higher

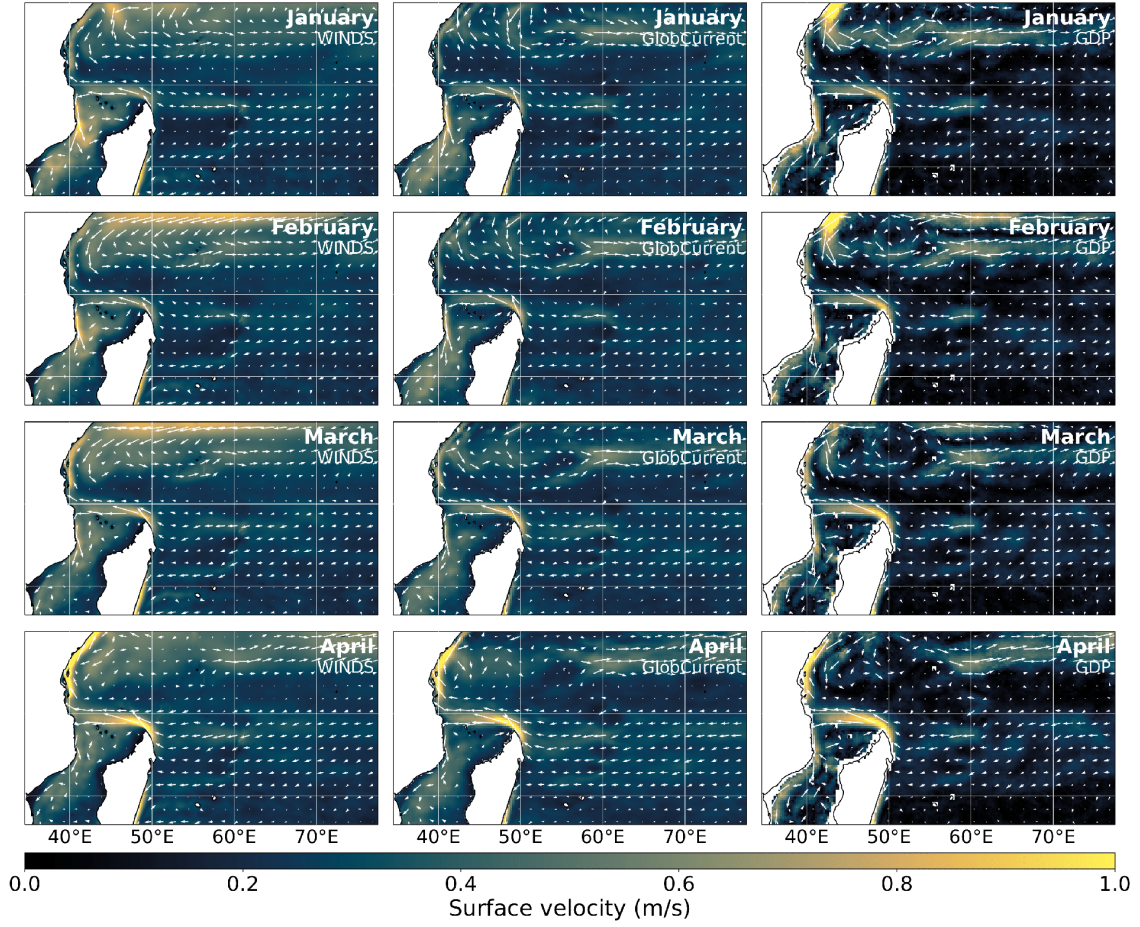


Figure 3.2: Monthly climatological surface currents (1993-2020) from WINDS (left), Copernicus GlobCurrent Surface (centre), and Global Drifter Program derived near-surface currents (right) for January to April.

in WINDS than Copernicus GlobCurrent, although this is likely in part due to finer-scale turbulence simulated by WINDS, which will not be captured by Copernicus GlobCurrent. Compared to in-situ observations at RAMA array moorings, WINDS and Copernicus GlobCurrent tend to respectively overestimate and underestimate EKE. The RAMA time-series is considerably shorter than WINDS-M, and most moorings do not record equal coverage across the seasonal cycle. However, there does not appear to be a strong seasonal cycle in EKE in most regions, so it is unlikely that this explains the systematically higher EKE in WINDS compared to RAMA. The currents measured at RAMA are also measured at a slightly greater depth (10/12 m) than WINDS (0-2 m). Nevertheless, this does suggest that eddies may be too energetic in WINDS. On the other hand, the variability of daily sea-surface

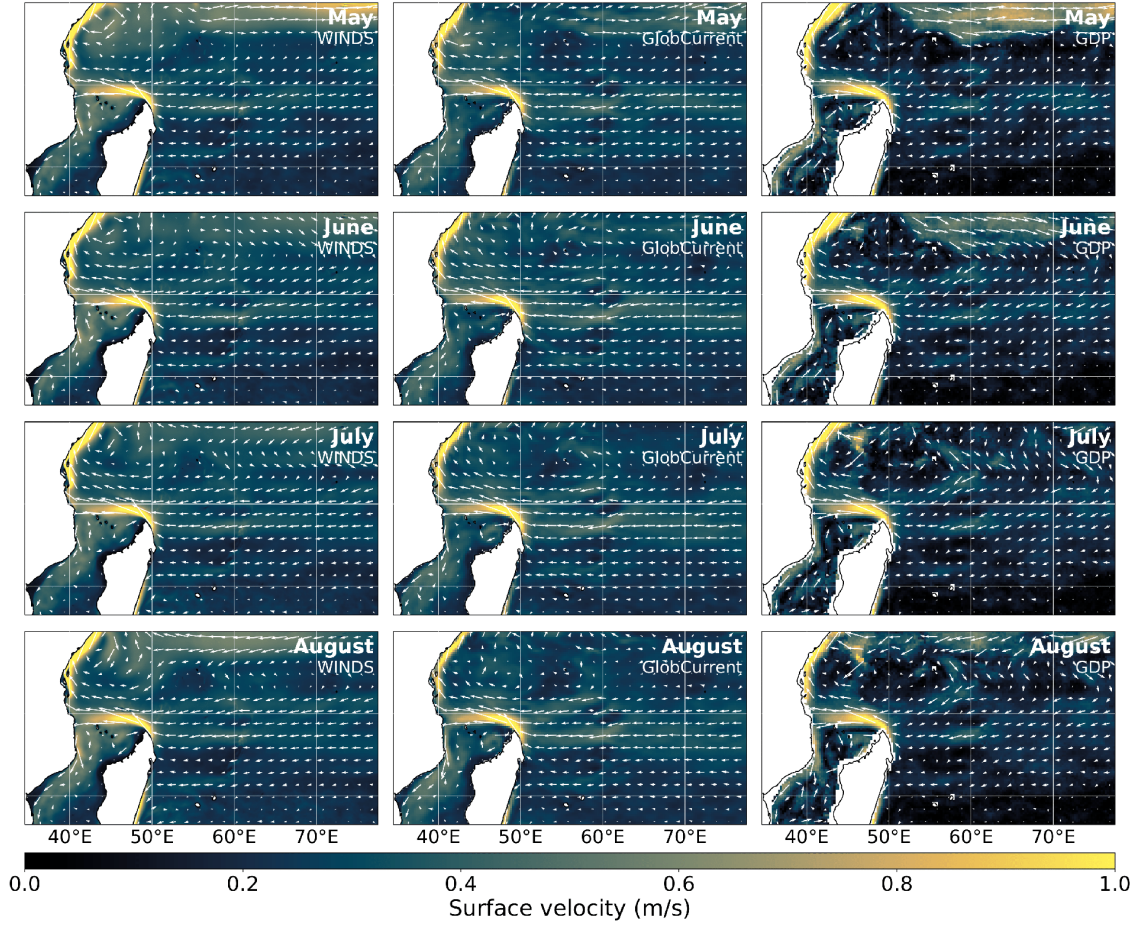


Figure 3.3: Monthly climatological surface currents (1993-2020) from WINDS (left), Copernicus GlobCurrent Surface (centre), and Global Drifter Program derived near-surface currents (right) for May to August.

height (figure 3.6), and therefore geostrophic surface currents, agrees very well with observations. This suggests that, at least away from the equator, mesoscale eddy activity is reasonably reproduced in WINDS.

The monthly mean surface current speed in WINDS associated with major surface currents in the SWIO is shown in figure 3.7, compared to a $1/12^\circ$ global ocean reanalysis (CMEMS GLORYS12) and Copernicus GlobCurrent. Particularly strong agreement between GLORYS12 and GlobCurrent is expected as the former is an assimilative model, but agreement is generally very good between all three products. One notable exception is the western South Equatorial Countercurrent, where current variability often appears to be greater in WINDS than GLORYS12

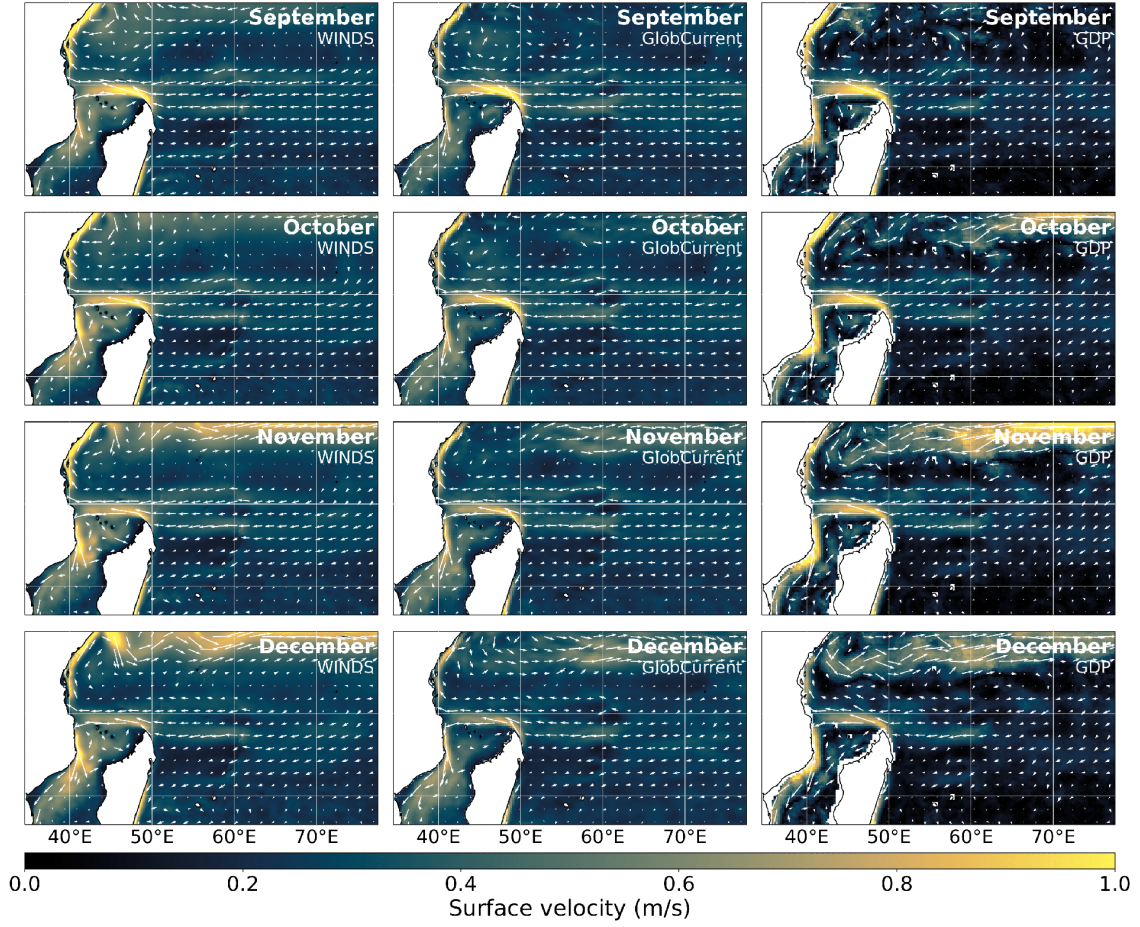


Figure 3.4: Monthly climatological surface currents (1993-2020) from WINDS (left), Copernicus GlobCurrent Surface (centre), and Global Drifter Program derived near-surface currents (right) for September to December.

and GlobCurrent (which is also reflected in EKE derived from RAMA moorings in figure 3.5). The seasonal cycle is also amplified in the NW Mozambique Channel in WINDS compared to GLORYS12 and GlobCurrent. Very high surface current speeds have been observed in this region from in-situ observations (Ridderinkhof et al., 2010), but it is not clear whether the stronger seasonality simulated by WINDS is real or an artefact. Although the seasonal monsoonal cycle dominates many of the time-series in figure 3.7, it is also clear that there is considerable interannual variability. This is generally reproduced very well by WINDS, but the magnitude of interannual variability is occasionally larger in WINDS than GLORYS12 or GlobCurrent.

As WINDS was designed for the primary purpose of simulating marine dispersal (for instance, for coral larvae), it is important to test whether WINDS can reproduce

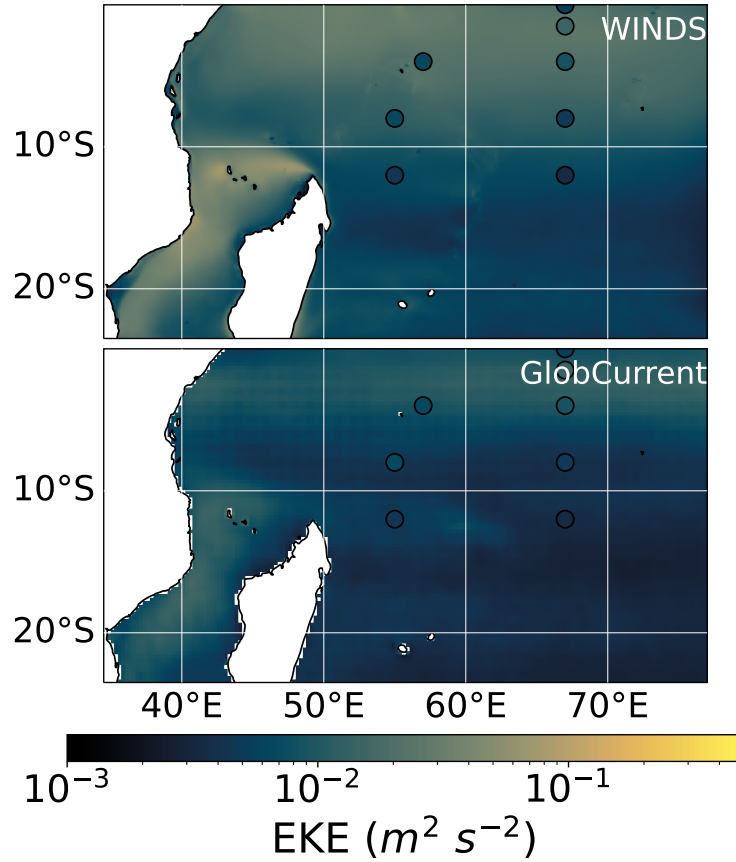


Figure 3.5: Eddy kinetic energy (EKE) from WINDS (top) and Copernicus GlobCurrent (bottom). EKE was computed by passing daily-mean surface velocity through a high-pass filter with a cut-off period of 30 days, thereby removing high-frequency variability associated with tides, and low-frequency variability associated with time-mean currents and the seasonal cycle. Circles represent the EKE at 10/12 m depth from the RAMA array.

observed pathways of surface drift in the ocean. Although Global Drifter Program (GDP) deployments are low in the SWIO (Lumpkin & Centurioni, 2019), sufficient drifters have passed through the region to evaluate first-order dispersal pathways simulated by WINDS. We released a large number of virtual Lagrangian particles at coral reef sites around 6 islands and banks within the WINDS domain on the 1st, 11th, and 21st of each month from 1993-2019, and advected them for 120 days following WINDS-M surface currents using OceanParcels (Lange & van Sebille, 2017), with a Runge-Kutta 4th order scheme and a time-step of 10 minutes. Figure 3.8 shows the proportion of these virtual particles that passed through each $0.5^\circ \times 0.5^\circ$ grid cell at least once within 120 days, overlaid with GDP drifter trajectories for

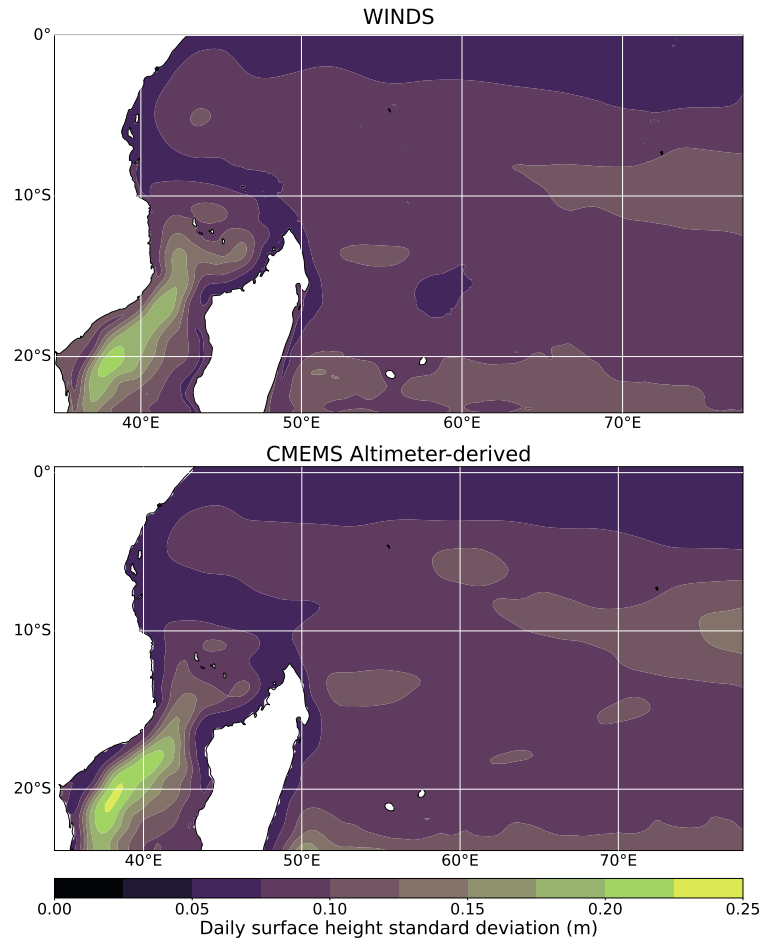


Figure 3.6: Variability of sea-surface height from 1993-2020 from WINDS (top) and the CMEMS Global Ocean Reprocessed Gridded L4 sea-surface Height product (bottom), computed as a standard deviation.

(up to) 120 days after their nearest approach to release sites. Although the Global Drifter Program sample size is small in some cases, agreement between observed drifter trajectories and WINDS is generally excellent, with observed trajectories usually confined to the ‘high-probability’ regions predicted by WINDS. Notable exceptions include some GDP drifters that travelled further eastward within the South Equatorial Countercurrent from Mayotte and Zanzibar than predicted by WINDS, and less zonal confinement within the South Equatorial Current for GDP drifters travelling westwards from the Chagos Archipelago as compared to WINDS. These trajectories are physically possible within WINDS, but improbable. Surface currents associated with the South Equatorial Countercurrent in WINDS are generally at least as strong as those diagnosed from GDP drifters (Figures 3.2-3.4), so the possible

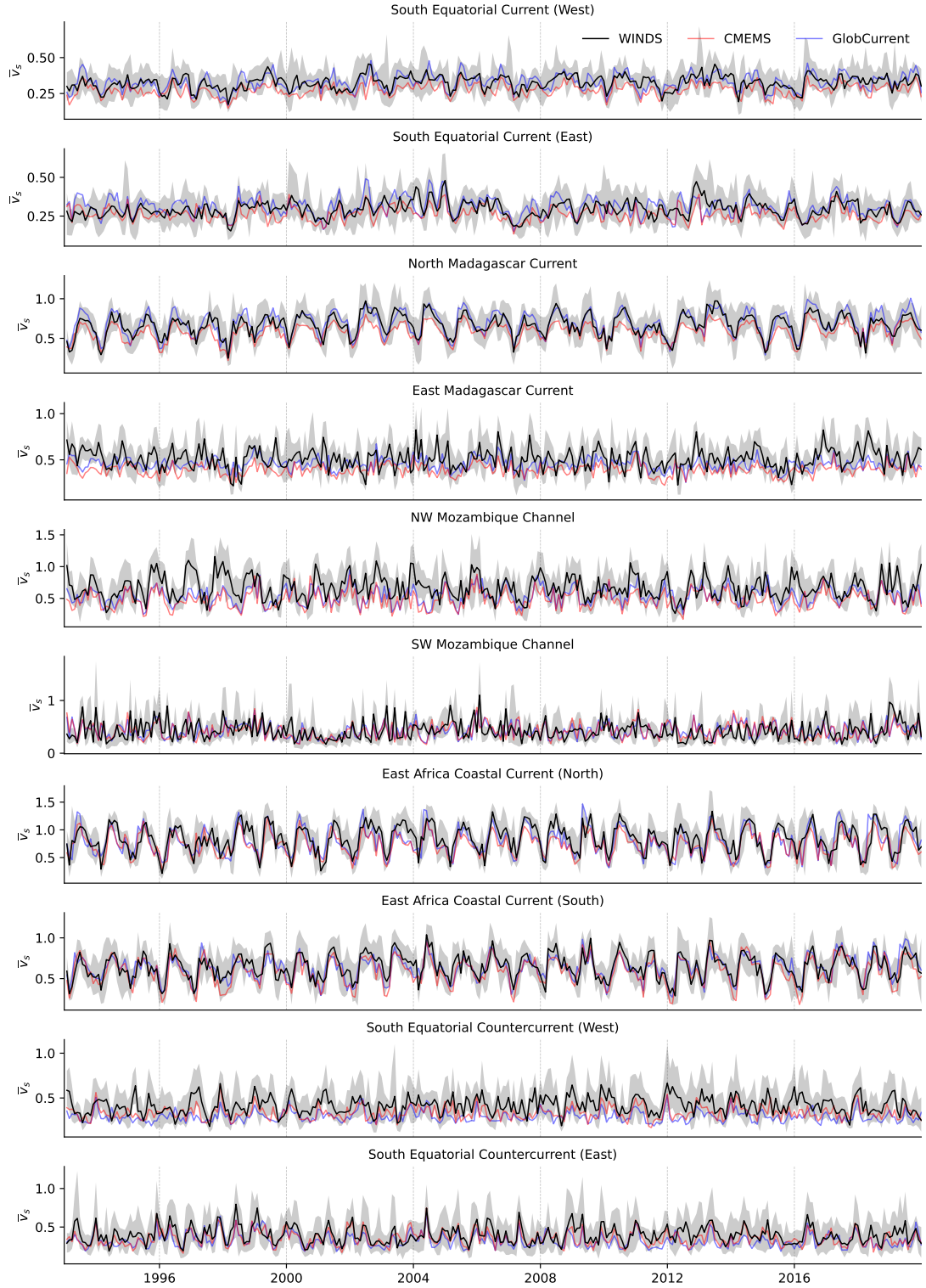


Figure 3.7: Monthly mean surface currents averaged across ten key regions for WINDS (black, with grey shading representing the monthly range), CMEMS GLORYS12 (red), and GlobCurrent (blue).

underprediction of eastward surface transport is instead likely due to the WINDS domain ending at the equator. In our Lagrangian analysis, any virtual particles crossing the equator are removed, so many virtual particles may be unable to enter the South Equatorial Countercurrent. For instance, most GDP drifters in figure 3.8 that travelled a significant distance within the South Equatorial Countercurrent passed the equator at least once. It is nevertheless possible that WINDS underestimates surface connectivity between the East Africa Coastal Current and the South Equatorial Countercurrent, as one GDP drifter followed a relatively direct pathway from Zanzibar to the Seychelles Plateau, which was improbable in WINDS. It is important to note that GDP drifters are drogued and have some wind exposure due to the buoy, and may therefore experience forces from winds, waves and subsurface currents which will not be captured by WINDS.

Long-distance dispersal patterns predicted by WINDS are similar to those predicted by the CMEMS GLORYS12 $1/12^\circ$ global ocean reanalysis (not shown), and, given the relatively small sample size of GDP drifters in the region, it is not clear which product performs better over these very large distances. Indeed, this is expected, as the $1/12^\circ$ horizontal resolution of GLORYS12 is likely sufficient to resolve the main processes relevant to the large-scale surface circulation in the Indian Ocean. The real potential advantage of WINDS is at finer scales, which is particularly important for local applications, or for modelling the dispersal of substances with a lifespan on the order of days to weeks (rather than months or longer), such as coral larvae (Connolly & Baird, 2010). For instance, figure 3.9 shows simulated trajectories of 25 virtual surface-confined particles, perhaps representing coral larvae, released from analogous reef sites in southern Zanzibar, Tanzania, in WINDS-M and GLORYS12, at the same time on July 1st 2019. Perfect agreement between the two is *not* expected as (i) WINDS is not assimilative and (ii) there was likely limited observational data available for assimilation in this region in the first place. However, it is clear from this figure that the representation of the coast and islands is significantly improved in WINDS relative to GLORYS12 (due to the more than four-fold increase in horizontal resolution). The approximately 2 km resolution of

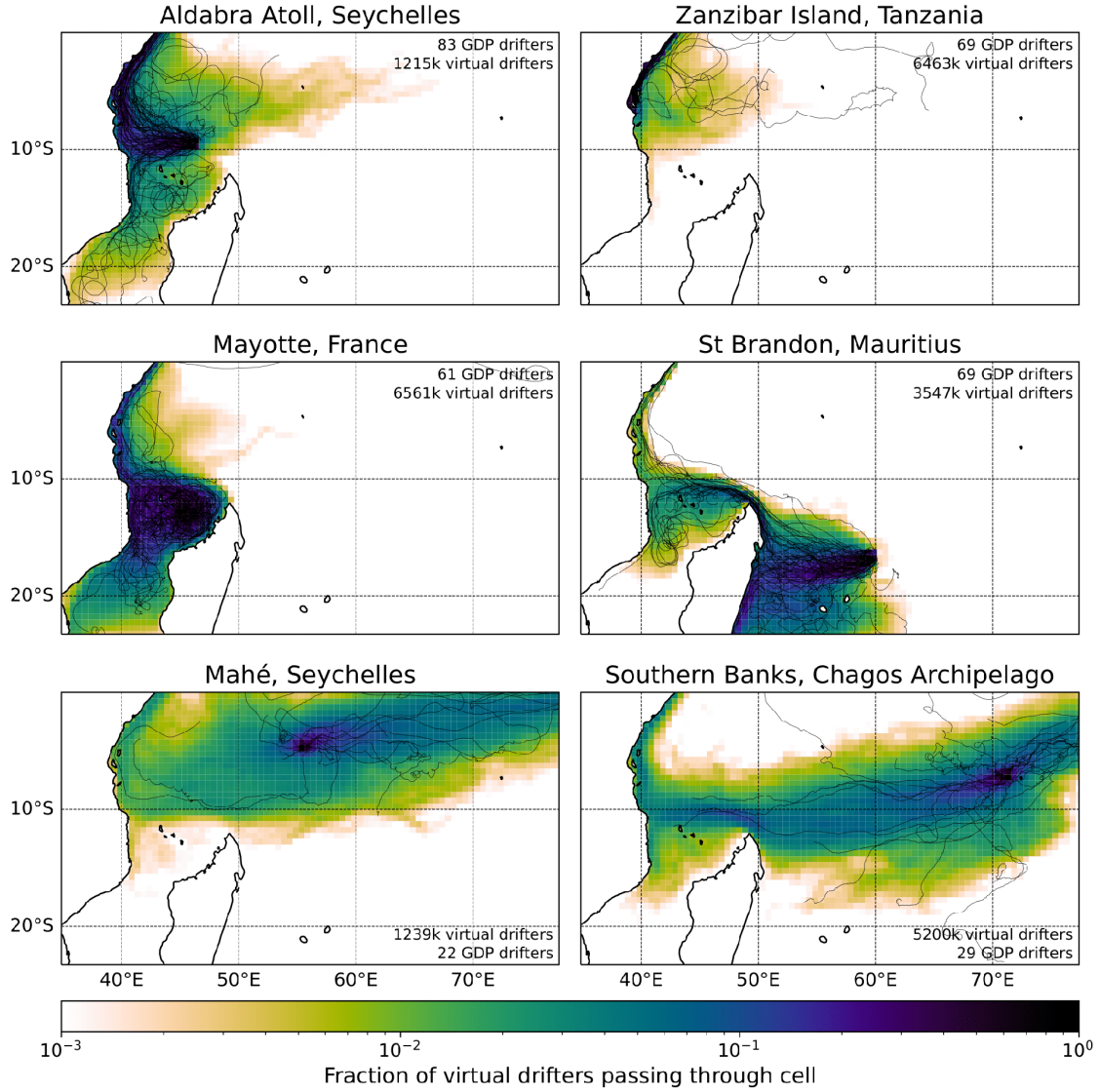


Figure 3.8: *Colour:* Fraction of virtual drifters advected with half-hourly WINDS-M surface currents that pass through each $0.5^\circ \times 0.5^\circ$ grid cell at least once within 120 days. Cells with less than 0.1% of virtual drifters passing through are shaded in white. *Lines:* Observed Global Drifter Program drifter trajectories, for 120 days following the nearest pass to the virtual drifter release site (or until beaching/death, if this occurred within 120 days).

WINDS is still too coarse to resolve the finest scales of motion that are important for reef-scale dispersal (Dauhajre et al., 2019; Grimaldi et al., 2022), but at intermediate scales of tens to hundreds of kilometres, we expect that WINDS will provide a significantly improved capacity for dispersal modelling and associated applications as compared to existing openly available regional and global ocean simulations.

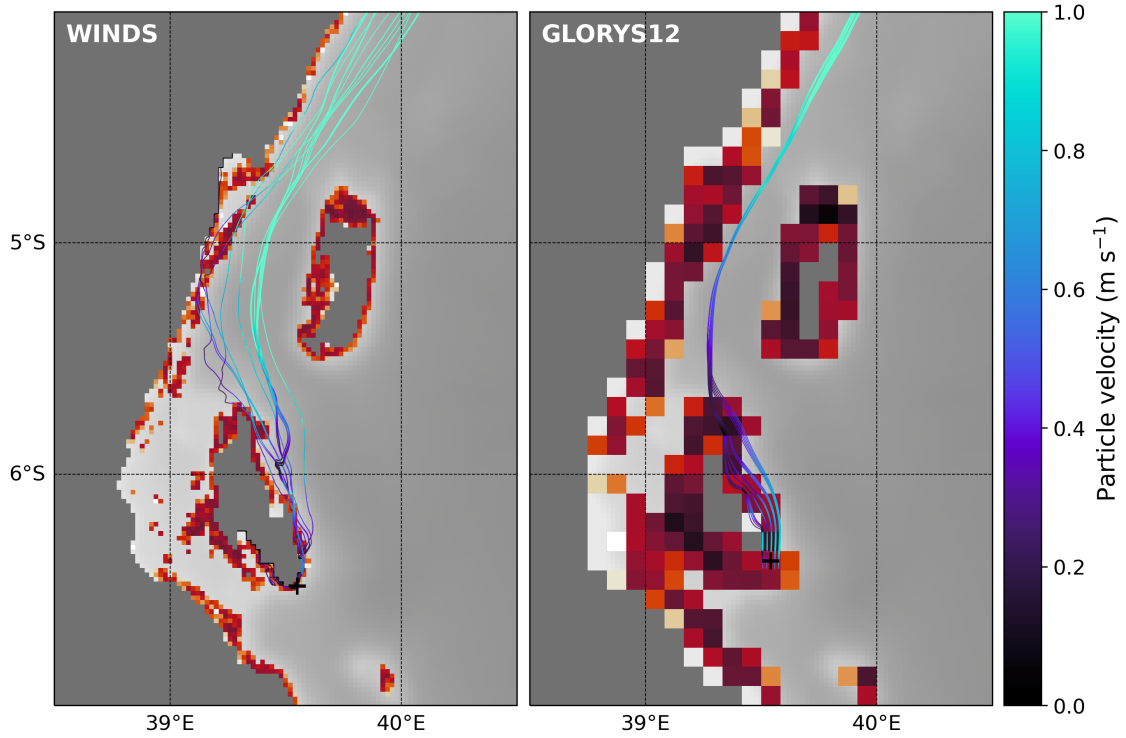


Figure 3.9: 25 virtual drifter trajectories, coloured by instantaneous speed, released from analogous coral reef cells at the southern tip of Zanzibar (Tanzania) on July 1st 2019 in WINDS-M (left) and GLORYS12 (right). Land cells for both models are shaded in dark grey. Red cells are coral reefs (Li et al., 2020), aggregated to the respective model grid, and shaded by total area per cell (shown for illustrative purposes only).

3.4.3 Sea-surface temperature (SST) and salinity (SSS)

Animation 3.1 (table 1.1) shows SST for one year in WINDS-C, demonstrating the combined effects of advection and surface forcing in setting spatial and temporal variability in SST. We have validated WINDS SST and SSS predictions by comparing monthly climatological SST and SSS from WINDS-M, to monthly climatological SST from OSTIA (Good et al., 2020) and SSS from ARMOR3D (Guinehut et al., 2012), all computed across 1993-2020 (both are independent of WINDS, although it is important to note that observations for sea-surface salinity are sparse in the SWIO). In general, WINDS performs well for both SST and SSS; the mean absolute error (MAE) for SST and SSS respectively ranges between 0.14–0.24 °C, and 0.06–0.1 PSU across the seasonal cycle (figure 3.10 and figure 3.11). There is a widespread and year-round cold and fresh bias across most of the SWIO in WINDS, although the

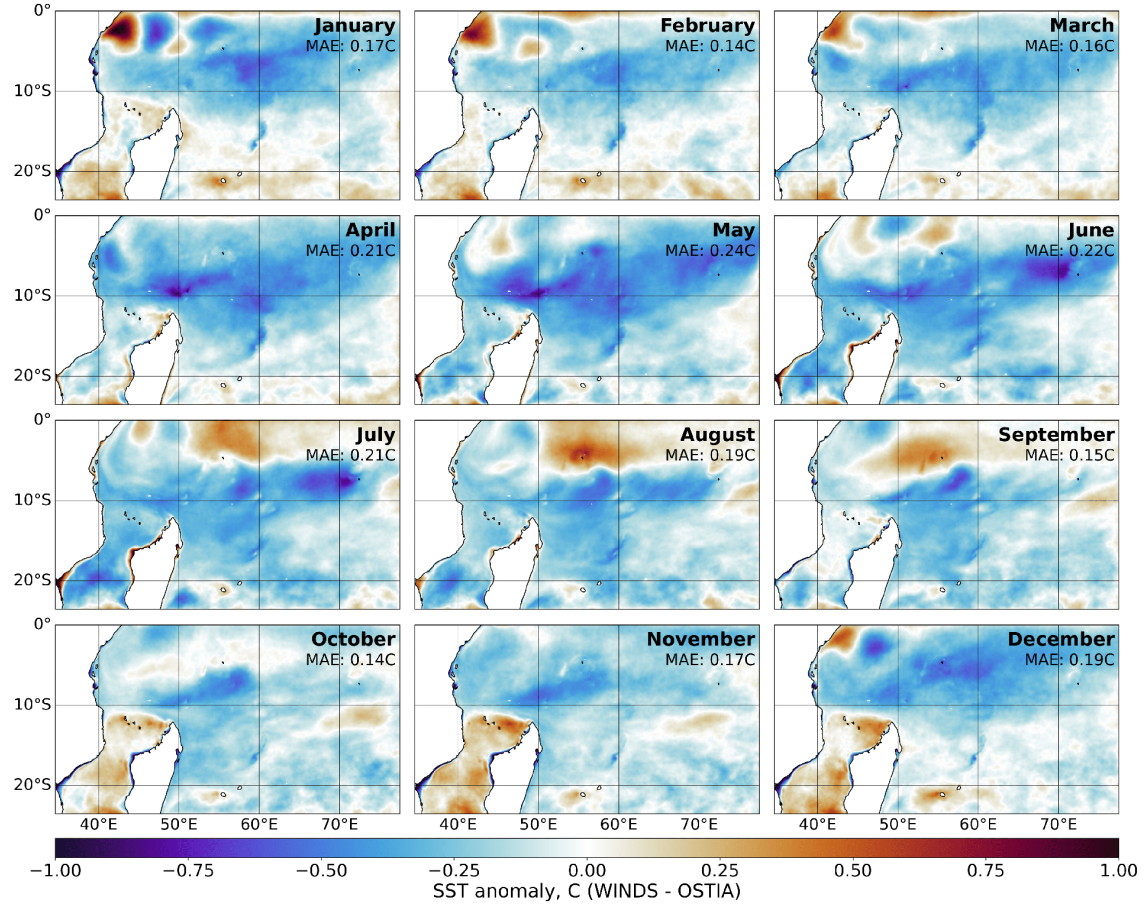


Figure 3.10: Difference between monthly climatological SST simulated by WINDS, and satellite and in-situ derived SST estimates from OSTIA. Blues indicate that WINDS simulates cooler temperatures, reds indicate that WINDS is warmer.

magnitude of this bias is small. There is also a warm bias within the Mozambique Channel during the northwest monsoon (November to February), and a salty bias year-round. We do not know for certain why these biases exist in WINDS. We hypothesised that WINDS may overestimate vertical mixing in the upper ocean, thereby entraining more cooler water into the surface layer, but comparison of the mixed-layer depth (MLD) in WINDS versus the GLORYS12 reanalysis (figure 3.12) shows that the MLD tends to be slightly *shallower* in WINDS. The different SST anomalies between the Mozambique Channel and the rest of the SWIO during the northwest monsoon (figure 3.10) is also not reflected in MLD anomalies. Finally, there is a spatially limited but relatively intense fresh bias in WINDS off the coast of Mozambique, associated with the Zambeze River. The implementation of rivers

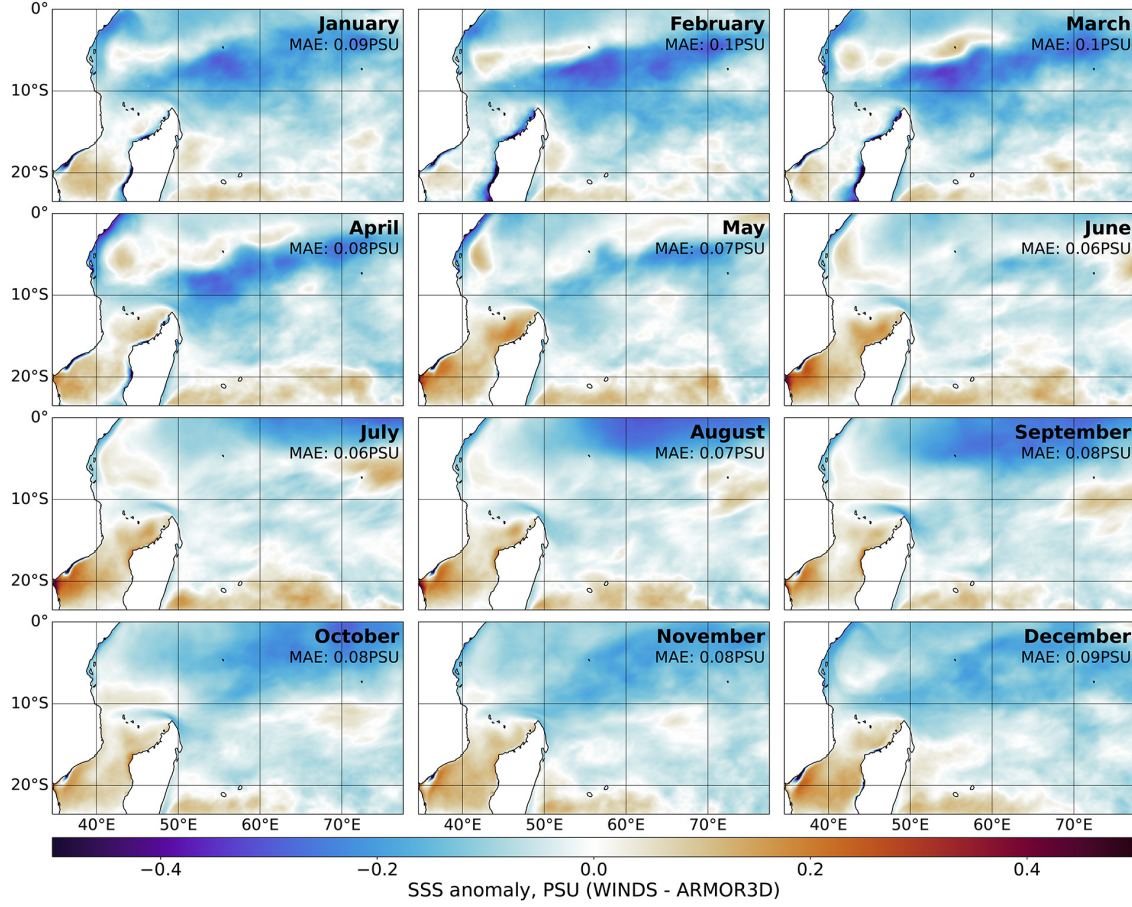


Figure 3.11: Difference between monthly climatological SSS simulated by WINDS, and in-situ derived SSS estimates from ARMOR3D. Blues indicate that WINDS simulates lower salinity (fresher), reds indicate that WINDS simulates higher salinity (saltier).

in WINDS is simplistic, so it is possible that the seasonal discharge climatology or physical water properties associated with the river mouth (15 PSU and 25 °C) were inappropriate, that the advection of the freshwater plume associated with the river is incorrectly simulated in WINDS, or that ARMOR3D does not fully capture the fine-scale freshwater plume associated with the Zambeze River.

3.5 Conclusions

WINDS, and specifically the realistic WINDS-M experiment, reproduces surface circulation well in the SWIO. Although surface current variability may be overestimated by WINDS in certain regions, such as within 5° of the equator, WINDS-M successfully reproduces the main features of surface circulation across the region, observed surface

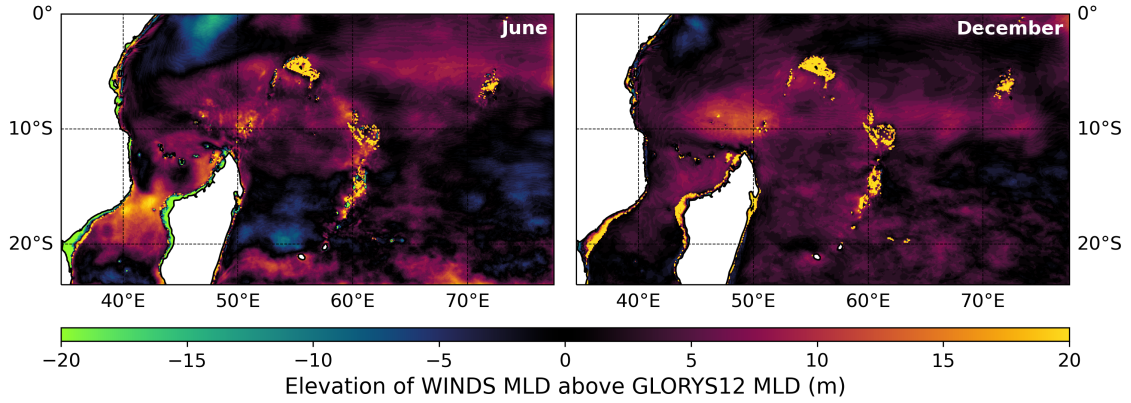


Figure 3.12: Difference in elevation of the mixed-layer depth (MLD), defined as the depth at which the climatological temperature first drops at least $0.2\text{ }^{\circ}\text{C}$ below the temperature at a depth of -3 m , in WINDS versus CMEMS GLORYS12. Positive values indicate that the MLD is *shallower* in WINDS. Plotted here are figures for June and December, two of the months with the largest SST anomalies in WINDS (figure 3.10).

drifter pathways, and surface properties such as temperature and salinity. Although observations of sub-mesoscale circulation in particular in the SWIO are lacking, our validation of WINDS-M suggests that this product is suitable for model-based studies investigating the dispersal of buoyant particles on scales of $\mathcal{O}(10^1 - 10^3)$ km. To our knowledge, the spatial resolution of WINDS-M is a four-fold improvement on the highest resolution publicly available time-varying dataset for surface currents in the SWIO ($1/12^{\circ}$ global ocean (re)analyses, such as GLORYS12 (Lellouche et al., 2021)), and the temporal resolution (30 minutes) is also sufficient to capture a wide range of current variability. We hope that the output of WINDS will be useful for those investigating marine dispersal (and, more broadly, marine science) in the SWIO.

With high-frequency surface current predictions for the entire SWIO generated, we can now simulate larval dispersal between coral reefs across the region. However, although our final goal is to predict connectivity and other conservation metrics which will be useful for marine practitioners, previous studies have raised the importance of considering the variability of reef connectivity in addition to the mean state (Thompson et al., 2018; Watson et al., 2012). As a result, we firstly use the output of WINDS to investigate the temporal variability of coral reef connectivity in chapter 4, to lay the foundations for chapter 5.

4

High-frequency variability dominates potential connectivity between remote coral reefs

4.1 Introduction

Coral larval dispersal is a coupled biological and physical process. Transport is largely driven by physical ocean currents as coral larvae are, to first-order, weak swimmers (Hata et al., 2017; Kingsford et al., 2002). Coral larvae have a limited competency window (usually on the order of days to weeks), outside of which they are unable to settle, and also die following a time-dependent mortality rate (Connolly & Baird, 2010; Graham et al., 2008). Early work often modelled larval dispersal as a time-independent advection-diffusion process, multiplied by functions incorporating competency and survival dynamics (Connolly & Baird, 2010; Largier, 2003). However, this static picture of potential connectivity contradicts observations of coral recruitment rates that can vary by orders of magnitude between years (e.g. Adjerdoud et al., 2022; Edmunds, 2023; Porter & Schleyer, 2017; Thomson et al., 2021). In fact, the time-varying flow field in the ocean introduces a significant stochastic component to potential connectivity (Mitarai et al., 2008; Siegel et al., 2008), where connectivity occurs in pulses driven by the filamentation of larvae in regions of high

strain and current convergence (Dauhajre et al., 2019; Harrison et al., 2013).

As broadcasting corals generally spawn infrequently in short-duration spawning events (Baird et al., 2009), most numerical modelling studies simulate spawning during a certain known (or suspected) spawning period, repeated annually over a certain number of years. Potential connectivity is then often integrated across each spawning period, with some studies focusing on the time-mean or seasonal picture (e.g. Gamoyo et al., 2019; Wood et al., 2014), whilst others also investigate interannual variability, with varying degrees of complexity (e.g. Thompson et al., 2018; Trembl et al., 2008; Wood et al., 2016). It is clear from the considerable effort that has gone into modelling coral larval dispersal that potential connectivity varies over a wide range of timescales, but few studies have investigated the consequences of high-frequency potential connectivity variability for ecological applications.

Consider the fate of a larval packet generated by a particular coral species at a particular reef site. Perhaps we are fortunate, and precisely know that spawning starts on day t every year (maybe we even know the exact time), taking place over Δt days. This may appear to be a very useful initial condition. However, in the absence of near-perfect data assimilation at an appropriate scale, or dominant oceanographic processes that are inherently predictable (e.g. a tidal lagoon), there is a strong stochastic component to short-term larval transport (Mitarai et al., 2008; Siegel et al., 2008). Even with appropriate data assimilation, the chaotic nature of turbulent flow results in uncertainty associated with larval position growing rapidly with time (e.g. Romero et al., 2013). A biophysical larval dispersal model hopefully captures the statistical properties of the turbulent flow, but the state of the system is highly unlikely to be correct at any one time. As a result, even in this best case scenario, quantifying the magnitude and timescales of this stochastic variability is essential for understanding uncertainty in potential connectivity predictions.

In many cases, however, the spawning timing and duration may *not* be precisely known. In the SWIO, temporal and spatial coverage of spawning observations is very poor (Baird et al., 2021). It is therefore also important to understand the magnitude and effects of seasonality on reef potential connectivity. This could be

particularly influential for the Indian Ocean, where monsoonal winds lead to a seasonal reorganisation of surface currents (Schott & McCreary, 2001), and therefore potential connectivity, between the northwest monsoon in the austral summer and southeast monsoon in the austral winter.

In addition to seasonality, connectivity may also vary from year to year. For instance, Thompson et al. (2018) demonstrated that at least 20 years of data were required to capture the interannual potential connectivity variability in the Coral Triangle (maritime Southeast Asia) region. However, given that Thompson et al. (2018) only considered two short spawning events per year, it is not clear to what extent this interannual variability in connectivity reflects low-frequency oceanographic variability, as opposed to being a sampling artefact due to the aliasing of high-frequency variability.

Regardless of its origin, stochastic variability in potential connectivity strongly affects metapopulation dynamics (Watson et al., 2012), but beyond the expectation of a seasonal cycle (Gamoyo et al., 2019), little is known about the magnitude, timescales, geography, or physical drivers of this variability in the SWIO. It is important to first investigate the temporal variability of potential connectivity in the region, to inform our approach to analysing geographic patterns and consequences for reef ecology in chapter 5. As a result, in this chapter, we set out to answer the following key questions:

1. How does potential connectivity vary over day-to-day, seasonal, and interannual timescales across the SWIO?
2. What are the physical oceanographic drivers of this variability?
3. To what extent is this variability important for understanding demographic and genetic connectivity?

To answer these questions, we present a modelled potential connectivity time-series, spanning all shallow-water coral reefs in the tropical SWIO, as a function of spawning time. We consider larval fluxes between over eight thousand 4 km^2 reef cells, across 27 years (for a total of almost 10,000 individual daily spawning events),

based on a state-of-the-art 2 km-resolution regional ocean model (chapter 3). This is the highest resolution (spatial and temporal) connectivity dataset ever generated in this region, allowing us to carry out a detailed investigation into the temporal variability of reef potential connectivity across scales and oceanographic regimes. The potential connectivity matrices and hydrodynamic data used in this study are freely available, and our analyses can be rerun under different biological parameterisations using the associated code (see table 1.1).

4.2 Methods

4.2.1 Hydrodynamical and larval dispersal models

We generated potential connectivity matrices for coral larval dispersal across the SWIO using SECoW (Simulating Ecosystem Connectivity with WINDS). SECoW is a modelling system combining hydrodynamic data from WINDS-M, a $1/50^\circ$ regional ocean simulation for the SWIO (chapter 3), with a larval dispersal model based on OceanParcels (Delandmeter & van Sebille, 2019; Lange & van Sebille, 2017). SECoW uses 30-minute frequency surface current output from WINDS-M for the years 1993-2020, thereby resolving hydrodynamic variability ranging from tidal to interannual.

The larval dispersal component of SECoW assumes that coral larvae physically behave as positively buoyant, otherwise passive particles, which are advected by surface currents for 120 days after spawning, using a fourth-order explicit Runge-Kutta scheme in OceanParcels. Coral larvae are weak swimmers compared to horizontal ocean currents (Hata et al., 2017; Kingsford et al., 2002) but the vertical position of coral larvae in the water column is more challenging to constrain. Although newly fertilised coral eggs are generally positively buoyant (Szmant & Meadows, 2006), larvae tend to lose buoyancy as they develop (Harri & Kayanne, 2003; Szmant & Meadows, 2006). However, the swimming speed of coral larvae can be significant compared to vertical velocities in the ocean (Hata et al., 2017), facilitating some measure of control over their vertical position in the water column. Under controlled conditions, some coral larvae move downwards towards settlement tiles after days to weeks (Szmant & Meadows, 2006; Tay et al., 2011) whereas others have been

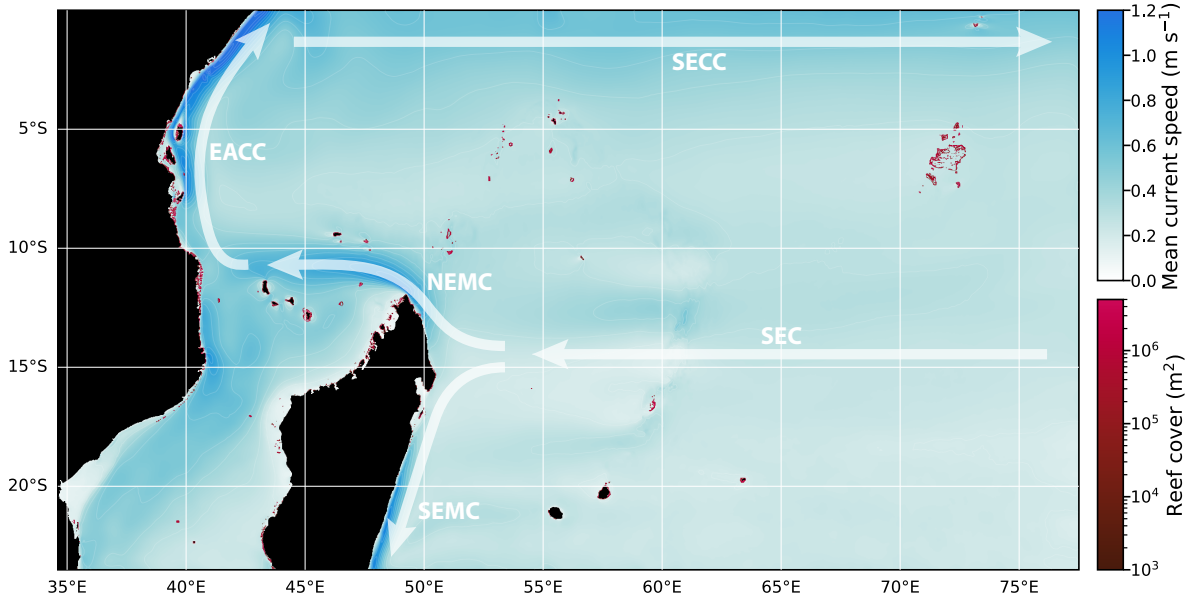


Figure 4.1: The model domain investigated in this study, with the time-mean surface current speed (blues) and reef surface area per grid cell (reds). Also shown is a schematic representation (after Schott et al. (2009)) of the major ocean currents in the region, namely the South Equatorial Current (SEC), Northeast Madagascar Current (NEMC), Southeast Madagascar Current (SEMC), East Africa Coastal Current (EACC), and South Equatorial Countercurrent (SECC). Note that circulation in the Mozambique Channel is dominated by eddies, wind-driven surface currents often reverse at the equator and, during the northwest monsoon, the southward-flowing Somali Current enters the domain and meets the East Africa Coastal Current between 0-5° S.

observed to actively swim upwards towards the light, with no dependency on larval age (Mulla et al., 2021).

Regardless, little is known about the vertical positioning of coral larvae in the open ocean so, for practical reasons (the excessive storage requirements of storing high-frequency 3D velocity fields for such a high-resolution domain, and the experimental flexibility offered by an offline particle tracking approach), in this study we assumed that they remain near the ocean surface. We did not use a parameterisation for sub-grid scale processes, as it is not clear that a simple random walk parameterisation would result in any meaningful improvement at the relatively high resolution and short connectivity timescales used in this study (Okubo, 1971; Reijnders et al., 2022; van Sebille et al., 2018). Using a stochastic parameterisation would also require an additional (and arbitrary) parameterisation to prevent particles from entering land

cells, and any uncertainty introduced by not resolving sub-grid scale processes is likely small compared to the biological uncertainties described above.

We released particles from every c. 2×2 km reef cell on the WINDS grid, based on an upscaled reef cover map derived from satellite imagery (Li et al., 2020). The resulting reef cover is likely higher than the actual coral cover (and clearly higher than the coral cover for any one species), but we choose this approach to broaden the applicability of our results, as taking subsets from the full dataset is straightforward. The Li et al. (2020) reef map is provided at a significantly higher resolution than WINDS, so some reefs are identified by the WINDS land-sea mask as being on land. In these cases, we redistributed the ‘land’ reef area onto the nearest ocean cells to conserve the total reef area (in rare cases, this results in an apparent reef cover $>100\%$), resulting in 8088 reef cells across the WINDS domain. We released $n = 1024$ (32×32) particles per reef cell, arranged in a regular grid, and simulated daily spawning events at midnight from 1 January 1993 to 31 December 2019, for a total of 9861 domain-wide spawning events, with c. 8.3×10^6 particles seeded per event.

Analogous to our treatment of MPP in chapter 2, each particle represents a large number of coral larvae, assumed to have an initial separation small enough such that they do not disperse significantly relative to one another. In the present study, we assumed a constant coral fecundity (i.e. the number of larvae generated) per unit area per day, ρ . In reality, coral fecundity is certainly not constant (e.g. Hartmann et al., 2018), but this is a necessary approximation for now, as no maps of coral fecundity exist spanning the southwest Indian Ocean. Therefore, each particle released in cell i represents $L_i^0 = \rho A_i / n$ larvae at spawning, where A_i is the reef cover of cell i for the purpose of this study.

Following Connolly and Baird (2010), we assumed that coral larvae gain and lose competency at constant rates after a minimum competency period, and die following a time-dependent mortality rate. We further assumed that competent larvae settle at a rate proportional to the reef cover in the occupied cell. This accounts for the capacity of upstream reefs to reduce the larval supply to downstream reefs, whilst sensibly handling sub-grid scale reef coverage and allowing for the possibility of a

larva passing over a reef without settling (Hata et al., 2017). Biological parameters are based on *Platygyra daedalea*, a widespread coral in the southwest Indian Ocean with an intermediate competency period and mortality rate (figure 4.2, table B.1). The results described in this study are robust with respect to biological parameters, but alternate versions of the figures in this manuscript for the other four coral species described in Connolly and Baird (2010) are included in dataset 4.2 (table 1.1).

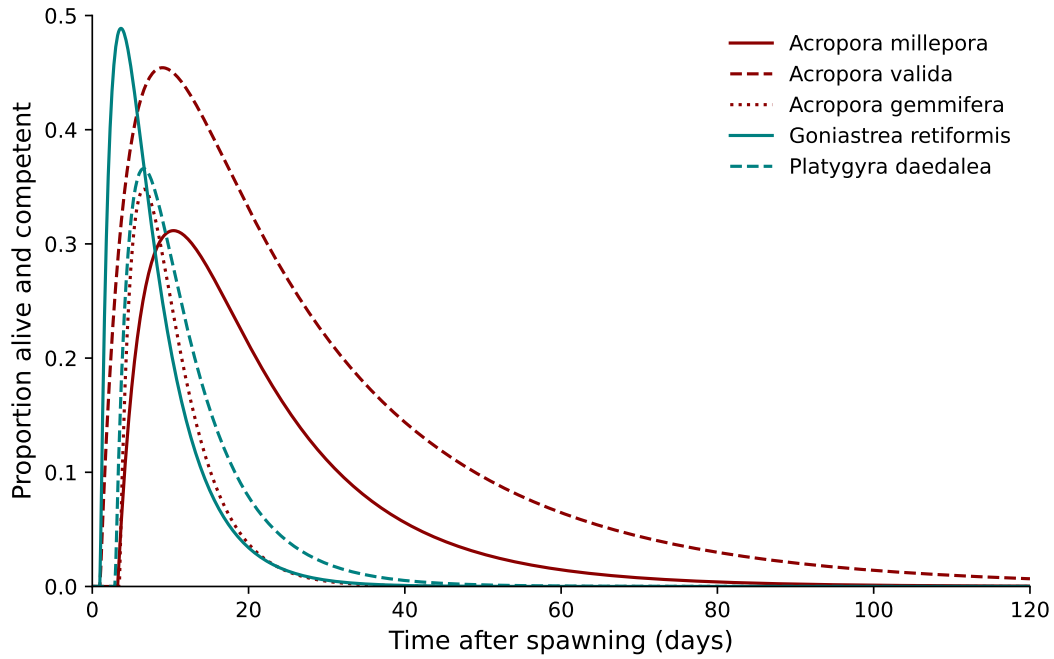


Figure 4.2: Proportion of larvae alive and competent as a function of time, for *P. daedalea* (used in the main text) and four other coral species (see dataset 4.2). Note that the minimum allowed competency period is set to 1 day in this study, contrary to the original form in Connolly and Baird, 2010.

Following Connolly and Baird, 2010, we assumed that the coral larvae represented by each particle are split across three larval reservoirs: a pre-competent reservoir L_1 , a competent reservoir L_2 , and a post-competent or dead larval reservoir L_3 . The pre-competent and competent reservoirs evolve through time according to the

following differential equations:

$$\frac{dL_1}{dt'} = -\alpha^*(t')L_1(t') - \mu_m(t')L_1(t'), \quad (4.1)$$

$$\frac{dL_2}{dt'} = \alpha^*(t')L_1(t') - \beta L_2(t') - \mu_m(t')L_2(t') - \mu_s F_r(t')L_2(t'), \quad (4.2)$$

$$\alpha^*(t') = \begin{cases} 0 & t' < t_c, \\ \alpha & t' \geq t_c, \end{cases}$$

where α^* is a competency acquisition rate (d^{-1}), β is a competency loss rate (d^{-1}), μ_m is a mortality rate (d^{-1}), μ_s is a settling rate (d^{-1}), and F_r is the fraction of a WINDS cell area covered by reef. The parameter α^* is equal to 0 before a larva has reached its minimum competency period t_c (d), and α thereafter. The settling term $\mu_s F_r(t)L_i^2(t)$ was not present in the original formulation of Connolly and Baird, 2010. Since SECoW cannot provide any physical insight into the position of a particle below the WINDS grid resolution (c. 2 km), we assumed that the particle is equally likely to be anywhere in the reef cell it currently occupies for the purpose of this biological parameterisation. The settling rate is therefore equal to a fixed settling rate μ_s assuming 100% reef coverage, multiplied by the actual proportion of the reef cell covered by reef. In this study, we set $\mu_s = 1 \text{ d}^{-1}$, assuming settling times on the order of a day (Tay et al., 2011). However, we also carried out tests with $\mu_s = 0.5 \text{ d}^{-1}$ and $\mu_s = 2 \text{ d}^{-1}$, and this primarily affects the absolute number of settling larvae rather than temporal variability.

4.2.2 Connectivity metrics

We could solve equation (4.1) and equation (4.2) directly by numerically integrating them, either ‘online’ during particle tracking, or ‘offline’ after regularly saving particle positions. However, as explained in section 2.2.2, this either requires poorly-constrained parameters to be set prior to particle tracking, an unrealistic amount of storage, or significant compromises in terms of data output frequency (leading to the loss of most settling events).

Instead, similarly to section 2.2.2, it is possible to reconstruct most information about larval settling events from a very small number of parameters recorded during each event:

- The cell ID (a 16-bit unsigned integer in our configuration, which is used as a key for dictionaries containing the reef area and other parameters).
- The event start time-step (a 16-bit unsigned integer in our configuration).
- The event duration (a 16-bit unsigned integer in our configuration).

Equation (4.1) and equation (4.2) are more complicated than the analogous equations in chapter 2 due to (1) the more complicated form of the survival curve (no longer assuming a constant mortality rate), and (2) the existence of competency. As a result, although an analytical solution exists when the mortality rate is constant, we are not aware of an analytical solution for the general case of time-varying mortality. Nevertheless, it is still possible to find an integral expression for the settling flux of larvae during a settling event (appendix B.1), which is smooth within an event and therefore possible to solve using a relatively small number of explicit fourth-order Runge-Kutta (RK4) steps. SECoW can use any number of RK4 steps to integrate events, but we found minimal loss of accuracy by using a single RK4 step. In this study, we use five RK4 steps as we had the available computational capacity, but those interested in using SECoW for different biological parameters can use a single step, which generates very similar results. We store a maximum of 60 events per particle, which captures almost all non-negligible settlement events.

The dispersal script generates a list of settlement events l , where each settlement event is associated with a source cell i , sink cell j , spawning time k , and larval settlement flux N_s^l . We will now define the larval flux, ρF_{ijk} ¹, as the total number of larvae spawning at source cell or group i (at time k) and settling at sink cell or group j :

$$\rho F_{ijk} = \sum^l \{N_s^l \mid i, j, k\}.$$

¹We define the larval flux as ρF_{ijk} rather than F_{ijk} as this clarifies which quantities are dependent on ρ and which are not. F_{ijk} therefore has units of m^2 .

Note that since ρF is computed using a simple summation, i and j in this expression can instead refer to source and sink *groups* (this is not the case for earlier expressions)².

We define the *out-strength* of site i , $S_{ik}^{\rightarrow}$, as the *fraction* of larvae setting anywhere, given that each larva originated from source cell or group i at time k :

$$S_{ik}^{\rightarrow} = \frac{\sum_j F_{ijk}}{A_i}.$$

In section 4.3, we focus on the out-strength matrix $S_{ik}^{\rightarrow}$ for individual reef cells. Contrary to flux, out-strength is a function of just one location (rather than a pair of locations), so it is more straightforward to investigate geographic dependence. In section 4.4, we also consider the flux matrix F_{ijk} for reef groups. The full flux matrix in SECoW has $8088 \times 8088 \times 9861 \approx 645 \times 10^9$ elements so, for tractability, we have formed 180 reef groups using an agglomerative clustering algorithm, resulting in a more manageable $180 \times 180 \times 9861$ matrix.

4.2.3 Data analysis

4.2.3.1 High-frequency variability

We quantified the high-frequency (day-to-day) variability of out-strength as the 1 day lagged temporal autocorrelation, r_{1d} . If r_{1d} is high, out-strength on day k is a good predictor of the out-strength on day $k+1$. Conversely, low r_{1d} indicates very high day-to-day reef connectivity variability. Examples are shown in figure 4.3(c-e); for instance, compare the relatively steady out-strength near Tanga in Tanzania ($r_{1d} = 0.86$) to the sporadic out-strength at Rémire Island in Seychelles ($r_{1d} = 0.24$). We computed r_{1d} independently for each cell, using the full 1993-2019 daily time-series.

²Since we have over 8,000 coral reef cells and over 10,000 release days in our simulation, the full ρF matrices at cell-level would contain around 660×10^9 entries. Computing and storing these full ρF matrices at cell-level would therefore either require the use of sparse matrix objects, or chunked file writing. At present, the post-processing scripts used in this study require around 600 core-hours on the JASMIN HPC for the entire 1993-2020 dataset. This is orders of magnitude less than the particle-tracking scripts, but it is still considerable. The use of sparse matrices or chunked file writing would add to the computational expense of post-processing, and we have therefore not attempted it in this study. As a result, we only compute the F matrices at group level. We can, however, compute out-strength at a cell level.

To investigate the physical drivers of r_{1d} , we first split all reef cells into six groups based on their hydrogeography, as different physical drivers may dominate in different oceanographic regimes:

1. Reefs influenced by the East African Coastal Current, specifically all reefs in Tanzania, Kenya, and Somalia ($N = 1822$).
2. All reefs in Mozambique, excluding St. Lazarus Bank ($N = 995$).
3. All reefs in Madagascar ($N = 1695$).
4. Remote islands and reefs near the rapid Northeast Madagascar Current, specifically the Comoro islands, St. Lazarus Bank, Banc du Geyser, Îles Glorieuses, and the Aldabra and Farquhar Groups of Seychelles ($N = 980$).
5. Other remote islands, specifically the rest of Seychelles, remaining French scattered islands, Mauritius, and the Maldives ($N = 1036$).
6. The Chagos Archipelago ($N = 1560$).

Within each group, we then carried out ordinary least-squares (OLS) regression with seven potential explanatory variables we hypothesised could explain spatial variation in r_{1d} , using the `statsmodels` Python package:

1. Mean surface current speed (m s^{-1}): the time-mean speed based on the daily mean velocity from 1993-2020, thereby averaging out sub-daily current variability.
2. Mean surface high-frequency current speed (m s^{-1}), based on the daily mean velocity from 1993-2020, with a high-pass filter to remove frequencies below $1/30 \text{ d}^{-1}$.
3. Mean surface sub-daily current speed (m s^{-1}), based on the half-hourly mean velocity from 2016-2020, with a high-pass filter to remove frequencies below $1/30 \text{ h}^{-1}$.

4. Nearby reef fraction (unitless), quantified as the reef fraction filtered by a 2D Gaussian kernel, with a standard deviation equal to the mean surface current speed at the cell multiplied by the minimum competency period t_c (roughly equal to the distance a larva may travel before its first chance of attaining competency).
5. Weighted connection distance (km), quantified as the average great-circle distance between a source cell and all of its downstream connections, weighted by the larval flux associated with each connection; in other words, the average great-circle distance a larva travels before settling.
6. Distance to land (km), quantified as the great-circle distance from the grid cell centre (ρ point) to the nearest coast (u/v point), identified by a Euclidean distance transform.
7. Mean out-strength (unitless), quantified as the time-mean out-strength for a cell from 1993-2019.

We also tested several other explanatory variables (such as the angle between the mean local current velocity and the vector pointing towards the nearest coast cell; and downstream reef fraction within a cone defined by the mean current speed and variability). However, we focused on these seven variables as they were relatively simple, and tended to have greater explanatory power. These variables were all strongly positively skewed, so we used the logarithm in the regression calculation. We identified the strongest explanatory variable on the basis of the R^2 value. Finally, to test whether the ‘best’ identified explanatory variable is substantially stronger than the others, we carried out multivariate OLS regressions using every pair of explanatory variables. We did not use OLS models with more than two explanatory variables, as we did not think that more complex models would provide significantly more physical insight.

4.2.3.2 Seasonal variability

To assess the strength of the regular seasonal cycle in out-strength, we computed the correlation for each reef cell between monthly mean out-strength and the regular seasonal cycle (i.e. the monthly climatological out-strength) averaged across 1993-2019, specifically extracting the R^2 value. We also carried out an Empirical Orthogonal Function (EOF) analysis of the monthly-mean out-strength matrix, decomposing the time-varying matrix into a set of principal components and associated basis functions. A similar analysis was previously carried out by Thompson et al. (2018) to investigate interannual connectivity variability. In our analyses, the first principal component (PC1) always corresponded to a seasonal cycle. To investigate how connectivity variability across the SWIO responds to the seasonal cycle, we then computed the correlation of the monthly-mean out-strength time-series at each reef cell with PC1, $r_{\text{PC1},S}$. To interpret the physical oceanographic drivers of this variability, we also computed the correlation between PC1 and the monthly-mean surface current speed, and the zonal u and meridional v components of the surface current velocity. The latter results in a new vector field ($r_{\text{PC1},u}, r_{\text{PC1},v}$) returning the correlation of each component with the seasonal cycle (PC1). For interpretation, this vector points in the direction of where the surface current is intensified (but not necessarily oriented) when PC1 is more positive, but the size of the vector depends on how closely correlated the local velocity is to PC1, rather than the magnitude of the velocity.

4.3 Physical drivers of reef connectivity variability

4.3.1 High-frequency variability

Temporal variability in reef out-strength across the SWIO is summarised in figure 4.3, spanning a wide range of timescales, from days to multiple years. However, the out-strength at most reefs simulated by SECoW is dominated by high-frequency variability on the order of days to weeks. As shown by figure 4.3(a), a low-pass filter with a threshold of longer than ~ 20 days removes most of the variance in

daily out-strength for the vast majority of reef cells within the SWIO. Although an annual and, in some cases, biannual cycle is detectable at most sites, this variability is only *dominant* at a small minority of sites.

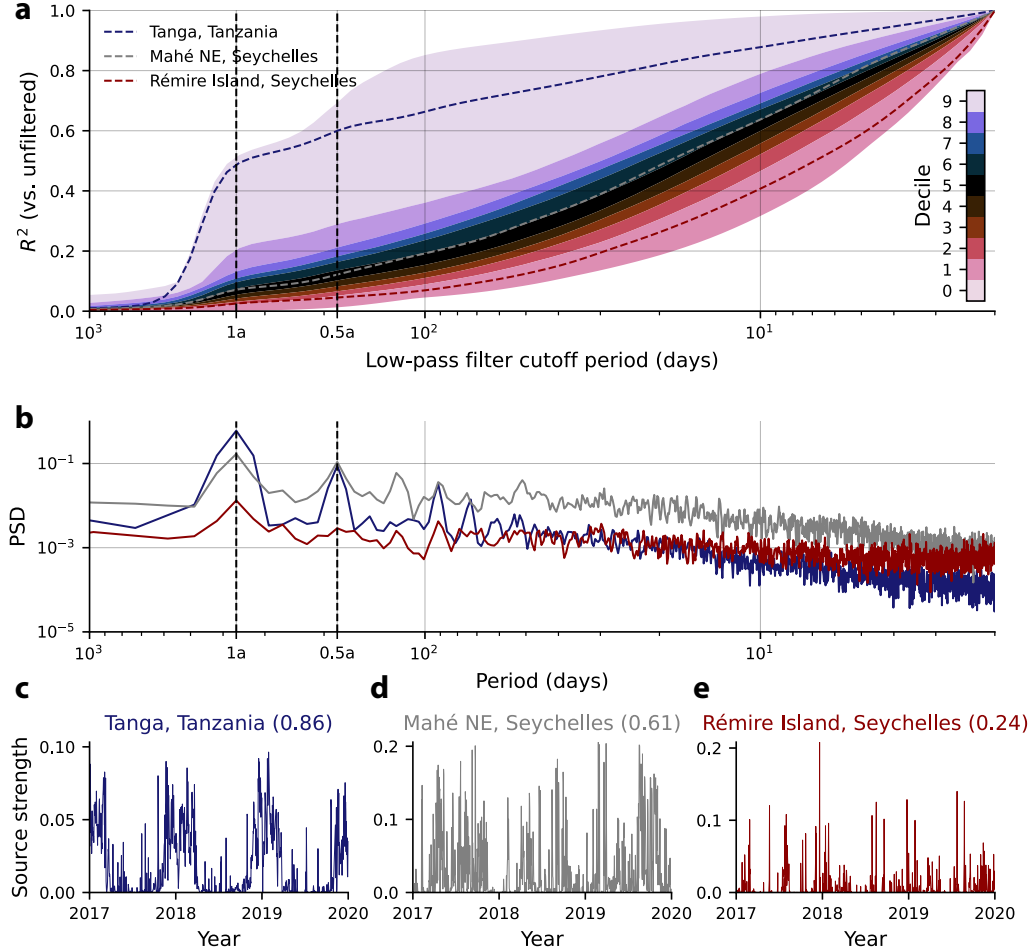


Figure 4.3: (a) Variance fraction of unfiltered (daily) out-strength explained by low-pass filtered out-strength, as a function of the low-pass filter cut-off period, expressed as deciles across the 8088 reef cells. Also shown in dashed lines are examples of three particular reef cells, dominated by low frequency variability (Tanga), high-frequency variability (Rémire Island), and a mixture (Mahé). Animations 4.1-4.3 (table 1.1) provide further insight into the day-to-day variability of out-strength at these sites, showing how destination sites can vary enormously (and rapidly) through time. (b) out-strength power spectral density for the three example reef cells using Welch's method. (c-e) Three years of the full out-strength time-series for the three example reef cells. The numbers in brackets in subplot titles refer to the 1 day lagged autocorrelation (see section section 4.2.3.1).

High-frequency potential connectivity variability (using the 1 day lagged autocorrelation of out-strength, r_{1d} , as a proxy, with lower values corresponding to greater high-frequency variability) varies enormously across the SWIO (figure 4.4). One clear

pattern from this figure is that remote reefs far from land are associated with a greater level of high-frequency potential connectivity variability, such as many of the atolls belonging to the Amirante Islands in Seychelles (figure 4.4(b), west) and Bank du Geyser (figure 4.4(e), east). The geographic remoteness reduces the probability that larvae spawning from these sites will be above a reef during its competency window, and the lack of nearby land allows larvae to pass over reefs without getting trapped against the coast, reducing the time spent above a reef environment. As a result, out-strength from these remote reefs is highly inconsistent and driven by short-lived settling pulses. A similar effect is seen at reefs further away from land along the Quirimbas Archipelago in Mozambique (figure 4.4(d)). Although some particularly remote reefs such as Bassas da India in the south Mozambique Channel (animation 4.4, table 1.1) and St. Brandon in Mauritius have a relatively high out-strength autocorrelation, this is because these sites are so remote that the out-strength is zero for many days, inflating the r_{1d} statistic. Highly variable and sporadic out-strength is therefore a robust characteristic of small and remote reefs in SECoW.

For some islands, the orientation of the coastline relative to prevailing ocean currents drives r_{1d} . The east and north coasts of Ngazidja and Mwali (Comoros, figure 4.4(e)) face surface currents entering the Mozambique Channel, thereby trapping larvae against the coast and resulting in consistent settling. For instance, practically all larvae spawning from the east coast of Ngazidja settle at reefs along the same coastline, whereas a greater proportion of larvae spawning from the opposite side of Ngazidja settle at other islands (which are lower-probability connections, and hence subject to greater variability). The interaction of ocean currents with the coastline, as previously described in depth by Mayorga-Adame et al. (2016, 2017) is also important in setting r_{1d} along the path of the East Africa Coastal Current (EACC, figure 4.4(a)). Larvae spawning from reefs around Chole Bay on the southeast coast of Mafia Island (by the ‘3’ label in figure 4.4(a)) get trapped within the bay and are therefore less likely to enter the EACC. Entering the EACC results in longer distance transport and less reliable connections, so larval retention around Chole Bay

results in higher r_{1d} . In contrast, larvae spawning from reefs in the west and northeast of the island are very likely to enter the EACC, and therefore have a much lower r_{1d} .

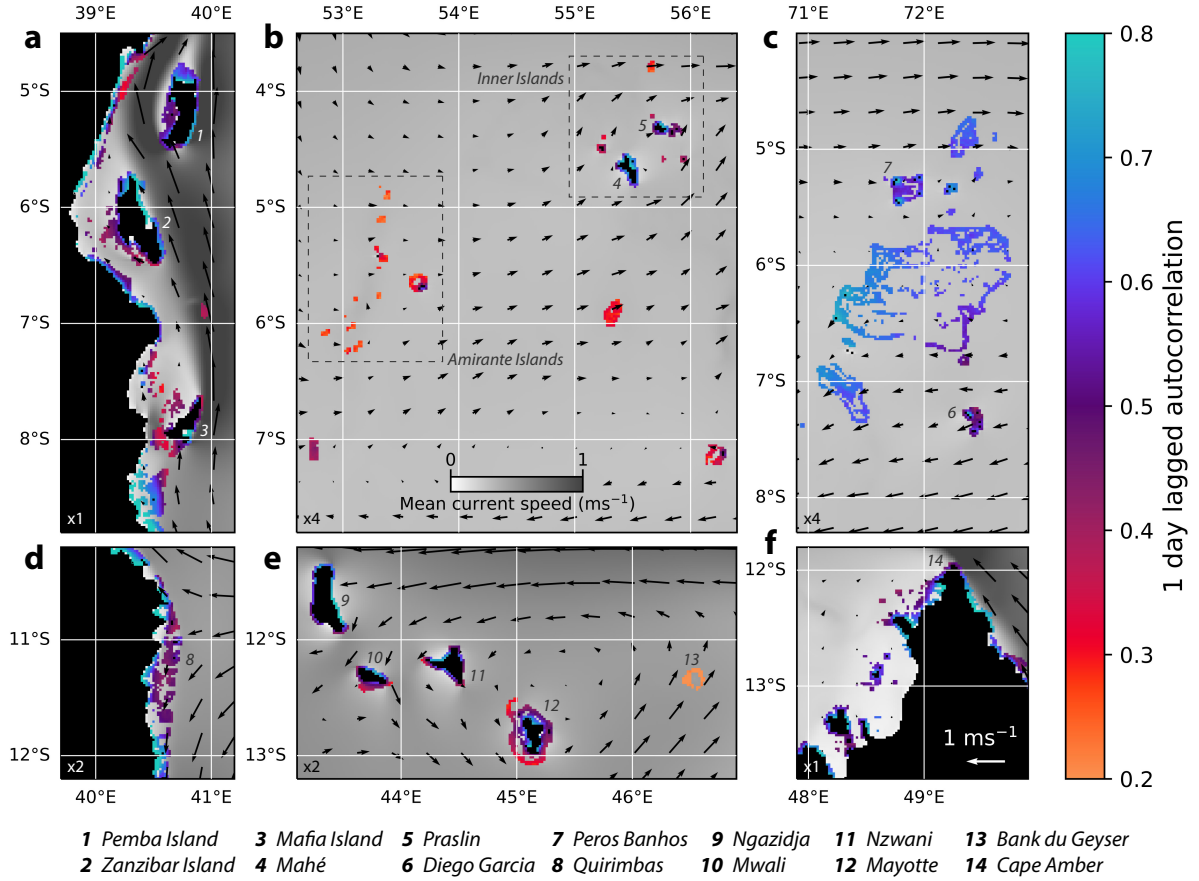


Figure 4.4: 1 day lagged autocorrelation, r_{1d} , for the out-strength time-series of individual reef cells. The corresponding figure for the full domain is provided in dataset 4.2 but, for clarity, this figure focuses on 6 sub-regions: (a) north Tanzania; (b) Seychelles, excluding the Aldabra and Farquhar Groups; (c) the Chagos Archipelago; (d) the Quirimbas Archipelago, Mozambique; (e) the Comoro Islands, including Banc du Geyser; and (f) north Madagascar. Background shading represents the mean current speed, with arrows representing the mean current velocity. For clarity, arrows are enlarged relative to the scale in panel (f) by the scale-factor indicated in the lower-left corner of each sub-plot.

A complex set of flow reversals and wake eddies are generated as the EACC is diverted by headlands and islands, resulting in highly localised connectivity regimes. For instance, similarly to the numerical model described in Mayorga-Adame et al. (2016), flow reversals are generated around Zanzibar Island and Pemba Island (figure B.1). Flow is weakened in the wake of a peninsula on the east coast of Zanzibar, trapping larvae near their source reefs, occasionally exacerbated by convergent flow

towards the coast. A similar effect is seen off the north tip of Pemba Island, where flow is slower in the wake of the island and is often oriented towards the coastline. Conversely, west of Pemba Island, currents are often seaward (perhaps associated with localised upwelling described by Painter et al. (2021)), enabling larvae to drift away from the coast and enter the EACC, again facilitating longer distance, less reliable connections. Similar explanations account for the pattern of high-frequency out-strength variability in northernmost Madagascar (figure 4.4(f)).

Figure 4.5 shows that, for much of the SWIO, a large proportion of this variability can also be *quantitatively* explained by several key metrics. For the EACC and islands in the path of the NEMC (figure 4.5(a, d)), the weighted connection distance (i.e. the weighted mean distance from a reef cell to downstream settlement reefs) explains around half of the variance in r_{1d} . For other remote islands (figure 4.5(e)), this rises to almost two thirds. Larvae in these settings tend to travel greater distances (due to a combination of current speed and/or relatively few nearby reefs) so the proximity of downstream reefs is a strong predictor of day-to-day potential connectivity variability. Reefs where the dominant larval destinations are within tens of kilometres tend to have less high-frequency potential connectivity variability. Unfortunately, weighted connection distance is a less-generalisable metric for decision-making, as this cannot be easily measured without running a larval dispersal model. For the EACC, weighted connection distance was the only metric acting as a reasonable predictor for r_{1d} . However, as can be seen in the insets in figure 4.5, there was a significant (negative) correlation between the local mean current speed and r_{1d} for NEMC islands ($R^2 = 0.47$) and other remote islands ($R^2 = 0.51$). The high-frequency current speed (associated with current variability in the 1-30 day range) was also strongly negatively correlated with r_{1d} for other remote islands ($R^2 = 0.53$). Therefore, the local current speed near remote island reefs may be a reasonable first-order predictor of the magnitude of high-frequency potential connectivity variability. The simple explanation is that greater current speeds are more likely to transport larvae away from the remote island, and into the open ocean, where chances for settlement will be rare and sporadic.

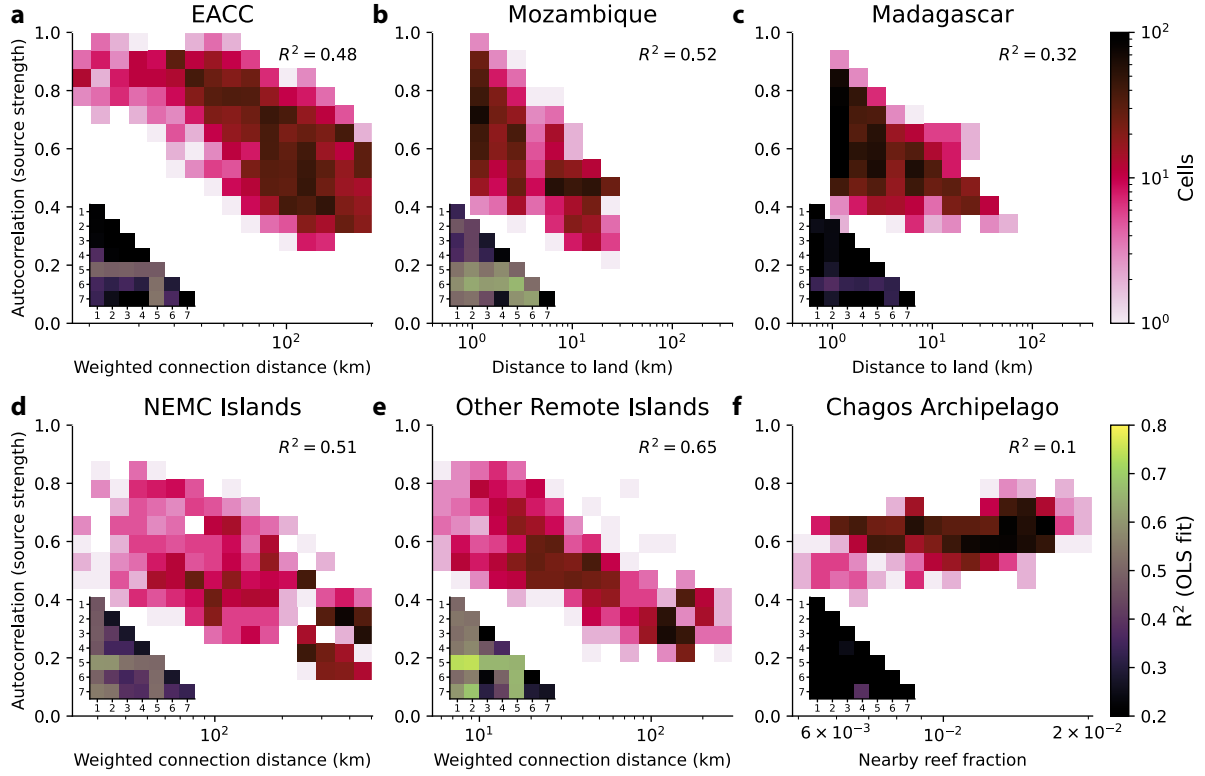


Figure 4.5: Histograms for the 1 day lagged autocorrelation of out-strength for individual reef cells, as a function of a predictor variable. The predictor variable plotted is the variable with the highest R^2 value from ordinary least-squares regression with the out-strength autocorrelation. The matrices in the lower-left corner of each sub-plot represent the R^2 value from ordinary least-squares regression based on all *pairs* of predictor variables, namely (1) Mean current speed; (2) Mean high-frequency current speed; (3) Mean sub-daily current speed; (4) nearby reef fraction; (5) weighted connection distance; (6) Distance to land; and (7) Mean out-strength.

For reefs along the coasts of Mozambique and Madagascar, the distance to land was generally the strongest explanatory variable for r_{1d} . In the case of Mozambique, this pattern is driven by the Quirimbas Archipelago (figure 4.4(d)), but several other explanatory variables also perform similarly well, namely the weighted connection distance ($R^2 = 0.50$) and the high-frequency current speed ($R^2 = 0.43$). For Madagascar, none of the predictor variables were particularly strong, and this may be due to the highly complex coastline and multiple oceanographic regimes (the eddy-dominated Mozambique Channel in the west, and the North and Southeast Madagascar Currents in the north and east).

Finally, high-frequency potential connectivity variability at the Chagos Archipelago

is only weakly correlated with any of the explanatory variables we tested. As hinted at by the general increase in variability towards parts of the Great Chagos Bank with lower reef cover, there is weak positive correlation between nearby reef fraction and r_{1d} . However, with minor exceptions, r_{1d} does not vary by much across the archipelago, with moderate-to-high r_{1d} across most reefs (figure 4.4).

For most regions, pairs of predictor variables lead to a slight, but not major, improvement in r_{1d} (figure 4.5 insets). The only very substantial improvement is for the Chagos Archipelago, where adding the time-mean out-strength to nearby reef fraction in the OLS regression model almost quadruples the R^2 value to 0.39. A high time-mean out-strength is indicative of many consistent nearby connections, although as with the weighted connection distance, this metric cannot be easily estimated without running a dispersal model.

In summary, a first-order rule of thumb for estimating high-frequency potential connectivity variability is as follows. For reefs at remote atolls lacking substantial land, r_{1d} is likely to be very low (with highly sporadic and pulsed out-strength). For reefs associated with substantial islands which are nonetheless remote, the local current speed may be a reasonable indicator of r_{1d} , with higher local current speeds associated with less reliable potential connectivity. For reefs near continental coasts, predicting potential connectivity variability without a larval dispersal model is likely to be challenging, although consideration of local geography and ocean dynamics may be helpful. For instance, potential connectivity variability will likely be greater for reefs further from the coast. Consideration of whether local ocean currents hinder or facilitate long-distance dispersal may also provide insights into potential connectivity variability as, the more likely long-distance dispersal is, the less reliable connectivity is likely to be. Finally, for exceptional regions of extensive reef cover such as the Chagos Archipelago, potential connectivity variability will generally be lower, but may increase in isolated sectors with lower reef cover.

4.3.2 Seasonal variability

Once high-frequency variability is removed from the out-strength time-series for each cell by computing monthly means, the dominant residual signal is the seasonal cycle. The regular (mean) seasonal cycle explains a median of 25.6% of the variance in monthly mean out-strength across reef cells, rising to 65.0% for reefs under the influence of the EACC. Since seasonal variability across much of the SWIO is driven by the monsoons, much of this variability is broadly in phase. Decomposing the monthly-mean out-strength matrix into a set of Empirical Orthogonal Functions, we unsurprisingly find that the dominant EOF corresponds to the seasonal monsoonal cycle (PC1, figure 4.6), switching sign between the northwest monsoon (broadly December to February) and southeast monsoon (broadly June to August). PC1 explains 26.9% of the variance in monthly mean out-strength, more than double that of the next principal component, and is very stable, with only minor interannual variation. PC1 is strongly linked to the strength of the EACC and NEMC, as well as to the position and strength of the South Equatorial Current (SEC) and South Equatorial Countercurrent (SECC) (e.g. Aguiar-González et al., 2016; Manyilizu et al., 2016; Painter, 2020; Schott et al., 2009; Swallow et al., 1991; Yamagami & Tozuka, 2015). In addition to current strength, current direction is strongly correlated with PC1, most notably for reefs in Somalia, Seychelles and the Chagos Archipelago.

In many cases, seasonal variability in current speed and out-strength are anticorrelated. For instance, the out-strength for most reefs along the path of the EACC is suppressed when the current is at its strongest (e.g. figure 4.7(a) - note how out-strength across most reefs is negatively correlated with PC1, and therefore the strength of the EACC, see also figure 4.6). Although faster currents tend to facilitate long-distance connections, due to the effects of mortality, dispersion and competency loss, these connections are practically always weaker than the short-distance connections that are simultaneously suppressed. Some local exceptions exist, such as in the west Zanzibar Channel, where stronger northward flow during the southeast monsoon facilitates the flow of larvae towards higher reef cover in the north. However, in general, this pattern is very robust along the Tanzanian and

Kenyan coasts, as well as across most islands directly in the path of the NEMC (such as the Aldabra and Farquhar Groups of Seychelles), and reefs at the north tip of Madagascar. Current speed also appears to be primarily responsible for the seasonal variability in the Comoro Islands (figure 4.7(e)). Flow here is highly complex due to strong eddy activity, but generally faster flow during the southeast monsoon results in lower retention within each island, and therefore lower out-strength. This pattern reverses at the south of each island, possibly due to flow reversals and current weakening in the island wakes.

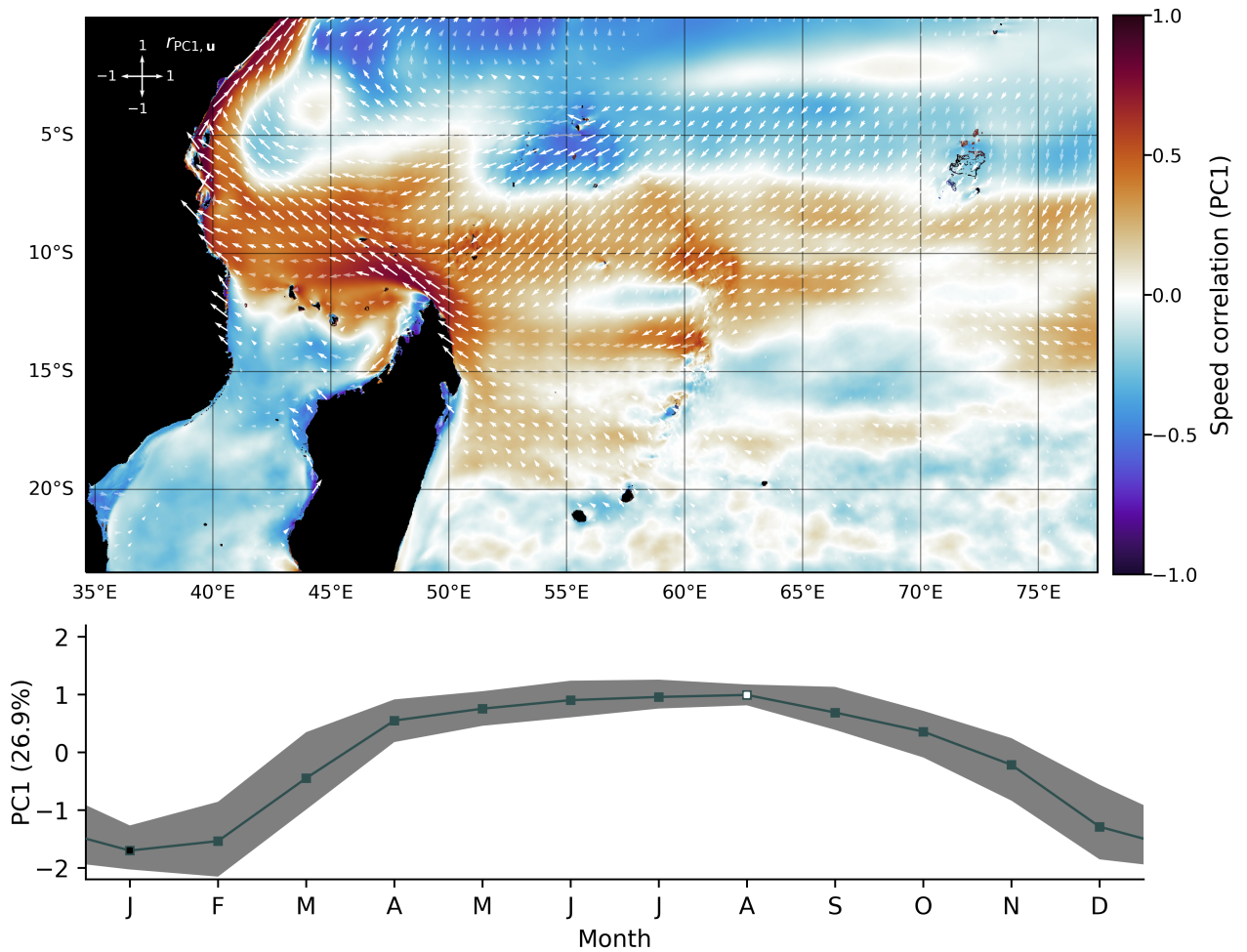


Figure 4.6: *Top:* Correlation of ocean current monthly mean speed with PC1 (from the out-strength matrix). *Bottom:* Seasonal cycle of PC1 computed as the monthly climatology, with the total range for monthly means across all years (1993-2019) shaded.

At other locations, seasonal variations in current *direction* appear to have a greater influence on out-strength variability. This is clearest at the Chagos

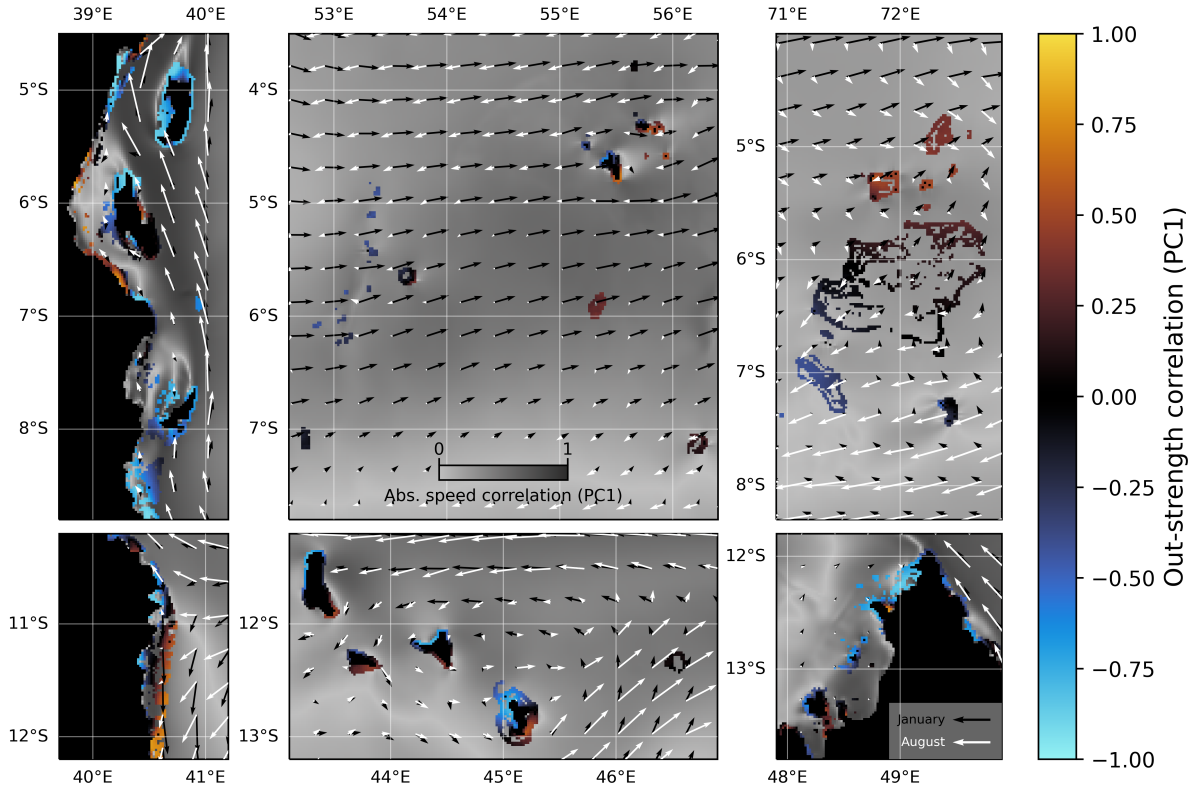


Figure 4.7: Close-up views of selected reefs from figure 4.6: (a) north Tanzania; (b) Seychelles, excluding the Aldabra and Farquhar Groups; (c) the Chagos Archipelago; (d) the Quirimbas Archipelago, Mozambique; (e) the Comoro Islands, including Banc du Geyser; and (f) north Madagascar. Colours represent the correlation of monthly mean out-strength with PC1. The background is shaded by the correlation between ocean current monthly mean speed and PC1 as in figure 4.6 but, for clarity, we show the magnitude only, in greyscale. Arrows show mean current velocities during minimum (January [northwest monsoon], black) and maximum (August [southeast monsoon], white) PC1.

Archipelago (figure 4.7(e)), where southwestward currents suppress out-strength in the southwest of the Archipelago during the southeast monsoon. For these marginal atolls, southwestward larval transport sends larvae directly into the open ocean, resulting in almost inevitable death. It is, however, important to note that correlation with PC1 is generally quite weak across the Chagos Archipelago. On Mahé in Seychelles, the seasonal cycle in out-strength is in antiphase for the south and north halves of the island (figure 4.7(b)). In the south, weaker currents during the southeast monsoon result in strong larval retention within Mahé (and therefore higher out-strength). However, a westward component to currents affecting the north of the island results in larval transport away from Mahé, locally reducing

out-strength. These patterns are reversed during the northwest monsoon. A similar effect occurs on the nearby island of Praslin.

Although the intensification of the NEMC during the southeast monsoon explains the anticorrelation of out-strength with PC1 in northernmost Madagascar, this anticorrelation continues along ocean-facing reefs across much of the northwest coast. Here, an offshore component to currents along the coast develops during the southeast monsoon, transporting larvae off the Madagascan shelf. An energetic mesoscale eddy field within the Mozambique Channel rapidly transports larvae away from Madagascar once they leave the shelf, resulting in low out-strength during the southeast monsoon (compare high retention during the northwest monsoon in animation 4.5, to low retention during the southeast monsoon in animation 4.6, see table 1.1).

4.3.3 Limitations

Although our simulations account simplistically for biological processes such as mortality, competency acquisition and loss, and settling rates depending on available reef cover, we do not incorporate environmental influences on coral larval mortality and competency, such as temperature (Figueiredo et al., 2022; Nozawa & Harrison, 2007). For instance, during IOD events, the temperature of the upper ocean rises in the west Indian Ocean. Although we found no significant effect of the IOD on potential connectivity in SECoW, it is possible that realised dispersal is nevertheless suppressed during IOD events due to the increased larval mortality rate. On the other hand, IOD events are generally most strongly expressed in the west Indian Ocean during October to November, which only partially overlaps with the general spawning season in the region (Baird et al., 2021; Koester et al., 2021; Mangubhai & Harrison, 2009). In addition to interannual temperature variability, temperature also varies over shorter timeframes and spatial scales, from meso- to frontal. This high-frequency temperature variability could add a further stochastic component to dispersal, particularly if a dense larval filament were subjected to protracted high or low temperatures by entrapment in an eddy or front. Including a dependence of larval mortality to temperature would add yet another degree of freedom to our

larval biological parameterisation, so we do not investigate this in the present study. However, daily surface temperature is available within WINDS (chapter 3), so this could be included in a future dispersal model.

Although WINDS is the highest resolution ocean model that has been run on such large spatial and temporal scales in the SWIO, the approximately 2 km resolution is still insufficient to resolve flow on a reef scale. As a result, although we expect SECoW to reasonably simulate larval dispersal within the open ocean, larval retention may be overestimated by our simulations along continental coastlines (Dauhajre et al., 2019), and underestimated around atolls (Grimaldi et al., 2022). Given that long-distance connections are associated with greater high-frequency potential connectivity variability (section 4.3.1), our study may underestimate out-strength variability for reefs across East Africa and Madagascar. Conversely, it is likely that our study overestimates potential connectivity variability for larvae originating from remote coral atolls. The highest frequency of variability we consider in this study is 1 d^{-1} . Larval dispersal will vary at even higher frequencies, for instance following tidal cycles (Green et al., 2018; Grimaldi et al., 2022). However, although particles in SECoW do experience tides, which are reproduced well by WINDS over the open ocean (chapter 3), complex, reef-scale interactions between tides, waves, and reef geomorphology will not be reasonably represented. We therefore do not investigate the variability of larval dispersal with respect to tidal phase.

By considering total reef area, SECoW certainly overestimates the distribution of any one particular coral species, and further assumes that coral fecundity is constant. These assumptions are necessary due to the lack of data in the SWIO, but they are nevertheless important limitations. Insofar as potential connectivity variability is concerned, temporal variability in fecundity, both stochastic and as a response to environmental stress (Hartmann et al., 2018; Leinbach et al., 2021; Levitan et al., 2014; Nakamura et al., 2022; Pratchett et al., 2019), may be particularly important. Again, it is not clear to what extent this may amplify or dampen connectivity variability induced by ocean currents.

4.4 Consequences for demographic and genetic connectivity studies

4.4.1 ‘Interannual’ variability for short spawning events is dominated by high-frequency variability

The importance of interannual variability for potential connectivity is recognised by some modelling studies. For instance, Thompson et al. (2018) investigated potential connectivity in the Coral Triangle using a 47-year hindcast, and found that at least 20 years of simulated spawning events were required to reasonably represent interannual connectivity variability. This is concerning, as many (if not most) larval dispersal modelling studies continue to use considerably shorter timespans. What was not clear, however, is whether this variability in potential connectivity between annual spawning events reflected genuine low frequency (interannual) oceanographic variability, or whether this simply reflects underlying high frequency variability in surface currents.

To test this, we compute the coefficient of variation (CV) for out-strength and flux (i.e. the standard deviation divided by the mean) as a function of the number of spawning events, for five different types of spawning behaviour: (1) a 1-day annual spawning event, (2) a 5-day annual spawning event, (3) a month-long annual spawning event, (4) year-round spawning, and (5) a 1-day spawning event every 10 days. Time-series 1-4 have a total length of 27 years, and time-series 5 has a total length of 270 days (i.e. all have 27 spawning events). For each time-series, we compute the median CV, and 5th - 95th percentile range, across all reef cells or connections. To eliminate biases associated with a particular season or year, we compute 12 different time-series for scenarios 1-3 (one for each spawning month) and scenario 5 (one for each year from 2008-2019), and average across them. Since many individual connections in the flux matrix are below the detection threshold of SECoW, we excluded all connections which are always zero.

The solid black line in figure 4.8 shows how the CV of (a) out-strength and (b) flux for an annual 1-day spawning event increases with the number of spawning events (years). Despite representing an entirely different region, figure 4.8(b) shows a strong resemblance to the results of Thompson et al. (2018), with several decades of data

(tens of spawning events) required to adequately characterise the variability associated with potential connectivity between reefs. In contrast to flux, interannual variability in out-strength (figure 4.8(a)) can be reasonably represented by only around ten years of data. In addition to reaching a plateau more quickly, the magnitude of the CV is generally significantly smaller for out-strength than flux. Out-strength is proportional to the integral of flux across all sink cells, so it is unsurprising that this metric is less variable than flux, despite flux being computed here using groups rather than cells.

If interannual variability in potential connectivity were driven by interannual oceanographic variability, we would not expect the CV to be sensitive to spawning duration (below a year). However, for out-strength, the interannual variability falls rapidly with increased spawning event duration. For instance, increasing the spawning event duration from 1 day to 5 days reduces the CV by about a third. This demonstrates that protracted spawning, even as little as a few days, is an effective method of improving out-strength stability (i.e. the likelihood of larvae settling anywhere). In contrast, the out-strength CV for year-round spawning is typically around 0.2 for many reefs (figure 4.8(a)), indicating that the mean out-strength over a year only varies slightly from the longer-term average. A qualitatively similar pattern is seen for flux, although the CV for 5-day spawning events is similar to 1-day spawning events (likely due to the highly transient nature of individual reef-reef connections).

The teal line in figure 4.8 shows the CV for out-strength (a) and flux (b) for a simulated 1-day spawning event occurring every 10 days, rather than every year. Despite the fact that this time-series captures zero interannual variability and is based on a biologically unrealistic spawning scenario, the median CV is practically indistinguishable between 1-day spawning events every 10 days versus every year. This strongly suggests that, to first-order, interannual dispersal variability for short spawning events reflects stochastic high-frequency oceanographic variability, rather than being driven by genuine interannual oceanographic variability. The out-strength variance for single day spawning events separated by 10 days versus a year begin to diverge slightly after around 15 spawning events. For spawning events separated by 10 days, this corresponds to a total duration of 150 days, which is sufficient time to

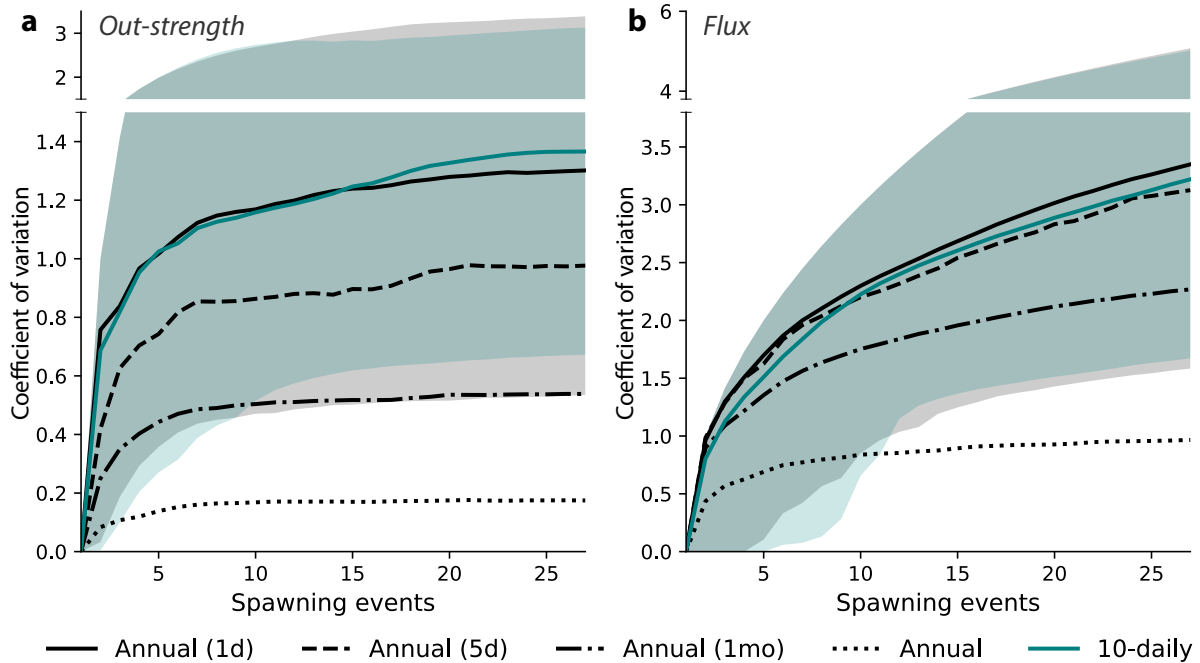


Figure 4.8: (a) out-strength CV across reef cells with a significant detectable out-strength in SECoW for (*black*) annual spawning events from 1993-2019, assuming spawning takes place over (solid) 1 day, (dashed) 5 days, (dash-dotted) 1 month, and (dotted) continuously on an annual basis; and (*teal*) spawning events lasting one day every 10 days. The shaded area represents the 5th - 95th percentiles for the annual 1-day spawning events (*black*) and 10-daily spawning events (*teal*). (b) As with (a), but for flux (based on groups, not cells). Note the different *y* scale.

switch between opposite monsoon phases (introducing additional variance due to seasonal variability). However, this is unlikely to be relevant for most corals, as few broadcast spawning corals spawn across different phases of the monsoonal cycle.

To summarise, although there is genuine interannual variability in the out-strength and flux time-series (reflecting the underlying oceanographic forcing, see chapter 3), most variation in potential connectivity across annual spawning events is simply an artefact arising from low-frequency sampling of a signal dominated by high frequency variability.

4.4.2 Most settling larvae are generated by a small minority of spawning events

Although protracted spawning periods have been observed or inferred for some broadcast-spawning corals in the west Indian Ocean (e.g. Mangubhai & Harrison,

2008; Sola et al., 2015), spawning is often short and synchronous, taking place over a few nights per year at most (e.g. Bronstein & Loya, 2011; Mangubhai et al., 2007; Sola et al., 2016). Since out-strength is generally dominated by day-to-day variability (section 4.3.1), the fate of coral larvae generated by a spawning event is very sensitive to exact timing of spawning.

Since the autocorrelation timescale for out-strength³ is less than 10 days for almost all reefs in SECoW (the 99th percentile is 9.9 days), we can approximate 1-day spawning events separated by 10 days as being independent. We thereby generated a synthetic multi-centennial out-strength time-series by imagining a coral species that spawns one day per year, and extracting the out-strength at each reef site every 10 days between December to February (within the general spawning period for broadcasting corals in the SWIO (Baird et al., 2021; Koester et al., 2021; Mangubhai & Harrison, 2008; Mangubhai, 2009)) from 1993-2019. This resulted in a time-series spanning 243 (9×27) spawning events (or years). From this time-series, we computed the smallest proportion of events that account for 50% of all successfully settling larvae. Finally, we repeated this process ten times to cover all simulated spawning events in December to February, and averaged across these ten initialisations.

SECoW predicts that half of all settling larvae were generated by only 13.3% of annual spawning events (the median across all reef cells). However, this falls to below 4.0% for the decile of reefs with the greatest out-strength variability and, for 47 reefs, this figure was less than 1%. In other words, for these reef sites, most settling larvae were generated by a once-in-a-century spawning event. Reefs with the most unequal temporal distribution of out-strength were almost always remote islands, including most of Seychelles, isolated reefs in Mozambique and Madagascar, Réunion, and the Outer Islands of Mauritius (figure 4.9). The reefs with the most consistent year-to-year out-strength were mostly along the path of the EACC, due to the relatively continuous reef along the coast and predictable, consistent ocean currents. This finding may have important implications for reef ecology, which we explore further in chapter 5.

³Computed based on r_{1d} assuming $r = \exp(-t/\tau)$, where τ is the autocorrelation timescale.

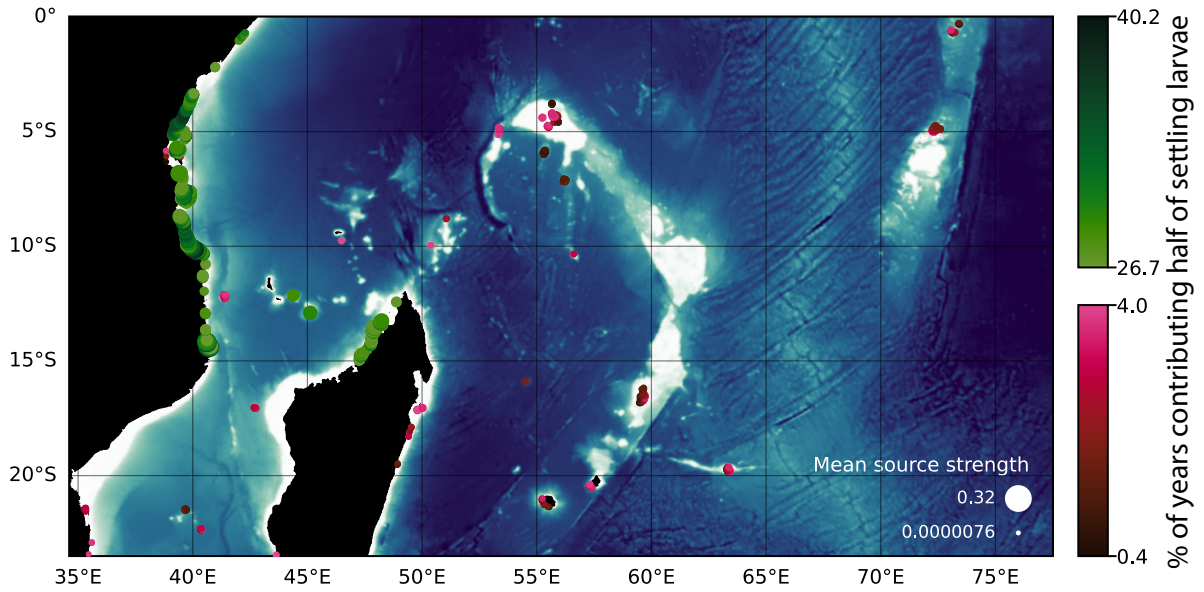


Figure 4.9: Percentage of years contributing half of successfully settling larvae (colours), shown for the lowest and highest decile of reef cells only. Markers are scaled by the mean out-strength, and do not represent the physical size of reef cells.

Some corals have been observed to ‘split spawn’, i.e. undergo multiple spawning events within a reproductive season, often (but not always) separated by a month (Bastidas et al., 2005; Foster et al., 2018; Willis et al., 1985). A previous modelling study based on the Great Barrier Reef found that split spawning separated by a month can significantly increase the reliability of larval supply (Hock et al. (2019), with similar results also found by Kough and Paris (2015). Our finding that a minority of spawning events generate most settling larvae supports this finding (in a very different and diverse oceanographic context), as a greater number of individual spawning events significantly increases the likelihood of a rare ‘high-impact’ dispersal event.

4.4.3 High-frequency oceanographic variability introduces considerable uncertainty to connectivity predictions

Dispersal variability significantly affects metapopulation dynamics (Watson et al., 2012), but this is neglected by many modelling studies, which generally only publish a time-mean potential connectivity matrix. Time-mean potential connectivity matrices are also widely used to explain genetic connectivity (e.g. Foster et al., 2012; Horoiwa et al., 2022; Padrón et al., 2018), and to explore long-term population persistence

and eco-evolutionary dynamics (e.g. Holstein et al., 2022; Kleypas et al., 2016; McManus, Forrest, et al., 2021). However, given the enormous variability in potential connectivity, it is pertinent to consider the uncertainty oceanographic variability may introduce into these predictions.

For this purpose, we consider the backward *cumulated multistep implicit connectivity*, hereon CMIC for brevity, defined by Ser-Giacomi et al. (2021). For a pair of nodes (reef groups) i and j , the CMIC for n steps gives the probability that a pair of random walks terminating at i and j passed through the same node within n steps. If post-settlement processes are neglected and steps of a random walk are interpreted as gene flow, the CMIC may reflect the degree of shared ancestry for a pair of reefs over a given number of generations (Legrand et al., 2022), with 1 indicating definite shared ancestry, and 0 indicating zero shared ancestry. We compute the CMIC between all pairs of reef groups across 100 steps, randomly sampling potential connectivity matrices, assuming spawning events occur across one day during the northwest monsoon. We repeat this process 1000 times, to generate a large set of possible dispersal histories, sampling across the range of primarily stochastic oceanographic variability.

This is shown in figure 4.10 for 100 randomly chosen pairs of sites. The CMIC computed from the time-mean flux matrix (black points in figure 4.10) is rarely close to the median CMIC (white points) across the 1000 realisations, and ordering CMIC using the time-mean flux matrix would result in a completely different ranking to most CMIC estimates based on time-varying flux matrices. For weaker connections (separated by more dispersal steps), the time-mean CMIC is generally lower than the median CMIC. This suggests that the pulsed nature of connectivity may play an important role in connecting distant populations, which is not adequately represented with the time-mean potential connectivity matrix. Even though we compute the CMIC over a significant number of steps (100), the 5th-95th percentile CMIC range (teal bars) is considerable. This uncertainty is fundamentally related to the turbulent nature of ocean currents, thereby imposing limitations on what we can infer about genetic connectivity between site pairs from physical larval dispersal (before even

considering uncertainty in biological parameters). These findings motivate our approach to assessing reef potential connectivity in chapter 5, by similarly considering the CMIC as the median across a range of random connectivity realisations, rather than just the time-mean.

For example, based on the time-mean potential connectivity matrix, high CMIC (and therefore low genetic differentiation) would be expected for the pair of sites marked with an asterisk (*) in figure 4.10. If the genetic differentiation between these sites were in fact observed to be high, this could be interpreted as overprinting of the physical connectivity signal by, for instance, selection. This may be correct but, as is clear from the teal bars in figure 4.10, high genetic differentiation is actually consistent with the CMIC uncertainty introduced by oceanographic variability. It is therefore not clear how much insight can be gained by, for instance, tuning biophysical models to best fit observed genetic differentiation (Legrand et al., 2022), particularly when CMIC uncertainty can span orders of magnitude when computed over fewer steps (not shown).

For demographic connectivity (for example, considering the role larval dispersal may play in driving recovery after mass-mortality events), the larval flux over a smaller number of spawning events is more relevant than the CMIC. Summed over a ten-year period, the total number of larvae transported between pairs of sites may vary over several orders of magnitude due to stochastic ocean variability (not shown), again introducing fundamental uncertainty to what we can predict about demographic connectivity. For instance, the importance for coral resilience of a particular reef-reef connection associated with high time-mean larval flux may be overestimated if that connection has a reasonable chance of being insignificant for a decade or longer. This is an important conclusion that informs our approach to identifying reefs that may act as important sources of larvae in the short term in the following chapter (chapter 5). We therefore argue that studies generating potential connectivity data to inform marine management efforts should discuss (and publish) data on dispersal *variability* rather than just the time-mean dispersal matrix (or the mean seasonal cycle). It is also questionable whether a time-mean dispersal matrix

should be used to explain recent inferred gene flow (e.g. Padrón et al., 2018), when model-data mismatch (or agreement) could simply be due to stochastic variability.

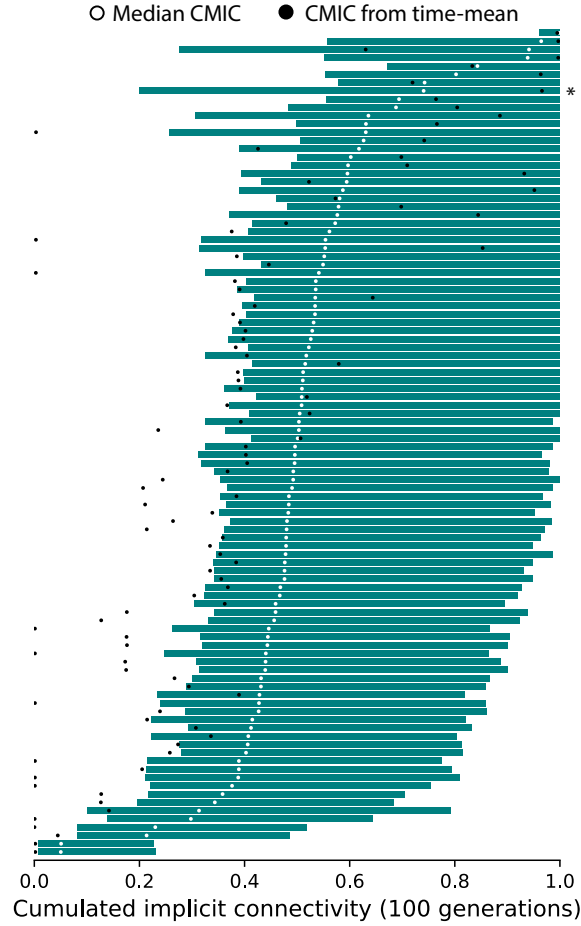


Figure 4.10: (Backward) cumulated multistep implicit connectivity (CMIC) over 100 steps for 100 randomly chosen connections (which have nonzero connectivity for at least 1% of spawning events). Connections for each step are selected based on a random time-slice during the northwest monsoon, and this is repeated 1000 times to obtain 1000 CMIC realisations. The teal bars show the 5th-95th percentiles across the 1000 realisations, and the white points represent the median. The black points represent the CMIC obtained from the time-mean potential connectivity matrix.

4.5 Conclusions

Coral potential connectivity is highly complex, with time-mean and seasonal signals often drowned out by high-magnitude, high-frequency variability. However, we have demonstrated that there is some order within this complexity.

Within the SWIO, there are relatively robust oceanographic and geographic predictors of high-frequency variability in potential connectivity, which is most extreme at remote islands and atolls under the influence of rapid ocean currents, and suppressed along near-shore reefs, particularly where ocean currents tend to trap larvae against the coast. These patterns will provide marine practitioners with an initial, qualitative indication of how significant high-frequency variability in potential connectivity may be at sites of interest. Although a predictable seasonal cycle is dominant at some reefs, particularly within the EACC, our results demonstrate that, at most reefs, day-to-day variability in potential connectivity is greater in magnitude than the mean connectivity, the seasonal cycle, and interannual variability.

Since most successfully settling larvae are generated by a small minority of spawning events, studies simulating only a small number of spawning events may significantly underestimate long-term potential connectivity, particularly at remote islands. This may have particularly important consequences for predicting genetic connectivity, in which rare but ‘high-impact’ dispersal events may play a disproportionately important role. Reasonably characterising the potential connectivity of a relatively sparse network of reefs therefore requires a large number of spawning events, ideally over multiple decades. If this is not possible (for instance, due to the costs associated with running a high-resolution hydrodynamical model), simulating a large number of spawning events over a smaller number of years likely gives a better indication of potential connectivity variability than simulating a smaller number of spawning events over a larger number of years. Neglecting this will severely under-represent uncertainty in potential connectivity from the dispersal model. However, even with a large number of simulated spawning events, the time-mean (or seasonal) connectivity matrix alone may be of limited utility for many ecological applications, since the actual potential connectivity over years and even decades may deviate massively from the long-term average.

Since the autocorrelation timescale for potential connectivity at most reefs is on the order of a few days, protracted spawning eliminates most variability associated with out-strength, and some variability associated with the strength

of individual connections. This suggests that the larval supply associated with broadcasting corals that spawn infrequently over a short duration is likely to be highly irregular, inconsistent and unpredictable, in comparison to corals carrying out split-spawning, asynchronous and protracted spawning, or continuous larval release by some brooding corals. Even with excellent data assimilation (which is rarely available at fine scales relevant for larval dispersal), day-to-day potential connectivity variability is chaotic and stochastic, and the exact timing of spawning therefore has limited practical significance.

We expect that these results will also apply to oceanographically and geographically analogous reef systems outside of the Indian Ocean. For example, remote coral islands influenced by equatorial currents - such as Seychelles - are abundant throughout the Pacific, and linear reef systems along the path of major western boundary currents - such as the coasts of Kenya and Tanzania - are also found in Florida and southern Japan. Despite the strong influence of the monsoons on surface circulation in our study region (which is unique to the Indian Ocean and some Southeast Asian seas), our results demonstrate that, at most reefs, day-to-day variability in potential connectivity is greater in magnitude than the mean connectivity, the seasonal cycle, and interannual variability.

Given these findings, it is clear that sensibly considering temporal variability will be important in drawing conclusions about the connectivity of reefs across the SWIO, and simply considering time-mean (or climatological-mean) potential connectivity matrices may not fully represent typical larval dispersal events. Bearing these conclusions in mind, in the final chapter, we finally attempt to map coral connectivity for the entire SWIO, with the intention of supporting marine practitioners in prioritising conservation efforts, and investigating to what extent physical larval dispersal explains population genetics and biogeography.

5

Coral connectivity and resilience in the southwest Indian Ocean

5.1 Introduction

As described in section 1.5, understanding large-scale patterns of coral connectivity is important data for effective marine spatial planning, which is lacking in the SWIO. At present, there is a basic understanding of reef connectivity in the tropical SWIO. The time-mean surface circulation in the SWIO is to first-order explained by Sverdrup transport, generating southward and northward interior transport north and south of $\sim 15^\circ\text{S}$ respectively (Godfrey, 1989; Talley, Pickard, Emery, & Swift, 2011) (section 1.3.2). This generates the westward flowing South Equatorial Current (SEC). When the SEC meets Madagascar, it splits into the Northeast Madagascar Current (NEMC) and Southeast Madagascar Current (SEMC), with the bifurcation latitude varying slightly following seasonal and interannual variability of interior Sverdrup transport (Yamagami & Tozuka, 2015). The SEMC flows southward along the east coast of Madagascar before feeding the Agulhas system, whilst the NEMC 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 NEMC then bifurcates, partially feeding the net-southward but eddy-dominated flow of the Mozambique Channel, but with most water entering the East Africa Coastal Current

(EACC), which flows northward along the coast of Tanzania and Kenya (Schott & McCreary, 2001; Swallow et al., 1991; Van Der Werf et al., 2010). The EACC tends to cross the equator during the southeast monsoon (austral winter), feeding the Somali Current. During the northwest monsoon (austral summer), the Somali Current reverses due to the monsoonal reversal of winds, causing the EACC to tend to separate from the coast south of the equator and feed the eastward South Equatorial Countercurrent (SECC) (Schott & McCreary, 2001), although there is considerable interannual variability (Nagura & McPhaden, 2010; Sachidanandan et al., 2017).

Qualitative interpretation of these patterns suggests that larval dispersal should be largely westward within the region dominated by the SEC, with eddy-mediated dispersal across the Mozambique Channel, and strong connectivity along the path of the EACC, which flows past mostly continuous reef along the coasts of Tanzania and Kenya. This is broadly supported by regional coral biogeography (Obura, 2012), coral population genetics (e.g. Keshavmurthy et al., 2013; van der Ven et al., 2022), and global (Wood et al., 2014) and regional (Crochelet et al., 2016; Gamoyo et al., 2019; Mayorga-Adame et al., 2017) larval dispersal simulations. These studies provide valuable insights into the connectivity of the SWIO, and generally support the existence of well-connected reef clusters in the north Mozambique Channel and along the path of the EACC, with Seychelles and the Mascarene Islands being more isolated.

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 larval dispersal studies relying on relatively coarse oceanographic data (Crochelet et al., 2016; Gamoyo et al., 2019; Wood et al., 2014), necessitating the use of finer resolution models to investigate to what extent these patterns can be explained through physical larval dispersal versus other biological processes such as selection. Using larval dispersal simulations based on a ~ 2 km resolution ocean model, Mayorga-Adame et al. (2017) found that sub-mesoscale flow around ocean islands indeed generates localised patterns of retention and dispersal, such as poor connectivity within the Pemba and Zanzibar channels, explaining observations from coral population genetics

(e.g. van der Ven et al., 2016). However, these simulations were temporally limited (which is potentially cause for concern, based on the conclusions from chapter 4), and are not available for the wider SWIO. A new coral population genetics dataset has also recently been made available for many sites across Seychelles (Burt et al., 2022). Genetic studies in the SWIO region have generally focused on the Mozambique Channel and Kenya-Tanzania regions, so investigating the physical drivers of coral connectivity across Seychelles in particular is valuable and novel. However, the very small size of most islands in Seychelles necessitates high resolution hydrodynamic data to resolve fine-scale flow patterns around islands.

Finally, although Crochelet et al. (2016), Gamoyo et al. (2019), and Mayorga-Adame et al. (2017) considered coral resilience and connectivity through metrics such as time-mean connectivity matrices, the number of upstream and downstream connections for sites, and betweenness centrality (the degree to which reefs act as bottlenecks for larvae), there is limited evidence that considering these metrics in marine spatial planning leads to improved conservation outcomes. Eco-evolutionary simulations based on realistic larval dispersal networks (e.g. McManus, Forrest, et al., 2021) also suggest that it is challenging to predict the resilience of corals *a priori*. This motivates an investigation of the response of corals in the tropical SWIO to future environmental change using an eco-evolutionary model, to identify reefs which might be particularly vulnerable and resilient in response to warming over the 21st Century (and the physical drivers of these patterns).

In this chapter, we set out to answer the following questions:

1. What is the large scale structure of coral potential connectivity in the SWIO?
2. To what extent does potential connectivity explain biogeography and coral population genetics, regionally and, in particular, across Seychelles?
3. How may potential connectivity affect the resilience and higher-level importance of coral reefs in this region?

5.2 Methods

5.2.1 Hydrodynamical and larval dispersal models

This study uses the same larval dispersal simulations (SECoW) as described in chapter 4 (section 4.2.1). Briefly, SECoW combines hydrodynamic data from the 2 km WINDS-M model (chapter 3) with Lagrangian particle tracking simulations using OceanParcels (Delandmeter & van Sebille, 2019; Lange & van Sebille, 2017). Coral larvae are represented as particles which are positively buoyant but otherwise passive. 1024 particles are released at midnight every day from 1 January 1993 to 31 December 2019 at 8088 2×2 km reef cells identified within the WINDS-M domain (figure 4.1) and are advected for 120 days following surface currents from WINDS-M. The number of virtual larvae initially represented by each particle is proportional to the reef area of the origin reef cell (i.e. constant fecundity is assumed), based on the satellite-derived reef map (Li et al., 2020). As in chapter 4, larvae experience competency acquisition and loss, and time-varying mortality according to parameters estimated by Connolly and Baird (2010), and a settling rate proportional to the fraction of a cell covered by reef (1.0 d^{-1}). We focus on the moderate parameters for *P. daedalea* in this study (figure 4.2), but, similarly to chapter 4, findings are relatively insensitive to most of these parameters (dataset 5.1).

5.2.2 Connectivity metrics

5.2.2.1 Potential connectivity

We here formally define the potential connectivity, C_{ijk} , as the likelihood that a larva from reef cell i settles at reef cell j from spawning event k (Mitarai et al., 2009):

$$C_{ijk} = \frac{F_{ijk}}{A_i} \quad (5.1)$$

5.2.2.2 Out-strength

We define the *out-strength*, $S_{ik}^{\rightarrow}$, as the likelihood that a larva from reef cell i settles anywhere. This metric is defined identically to section 4.2.2, i.e.

$$S_{ik}^{\rightarrow} = \frac{\sum_j F_{ijk}}{A_i}. \quad (5.2)$$

In section 5.3.3, we also consider the related *in-strength* metric $S_{jk}^{\leftarrow}$, which is equivalent to the ratio between the number of larvae settling and spawning at a site, which has the same value as the number of larvae settling per unit area of reef when $\rho = 1 \text{ m}^{-2}$.

$$S_{jk}^{\leftarrow} = \frac{\sum_i F_{ijk}}{A_j} \quad (5.3)$$

5.2.2.3 Out-consistency

We define the *out-consistency*, $E_i^{\rightarrow}$, as the minimum proportion of spawning events at site i responsible for 50% of larvae settling anywhere.

This is a novel metric introduced in this thesis, and is identical to the metric used in section 4.4.2. If all spawning events at site i are associated with equal out-strength (i.e. all spawning events result in the same number of larvae from i settling anywhere), then site i is highly consistent as a larval source and $E_i^{\rightarrow} = 0.5$. As larval settling becomes increasingly sporadic and associated with a smaller proportion of spawning events, $E_i^{\rightarrow}$ approaches 0. We compute $E_i^{\rightarrow}$ by sorting $S_{ik}^{\rightarrow}$ along k , and finding the smallest number of events such that the cumulative out-strength exceeds half of the total out-strength across all k .

5.2.2.4 Out-entropy

We define the *out-entropy*, $H_{ik}^{\rightarrow}$, as the entropy associated with larval destinations for larvae spawning from source site i and event k . In other words, $H_{ik}^{\rightarrow}$ represents the uncertainty associated with (or information required to describe) where larvae spawning at site i settle. $H_{ik}^{\rightarrow}$ has units of bits, and is computed through the following:

$$H_{ik}^{\rightarrow} = - \sum_j \left(\hat{F}_{ijk} \cdot \log_2 \hat{F}_{ijk} \right), \quad (5.4)$$

$$\hat{F}_{ijk} = \frac{F_{ijk}}{\sum_j F_{ijk}}. \quad (5.5)$$

The out-entropy is maximised by larval destinations being distributed equally across a large number of reef cells. As an example, $H_{ik}^{\rightarrow} = 4$ bits could represent larvae settling in equal numbers across $2^4 = 16$ destination reef cells. Note that it is possible for the out-entropy to be large whilst the out-strength is small (and vice versa).

To our knowledge, this is a novel metric for considering larval dispersal (although it is similar to the concept of diversity in ecology).

5.2.2.5 Out-bleaching alert dissimilarity (BAD)

NOAA Coral Reef Watch defines the Coral Bleaching HotSpot value as the difference between the SST, and the maximum monthly mean (MMM) temperature in the SST climatology. The Degree Heating Week (DHW) is a measure of accumulated thermal stress, and is defined as the time-integral (unit weeks) of the HotSpot value over a rolling 12-week period, where the HotSpot value exceeds 1. Whilst imperfect, $DHW > 4$ is indicative of elevated bleaching risk (Donner et al., 2005; Liu et al., 2003; NOAA Coral Reef Watch, 2020; Sully et al., 2019). Based on the NOAA Coral Reef Watch daily global 5 km satellite coral bleach DHW product from 25/03/1985 to 12/04/2023 (NOAA Coral Reef Watch, 2023; Skirving et al., 2020), bilinearly interpolated to the WINDS grid, we compute a binary ‘bleaching risk’ time-series B_{ik} for each site i and day k , defined as the following:

$$B_{ik} = \begin{cases} 1, & \text{if } DHW_{ik} \geq 4, \\ 0, & \text{if } DHW_{ik} < 4. \end{cases}$$

For all pairs of reefs i and j , we then compute $B_{ij}^{\rightarrow}$, the proportion of time that j is at bleaching risk given that i is *not* at bleaching risk,

$$B_{ij}^{\rightarrow} = \frac{\sum_k ((1 - B_{ik}) B_{jk})}{\sum_k (1 - B_{ik})}.$$

From a connectivity perspective, $B_{ij}^{\rightarrow}$ is a measure of the usefulness of i to j from the perspective of i (the proportion of time i is not under thermal stress that j is under thermal stress).

Finally, we define the out-bleaching alert dissimilarity (BAD), $BAD_{ik}^{\rightarrow}$ as the average $B_{ij}^{\rightarrow}$ across the larval sinks for i (weighted by larval fluxes),

$$BAD_{ik}^{\rightarrow} = \sum_j (B_{ij}^{\rightarrow} \hat{F}_{ijk}), \quad (5.6)$$

where $\hat{F}_{ijk}$ was defined in equation (5.5). This is a novel metric. In short, high out-BAD for i means that many larvae from i are being distributed to reefs that are at bleaching risk, when i is not at bleaching risk, and therefore indicates that the site may be very useful for the recovery of its downstream reefs.

5.2.2.6 Out- Δ TST (thermal stress threshold)

If a coral reef is connected to reefs in different thermal environments, larvae may be exchanged with genotypes adapted to different thermal regimes (Kleypas et al., 2016). The thermal stress threshold (TST) is defined as the temperature threshold at which a coral begins to experience thermal stress. Although various definitions exist (Kumagai et al., 2018; Logan et al., 2012), we use a TST parsimonious with our definition of the BAD, taking the maximum monthly mean (MMM) SST +1 °C from the NOAA Coral Reef Watch daily global 5 km satellite SST product. Similarly to Kleypas et al. (2016), we define the out- Δ TST, $\Delta\text{TST}_{ik}^{\rightarrow}$, as the difference between the TST of a source site i and the weighted average of the larval destinations.

$$\Delta\text{TST}_{ik}^{\rightarrow} = \sum_j (\text{TST}_j \hat{F}_{ijk}) - \text{TST}_i, \quad (5.7)$$

where, again, $\hat{F}_{ijk}$ was defined in equation (5.5). If the out-TST is positive, the site is sending larvae to reefs that, on average, have a higher TST.

5.2.2.7 Betweenness centrality

Betweenness centrality is a measure of the extent to which a node acts as a bottleneck in a network. Specifically, the betweenness centrality of a node i is the proportion of the shortest paths between all pairs of nodes in a network that pass through i (Freeman, 1977). Although there is little empirical data demonstrating its utility in marine spatial planning (along with most metrics described here), nodes with high betweenness centrality are suspected to play an important role in maintaining network resilience, since the elimination of these nodes would result in network fragmentation (e.g. Brunner et al., 2022; Treml et al., 2008). Traditionally, the ‘shortest’ path between a pair of nodes i and j in a weighted network G is defined as the path that minimises the sum of weights along the path. However, as pointed out by Costa et al. (2017), this definition is not sensible when the weights in G represent dispersal probabilities, since the probability of dispersal from i to j is the product of edge weights, not the sum (although noting the more elaborate methods for computing connectivity in Ser-Giacomi et al. (2015)). As a result, we compute

the betweenness centrality on a network with modified weights $w'_{ijk} = -\log w_{ijk}$ using a standard algorithm in Networkx (Brandes, 2001; Hagberg et al., 2008).

5.2.2.8 Temporal variability

As was discussed in depth in chapter 4, the structure of a dispersal network can vary significantly with time due to stochastic, seasonal, and interannual variability. We compute the strength, entropy, BAD, Δ TST, and betweenness centrality using the time-varying flux matrix, and use the median across time to represent a typical value for a spawning event. We compute these quantities during post-processing, so can export them at the cell-level. In the case of the betweenness centrality, this computation is relatively expensive, as it requires the shortest path to be computed between all pairs of nodes in the network. As a result, we compute this metric at the group level.

5.2.2.9 Importance

We also compute a composite metric, which we call *importance*. This metric is an attempt to quantify the importance of a reef cell for maintaining the resilience of the reef network as a whole, and depends on out-strength, out-consistency, out-entropy, out-BAD, negative out- Δ TST, and betweenness centrality. The rationale is as follows:

- **Out-strength:** Reefs with high out-strength generate a large number of larvae (relative to the reef's size) that successfully settle, and are therefore more likely to play an important role in supporting demographic growth/stability in other reefs.
- **Out-consistency:** Reefs with a high out-consistency *consistently* generate larvae that successfully settle, and are therefore more reliable larval sources.
- **Out-entropy:** Reefs with high out-entropy distribute larvae in similar numbers across a large number of destinations, and are therefore more likely to play a significant role in connectivity for many other reefs.

- **Out-BAD:** Reefs with high out-BAD act as potentially particularly important larval sources for other reefs, as they are less likely to be under thermal stress when downstream reefs are (and therefore have a particularly high need for larval supply for recovery).
- **Out- Δ TST:** Reefs that supply larvae to cooler reefs are potentially a source of larvae with more heat-tolerant genotypes, and may therefore support downstream reefs in adapting to warming.
- **Betweenness centrality:** Reefs with a high betweenness centrality may act as bottlenecks for gene flow across the reef network, and therefore play an important role in minimising network fragmentation.

We compute importance by ranking reefs for each of the six metrics above (with a higher rank = better), normalising in the interval $[0, 1]$, and taking the mean across the six metrics. We use the term ‘importance’ for simplicity, but specifically mean ‘importance for the resilience of the reef network through larval dispersal’. The actual ‘importance’ of a reef is, of course, multifaceted and dependent on a much greater range of environmental, ecological and social factors. We also stress that the basis for assuming any of the above metrics are useful indicators of a reef’s importance is largely theoretical. Although there is some empirical evidence for the importance of connectivity in promoting resilience and biodiversity (Fontoura et al., 2022; Gouezo et al., 2019; Harris et al., 2020) and connectivity-related metrics are considered as important by reef experts (McClanahan et al., 2012), most evidence is based on theoretical ecology (Almany et al., 2009; Elmhirst et al., 2009; McManus, Forrest, et al., 2021). It has also been argued that connectivity may not be a key parameter in marine conservation, on the basis of observations (Graham et al., 2011) and theory (Costello & Connor, 2019). As a result, although our ‘importance’ metric represents a diversity of reasonable indicators for the importance of reefs in maintaining the resilience of the wider reef network, this metric should absolutely *not* be used as a primary metric for prioritising reef conservation efforts since there is insufficient empirical evidence to support this.

5.2.2.10 CMIC

Finally, we also consider the *backward cumulated multistep implicit connectivity* between reefs (Ser-Giacomi et al., 2021), hereon *CMIC*. For a pair of nodes i and j , the CMIC is the probability that a pair of random walks arriving at i and j once passed through the same node within k steps. With well-mixed populations within nodes and in the absence of selection or other post-settlement processes, the CMIC_{ij} can be interpreted as the number of generations of dispersal separating a random pair of corals in two sites from a common ancestral population (Legrand et al., 2022). Based on this interpretation, we would expect less genetic differentiation between coral populations separated by fewer steps (or generations) of dispersal. We estimate this number of generations G_{ij} by computing the number of steps k required for $\text{CMIC}_{ij} > 0.5$. We base this calculation on the median across 100 random temporal connectivity matrices, and also compute the 5th-95th confidence interval across these matrices to gauge how sensitive G is to stochastic oceanographic variability. Note that, contrary to potential connectivity, the CMIC is not associated with a direction, i.e. $\text{CMIC}(i, j) = \text{CMIC}(j, i)$.

5.2.3 Clustering

It is difficult to obtain an intuitive understanding of the network structure (e.g. dispersal barriers, clusters of reefs that tend to retain larvae) from connectivity matrices. To identify clusters of reefs that tend to retain coral larvae, we partition the network using the Infomap implementation of the map equation (Edler et al. (2023) and Rosvall et al. (2009), and appendix C.1) which has previously been used to identify community structure in the marine environment (Deauna et al., 2021; Reijnders et al., 2021). Infomap partitions a network by minimising the information required to describe a random walk, thereby identifying clusters of nodes with a high residence time. It is therefore very well suited for identifying partitions that tend to retain ‘flow’, compared to other metrics to identify community structure such as modularity which only consider pairwise interactions (appendix C.1, Rosvall et al. (2009)). In this case, the flow being described is that of larvae, with

flow between nodes being proportional to the probability of larval dispersal. Over multiple steps, the random walk could be interpreted as gene flow (in the absence of external factors such as selection).

Since potential connectivity varies with time, the community structure identified by Infomap is also time-varying. Rosvall and Bergstrom (2010) considered change in community structure by mapping node membership through time using alluvial diagrams. However, in our case, most temporal variability in the reef network is stochastic (chapter 4), and our goal is to identify *persistent* network structure. Reijnders et al. (2021) identified persistent transport barriers to flow in the Arctic Ocean by mapping nodes that are consistently situated on boundaries between clusters. This method is well suited to networks defined on a regular grid (as was the case for Reijnders et al. (2021)), but is difficult to visualise for an irregular, sparse network such as ours, and also obfuscates the ‘distance’ between nodes.

Instead, we identify *meta-clusters* of reefs that are persistently members of the same Infomap clusters throughout stochastic oceanographic variability, through a method inspired by common approaches in population genetics. To do this, we firstly subsample the full potential connectivity matrix by extracting ten randomly chosen time-slices, taking the mean across these time-slices (thereby finding the total potential connectivity across ten random spawning events), and repeating this process 1000 times. We thereby end up with 1000 random, static, ‘short-term’ potential connectivity matrices, sampling across the range of stochastic oceanographic variability. We then independently partition the 1000 potential connectivity matrices using Infomap, storing the partitions as a 180×1000 partition matrix (180 nodes (groups) and 1000 partitions), where each element is the cluster membership of a node within a particular potential connectivity matrix. For the Infomap algorithm, we use 10 iterations of the outer optimisation loop (there is little difference in code length between iterations) and the default teleportation probability. The solution is very robust with respect to these parameters. The Markov-time determines the spatial scale of clusters identified by Infomap, and there is no obvious *a priori* value for this parameter (Reijnders et al., 2021; Schaub et al., 2012). Since the default

value generates a reasonable number of top-level clusters (typically 5-10) and the basic large-scale structure as described below does not fundamentally change with the Markov-time, we use the default parameter of 1.0.

Since the large-scale structure of the network is relatively persistent through time, there is a large amount of redundancy across partitions. A principal component analysis (PCA) identifies that most variance in cluster membership is explained by the top three principal components, so we reduce the 180×1000 partition matrix to a 180×3 matrix based on these three principal components. Finally, we map each node (group) to a colour by assigning its position in this three-dimensional space to values of red, green and blue (RGB) (figure 5.6). The distance between nodes in RGB space therefore represents how consistently nodes appear in the same cluster, with significant differences in colour representing persistent dispersal barriers. We define reefs that consistently appear in similar clusters (i.e. are close in RGB space) as *meta-clusters*.

5.2.4 Eco-evolutionary simulations

Most predictions for future coral decline do not consider the potential for evolution, but since thermal tolerance is somewhat heritable (e.g. Dixon et al., 2015), it is possible that rapid adaptation could occur in response to ocean warming (thereby potentially preventing population collapse). To investigate this, we adapted the eco-evolutionary model described by McManus, Forrest, et al. (2021) and McManus, Tekwa, et al. (2021) to SECoW. This model simulates ecology (hard coral cover) at reef nodes j , where each node has habitable area A_j (equal to the reef cover in SECoW multiplied by a constant tunable parameter representing the carrying capacity), and is associated with hard coral cover $N_j(t)$, $N_{\min} \leq N_j(t) \leq 1$. We initialise hard coral cover at the carrying capacity, although note that the model is not sensitive to the initial conditions. We assume that coral fitness $g_j(z_j(t), T_j)$ is based on a single trait, optimal annual mean SST (z_j), and its distance from the actual annual mean SST in a cell (T_j), following a Gaussian with a temperature scale w . Fitness can become negative when $T_j \gg z_j$. The growth rate also depends on density-dependent immigration (larval dispersal from other reefs), and genetic

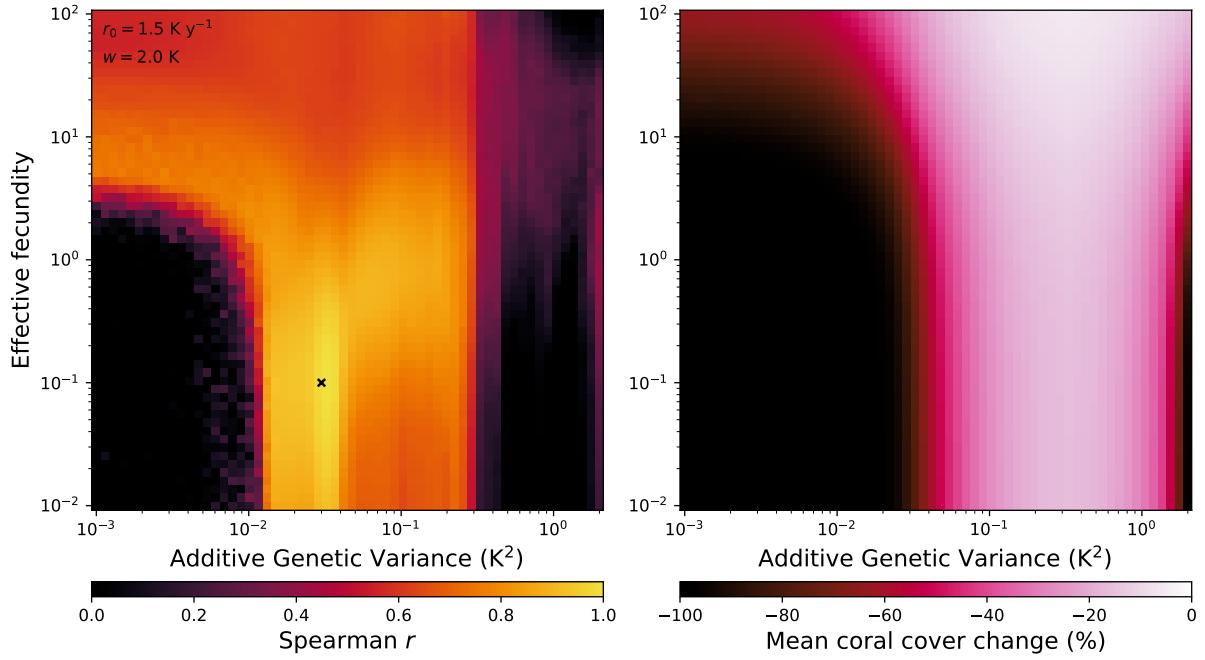
load (additive genetic variance V resulting in a reduction in mean population fitness when z_j is close to T_j , and an increase in mean population fitness when z_j is far from T_j). The trait value of a population can change through time (evolution), through the introduction of genotypes adapted to different thermal regimes (through larval dispersal from other reefs), and selection (depending on the additive genetic variance, and local slope of the fitness curve).

To investigate the response of reefs in the SWIO to future warming, we impose annual-mean sea surface temperature based on an MPI-ESM-LR (CMIP5) simulation from 1850-2300 under the moderate RCP4.5 scenario (Giorgetta et al., 2013), statistically downscaled using satellite-based OSTIA SST (Good et al., 2020) using the Delta method (Hay et al., 2000) (section 5.2.4.3).

In this study, we use similar parameters to McManus, Forrest, et al. (2021), as listed in table 5.1. However, many of these parameters are highly uncertain, particularly the additive genetic variance V and effective fecundity f . A sensitivity analysis (figure 5.1) shows that the *ranking* of reef response to warming is fairly insensitive to additive genetic variance within the range characterised as ‘low-to-high’ (0.01-0.1, McManus, Forrest, et al. (2021)). However, the actual decline simulated is highly sensitive within this feasible range. Sensitivity to the effective fecundity is low; however, exceptionally high effective fecundity may be able to compensate for very low additive genetic variance. Although long-term monitoring is sparse in the western Indian Ocean, our results agree reasonably well with observations of coral cover over the past three decades (Souter et al., 2021) based on a carrying capacity of 0.4, aside from the Chagos Archipelago, where the model is unable to reproduce the decadal-scale variability in coral cover inferred from observations (figure 5.2).

Although temporal variability in connectivity may be very important in understanding the short-term dynamics of connectivity and particular connections between reefs (section 4.4.3), it appears to be less important in long-term reef resilience in this eco-evolutionary model. Although we cannot run these simulations with time-varying potential connectivity at the cell-level (the full matrix is too large), simulations run at a group-level show little difference between time-varying and time-mean

Parameter	Definition	Value
r_0	Scaling factor for growth rate	1.5 K y^{-1}
w	Thermal tolerance	2 K
f	Effective fecundity	0.1
V	Additive genetic variance	0.03 K^2
K	Carrying capacity	0.4

Table 5.1: Parameters used for main eco-evolutionary simulations.**Figure 5.1:** *Left:* Correlation (Spearman's r) of coral decline section 5.2.4.4 with the base case used in this study (cross), as a function of the additive genetic variance and effective fecundity. *Right:* Mean coral decline as a function of the additive genetic variance and effective fecundity.

connectivity matrices under the parameters used in this study (figure C.2). Only under exceptionally high effective fecundity does a difference emerge. As a result, we use the time-mean connectivity matrix (for spawning events between October and March), and can therefore run simulations at the cell-level.

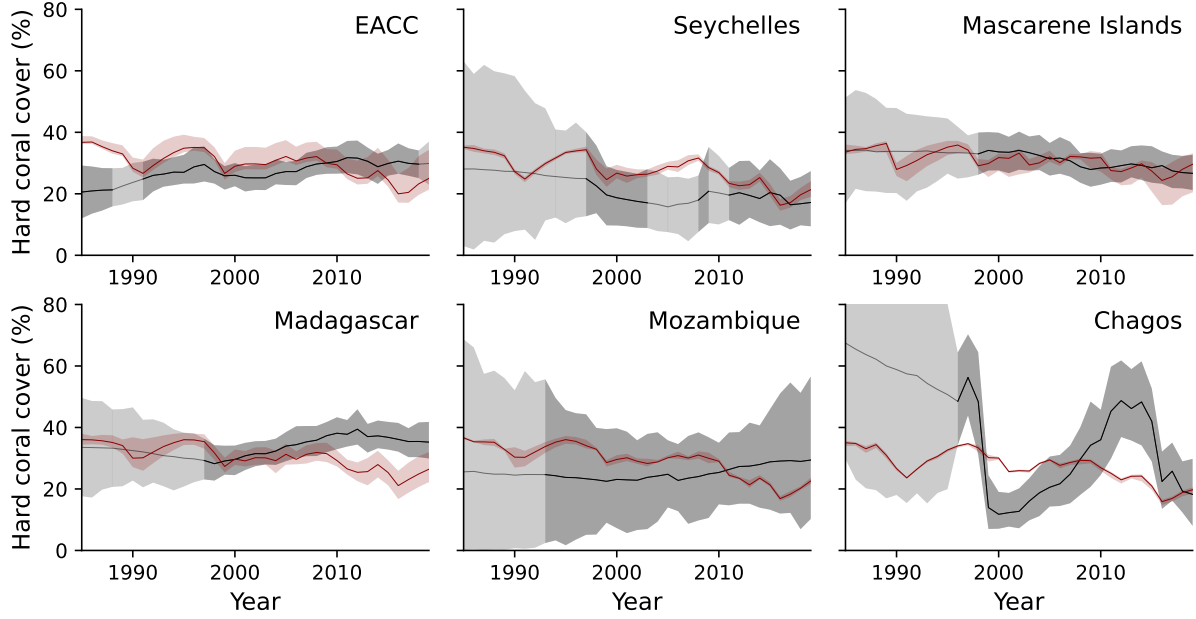


Figure 5.2: *Red:* Modelled hard coral cover (with 5th-95th range across reef cells) for six ecoregions considered by Souter et al. (2021) that have significant representation in SECoW, assuming a carrying capacity of 0.4. *Black:* Mean coral cover estimated by Souter et al. (2021) within each ecoregion (with 5th-95th confidence intervals). Pale lines indicate that data is missing from the observational records. Note that, although SECoW does include the Addu and Fuvahmulah atolls of Maldives, this only represents a very small proportion of reefs within Maldives, so we do not include a comparison with the assessment of Maldives in Souter et al. (2021).

5.2.4.1 Ecology

Change in coral cover is driven by (1) population growth, (2) immigration, and (3) genetic load:

$$\frac{dN_j}{dt} = g_j N_j + \rho a I_j (1 - N_j) + \frac{1}{2} V \left. \frac{\partial^2 g_j}{\partial z^2} \right|_{z=z_j} N_j, \quad (5.8)$$

$$I_j = \frac{1}{A_j} \sum_i F_{ijk}, \quad (5.9)$$

$$g_j = r_j (1 - N_j) - m_j, \quad (5.10)$$

$$r_j = \frac{r_0}{\sqrt{2\pi w^2}} \exp\left(\frac{-(T_j - z_j)}{w^2}\right), \quad (5.11)$$

$$m_i = \begin{cases} 0 & T_j \leq z_j, \\ 1 - \exp\left(\frac{-(T_j - z_j)}{w^2}\right) & T_j > z_j. \end{cases} \quad (5.12)$$

Population growth

The population growth rate term is similar to the standard logistic differential

equation, with the addition of a mortality term. The population growth rate is maximum when the annual mean SST at j , T_j , is equal to the population mean trait value z_j . Fitness decreases following a Gaussian as the annual mean SST at j increases in distance from z_j . The width of this distribution is set by the parameter w (K), where higher values of w represent a lower sensitivity to T_j . The maximum growth rate is $r_0/\sqrt{2\pi w^2}$, where r_0 is a scaling parameter. The mortality term m_j allows the growth rate to become negative when the coral population is under significant thermal stress.

Immigration

I_j (d^{-1}) represents the supply of (larval) immigrants to j relative to the habitat area at j , ρ is the coral fecundity (m^{-2}), and a is the area occupied per settled coral spat multiplied by the survival probability during settlement (m^{-2}).

Assuming all settlement occurs quickly enough such that population growth and genetic load are insignificant and that the coral cover before settlement was N_j^0 then, after one spawning event:

$$\begin{aligned}\frac{dN_j}{dt} &= \rho a I_j (1 - N_j), \\ \Delta N_j &= (1 - N_j^0) (1 - e^{-\rho a I_j \Delta t})\end{aligned}$$

The parameters ρ and a are very poorly constrained. As a first guess, Álvarez-Noriega et al. (2016) observed $\sim 10^7$ oocytes m^{-2} being generated by broadcast spawning corals after spawning. If 1% of oocytes develop into larvae, then the fecundity ρ of the reef following our definition is 10^5 m^{-2} . A typical coral spat occupies an area of order 10^{-5} m^2 (Bauman et al., 2015; Nozawa, 2012) and assuming a survival chance of 10% (Edmunds, 2023), we may therefore expect $a \sim 10^{-6} \text{ m}^2$. We call the product $\rho a = f$, the effective fecundity (McManus, Tekwa, et al., 2021).

Genetic load

V represents the additive (heritable) genetic variance around the mean trait value z_j . When the population is well adapted to the environment (i.e. the mean trait value z_j

is close to the annual SST, $\left. \frac{\partial^2 g_j}{\partial z^2} \right|_{z=z_j} < 0$), genetic variance results in a *reduction* in the mean fitness of the population, as the average coral will have $g < g(z_j)$. Conversely, when the population is poorly adapted to the environment and $\left. \frac{\partial^2 g_j}{\partial z^2} \right|_{z=z_j} > 0$, genetic variance results in an *increase* in the mean fitness of the population.

5.2.4.2 Evolution

The mean trait value of a population can change through time based on (1) the introduction of genotypes through immigration, and (2) selection:

$$\frac{dz_j}{dt} = (z_j^c - z_j) \left(\frac{\rho a I_j (1 - N_j)}{N_j} \right) + q_j V \left. \frac{\partial g_j}{\partial z} \right|_{z=z_j}, \quad (5.13)$$

$$q_j = \max \left(0, 1 - \frac{N_{\min}}{\max(N_{\max}, 2N_j)} \right). \quad (5.14)$$

Immigration

Larvae settling at reef j will be associated with genotypes that are adapted to the environment of their source reef. z_j^c is the mean trait value across the larval sources for j , and $\frac{\rho a I_j (1 - N_j)}{N_j}$ is the ratio between the existing population at j , and the new immigrant population. As a result, the larger the proportion of immigrants relative to N_j and the greater the difference in mean trait value between j and its larval sources, the faster the mean trait value at j will evolve due to the introduction of new genotypes.

Selection

Selection at j selects for genotypes that are adapted to the local environment (mean annual SST), with the mean trait value moving towards the local optimum in g_j . Selection is stronger when the fitness curve is steeper, and when there is greater additive genetic variance. When the population size is extremely small, selection is inhibited, implemented through the function q_j .

5.2.4.3 Data sources

As in McManus, Forrest, et al. (2021), we generate a simple, statistically downscaled time-series of annual-mean SST based on the delta method (Hay et al., 2000), by adding SST *changes* from a coarse-resolution climate model to a high-resolution mean state from satellite observations. This method assumes that the present mean state fully captures fine-scale (< 100 km) spatial variability in SST, and that temporal changes in SST have a comparatively weak spatial dependence (and can therefore be captured by the coarse-resolution climate model).

We obtain the high-resolution satellite-derived foundation SST from OSTIA (Good et al., 2020), and the coarse-resolution climate data from the r1i1p1 run of MPI-ESM-LR (CMIP5) under the RCP4.5 (mid-range) scenario (Giorgetta et al., 2013). MPI-ESM-LR has a resolution in the ocean of around 150 km, has an intermediate transient climate response and equilibrium climate sensitivity within CMIP5 (Meehl et al., 2020), and reproduces SST well over the historical period in the Indian Ocean (Jungclaus et al., 2013). We may explore the sensitivity of findings to different CMIP models and scenarios in the future but, for now, we focus on MPI-ESM-LR RCP4.5 as a moderate, representative CMIP contribution, with long-term experiments until 2300.

We gap-fill SST from OSTIA and MPI-ESM-LR using nearest-neighbour interpolation to account for differences in land-sea mask with WINDS, and then bilinearly interpolate both to the WINDS grid. We compute the mean SST from 1993-2020 for both, and compute anomalies with respect to this mean for MPI-ESM-LR. We finally add the MPI-ESM-LR anomalies to the OSTIA mean state to obtain our simple downscaled annual-mean SST time-series, from 1850-2300.

5.2.4.4 Decline

On the basis of these eco-evolutionary simulations, we compute a baseline mean reef cover N_i^0 over the 100-year period between 1875-1975 (before most recent anthropogenic warming began). We pass the reef cover time-series through a 10-year

rolling average to remove high-frequency variability, and extract the lowest reef cover during the 21st Century, $N_i^{\min}$. We then define the *decline* metric as the following:

$$\text{Decline}_i = \frac{N_i^{\min} - N_i^0}{N_0^i}. \quad (5.15)$$

This metric is analogous to the concept of *resistance* in resilience literature (Capdevila et al., 2020).

5.2.5 Comparison with population genetics in Seychelles

Burt et al. (2022) sampled coral fragments from 241 colonies of the broadcast-spawning coral *Porites lutea*, from 19 reef sites across Seychelles. The genomes were sequenced, mapped against a reference genome for *P. lutea*, and 120,538,781 Single Nucleotide Polymorphisms (SNPs) were extracted (Burt et al., 2022). SNPs are highly abundant, single base pair differences in DNA sequences between individuals caused by random mutations (with more differences representing greater genetic differentiation), and are widely used for analysing population structure. Burt et al. (2022) filtered out SNPs that were only present in a minority of samples, and those under natural selection (thereby only leaving neutral genetic markers), leaving 182,511 SNPs. Passing SNPs through PCA and ADMIXTURE analyses (Alexander et al., 2009) revealed that the 241 colonies likely represented two different clades with no geographic structure, hereon the *blue* and *green* clades (Burt et al., 2022). A further ADMIXTURE analysis on the individual clades identified two SNP clusters within each clade, representing shared ancestry (Burt et al., 2022).

To qualitatively compare the genetic structure of *P. lutea* corals across Seychelles with SECoW, we carry out a similar meta-clustering analysis as described in section 5.2.3, but performing the PCA on groups within Seychelles only. The first principal component explains 63.8% of the variance in cluster membership, so we use PC1 as a model analogue for attribution between the two genetic clusters in the ADMIXTURE analysis.

Finally, Burt et al. (2022) also estimated recent rates of gene flow between sampled sites using BayesAss (Mussmann et al., 2019; Wilson & Rannala, 2003), a

Markov-chain Monte Carlo algorithm that fits immigrant ancestries to SNP data, thereby inferring (directed) migration rates between populations (with 95% confidence intervals). We quantitatively compare these estimates to results from SECoW by computing the median and 95% confidence intervals of potential connectivity between reefs in Seychelles, based on 1000 randomly generated potential connectivity matrices based on 10 spawning events, assuming this represents the range of possible ‘recent’ gene flow due to oceanographic variability.

5.3 Results and Discussion

5.3.1 Coral connectivity across the SWIO

5.3.1.1 Potential connectivity

Aside from the general pattern of potential connectivity falling with distance, there is strong asymmetry in the potential connectivity matrix in figure 5.3, as expected from a region influenced by strong ocean currents. For instance, there is relatively strong potential connectivity ($> 10^{-5} \text{ d}^{-1}$) from the Outer Islands of Seychelles to sites in East Africa due to the rapid NEMC, whereas potential 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), but rather between the relatively nearby Aldabra and Farquhar Groups, which would require larval transport in the opposite direction to the NEMC (figure 1.2). Asymmetric dispersal is also pronounced along the path of the northward EACC from Tanzania to Kenya.

The strongest connection between the Chagos Archipelago and the rest of the SWIO is predicted to be with the Inner Islands of Seychelles, with mean potential connectivity that can approach 10^{-6} d^{-1} from some islands in Seychelles. The seasonal, eastward SECC is often around the Inner Islands of Seychelles during the northwest monsoon (the general spawning period in the region), providing a feasible pathway for eastward larval dispersal. For other sources of coral larvae, eastward dispersal towards the Chagos Archipelago is not predicted by SECoW to be significant. Aside from the Inner Islands of Seychelles, most connections with

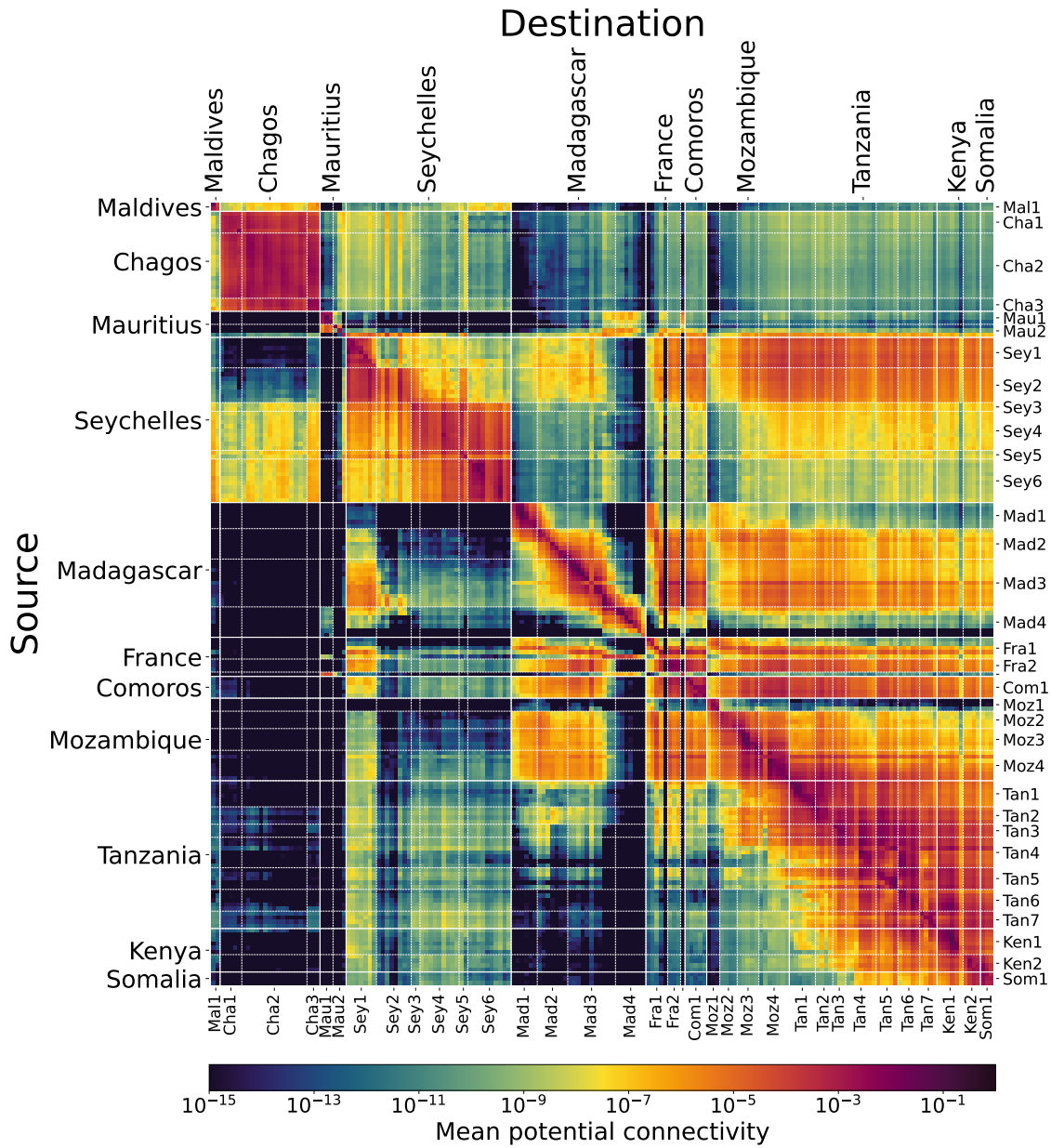


Figure 5.3: Time-mean potential connectivity between pairs of reef groups. We show the mean rather than median potential connectivity, as the latter is zero for most connections. Subregion codes are as follows: **Mal1**: Maldives; **Cha1**: S Banks; **Cha2**: Great Chagos Banks; **Cha3**: N Banks; **Mau1**: 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

the Chagos Archipelago are expected to be stronger in the opposite (westward) direction. Since westward potential connectivity from the Chagos Archipelago is strongest with the Outer Islands of Seychelles and southern Tanzania, it is likely that larval dispersal from the Chagos Archipelago occurs through an initially very slow southward pathway, before entering the westward SEC and joining the NEMC.

Potential connectivity is consistently strong throughout the Chagos Archipelago, which is unsurprising given the expansive area of reef cover and the lack of overwhelming unidirectional ocean currents (although seasonal currents do exist, see section 4.3.2). Larval dispersal is also strong within the constituent island groups of Seychelles. Due to the dominance of powerful mesoscale eddies within the Mozambique Channel, there is a fairly strong and symmetric exchange of larvae between west Madagascar and Mozambique, with potential connectivity exceeding 10^{-6} d^{-1} between many sites.

These results are supported by previous coral connectivity studies in the region, including Crochelet et al. (2016), Gamoyo et al. (2019), Mayorga-Adame et al. (2017), and Wood et al. (2014). Although the raw results were not reported, Wood et al. (2014) predicted nonzero connectivity between Seychelles and the Chagos Archipelago using comparable parameters for larval biology as this study. It is possible that Wood et al. (2014) also predicted stronger connectivity from Seychelles to the Chagos Archipelago than *vice versa*, although we cannot tell this for certain from their results. Mayorga-Adame et al. (2017) also predicted highly asymmetric larval dispersal within the Kenya-Tanzania region using a numerical model with a similar resolution to WINDS. Potential connectivity matrices for the SWIO from Crochelet et al. (2016) and Gamoyo et al. (2019) are qualitatively similar to ours, although only the most probable connections were within the detection limits of these studies due to the much smaller number of particles and spawning events simulated. For instance, whereas we predict significant, large-scale larval exchange across the Mozambique Channel, this is not supported by Crochelet et al. (2016) and Gamoyo et al. (2019), who both only predict nonzero connectivity between a very small number of sites. This contrasts with previous biogeographic and genetic studies indicating that there

is significant connectivity between Mozambique and west Madagascar (Obura, 2012; van der Ven et al., 2022; van der Ven et al., 2021), with Obura (2012) finding a high level of similarity between the coral faunas of northwest Madagascar and northern Mozambique. Unfortunately, none of the modelling studies above made their results publicly available, so a quantitative comparison with our results is not possible.

Due to the large number of connections between reefs, a connectivity matrix is the most straightforward way of visualising potential connectivity. However, in collaboration with Otis Brunner (development and funding) and Julia Janicki (software engineering), we have also developed *Sea the Connectivity*, an interactive application to visualise connections between reefs and reef metrics such as out-strength in a clear and geographic manner. We hope that this tool will be useful for marine practitioners, and it can be found in dataset 5.2 (table 1.1).

In line with our findings in chapter 4, the time-mean potential connectivity matrix obfuscates the enormous temporal variability in connectivity. The standard deviation of potential connectivity across daily spawning events within the broad northwest monsoon spawning season is greater than the mean between practically all pairs of reef groups, with this ratio frequently exceeding 10, and even 100 for distant connections (figure 5.4). This may in part explain the sparse potential connectivity matrices simulated by Crochelet et al. (2016) and Gamoyo et al. (2019), as the relatively small number of spawning events considered by these studies may have been insufficient to capture the magnitude of long-term mean potential connectivity between sites. Short-distance dispersal (close to the diagonal) is generally associated with low temporal variability, although this is not always the case in the Outer Islands of Seychelles due to how remote many of these islands are. Potential connectivity across the Chagos Archipelago is highly consistent, as is northward larval dispersal within Kenya and Tanzania, due to the effects of the EACC. Although southward dispersal within Kenya and Tanzania is non-negligible in SECoW (in contrast to Gamoyo et al. (2019)), it is highly irregular in comparison to the much more likely northward dispersal pathways.

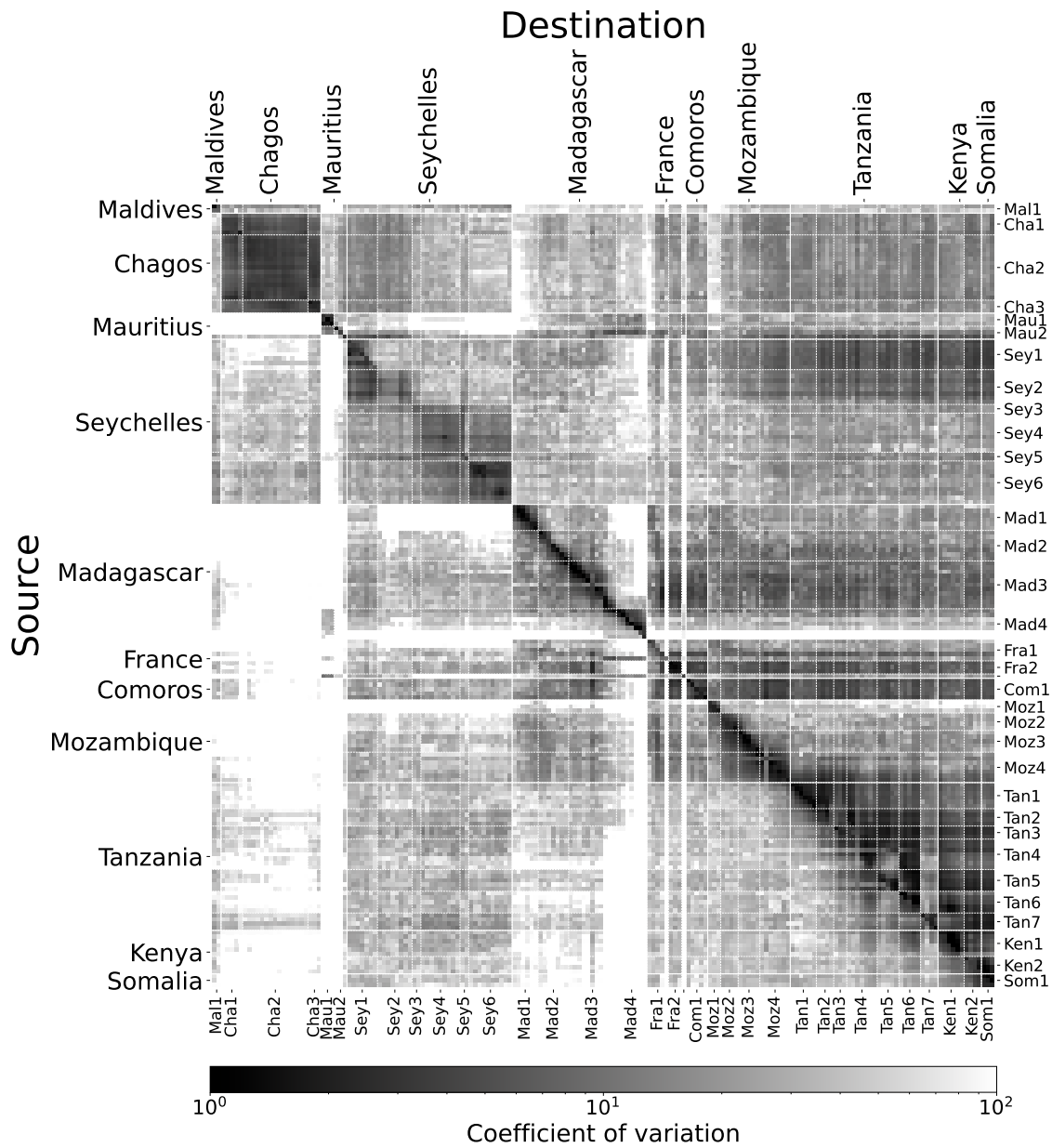


Figure 5.4: Coefficient of variation (standard deviation divided by the mean) of potential connectivity between all pairs of reef groups.

5.3.1.2 Implicit connectivity

The genetic differentiation between two individuals depends, in part, on the number of generations separating them from a common ancestor. As a result, although potential connectivity provides useful information on the rate of migration (through larval dispersal) between coral populations, it may not be the best proxy for predicting the genetic differentiation between populations. The (backward) cumulated multistep

implicit connectivity (CMIC, Ser-Giacomi et al. (2021)) is the likelihood that a pair of random walks terminating at sites i and j passed through a common site within k steps. By modelling gene flow as a random walk through the potential connectivity network, the CMIC may therefore represent the likelihood of a random pair of corals from two sites sharing a common ancestor from the same population within k generations. The CMIC has previously been suggested to better explain genetic differentiation in the marine environment than traditional ‘explicit’ metrics such as potential connectivity (Legrand et al., 2022).

Figure 5.5 shows the typical number of steps (or generations) of dispersal such that the CMIC exceeds 50% for a pair of reef groups (taken as the median across 100 CMIC realisations computed from random subsets of the full potential connectivity matrix). Since the CMIC is nondirectional, the upper triangle of figure 5.5 represents the relative uncertainty of the generational distance between sites (the ratio of the 95% confidence interval to the median across the 100 CMIC realisations). Figure 5.5 indicates that genetic differentiation within the Chagos Archipelago would be expected to be low, with less than 10 generations separating most pairs of sites. Populations within island groups in Seychelles are expected to be very well-mixed, although tens of generations of dispersal separate the Outer and Inner Islands. Examination of the block representing dispersal within Madagascar indicates that three well-mixed reef clusters may exist on the island, in southwest, north, and east Madagascar. Figure 5.5 predicts that corals in Seychelles should show the least genetic differentiation with respect to the Chagos Archipelago, connected on timescales of tens of generations. The Chagos Archipelago is connected to the rest of the SWIO over timescales of over 100 generations, except for the Outer Islands of Mauritius and Tromelin Island (France).

Contrary to potential connectivity, where the connectivity between distant sites is generally more variable due to sporadic and rare long-distant dispersal events, uncertainty in the CMIC generally *decreases* with distance. This is because the CMIC for distant sites is integrated over a large number of spawning events, smoothing out temporal variability. The relative uncertainty in the number of generations

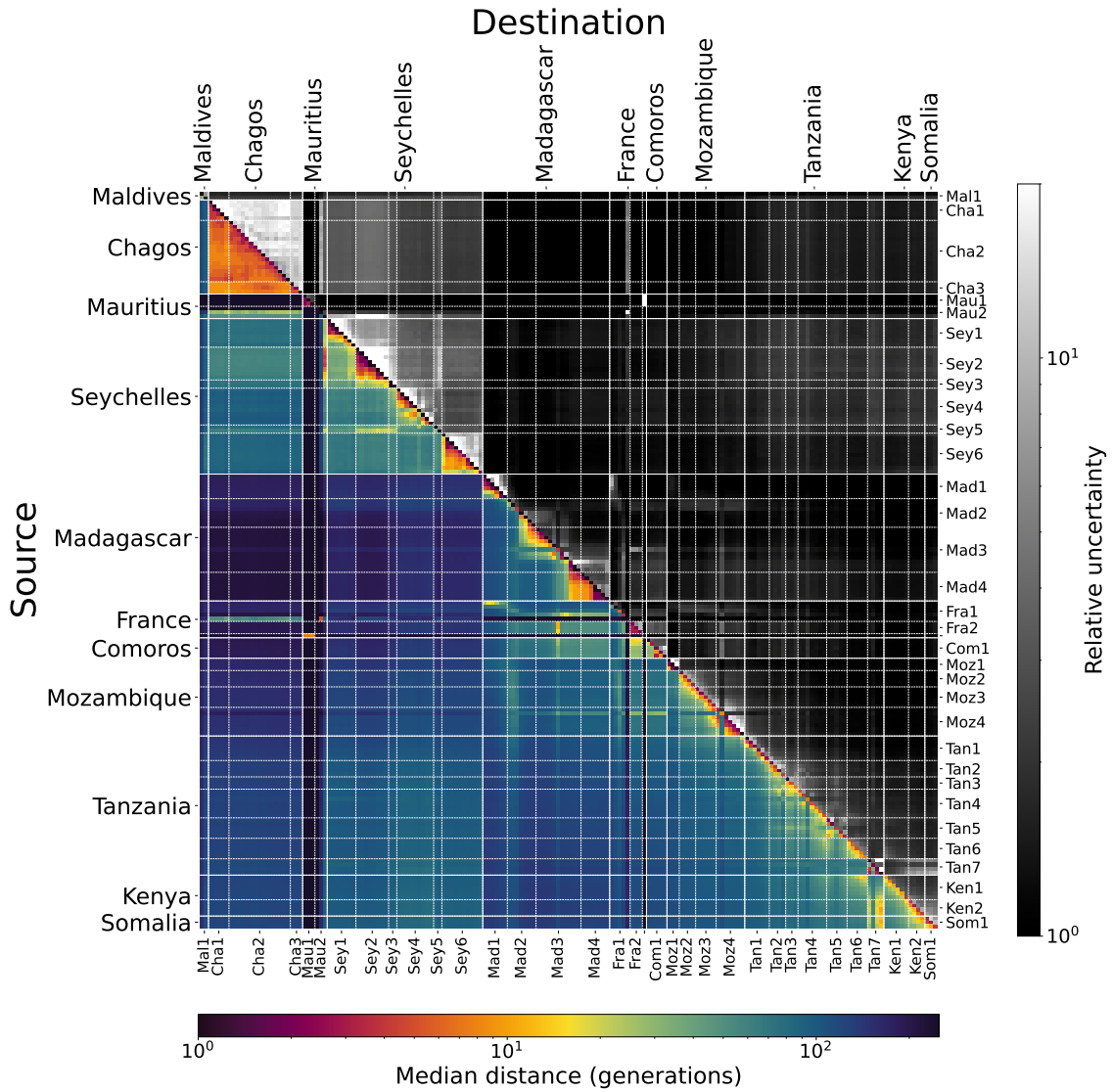


Figure 5.5: *Lower triangle:* Distance between pairs of sites in generations or steps according to CMIC, taken as the median across the CMIC computed from 1000 random subsets of the full potential connectivity matrix. *Upper triangle:* 95% confidence interval across the 1000 random matrices divided by the median.

separating sites within Seychelles is particularly high (often over 10), indicating that genetic differentiation within Seychelles may be very challenging to predict due to oceanographic variability. In contrast, as with the potential connectivity, the uncertainty in CMIC for sites influenced by the EACC is generally very low, due to the consistency and regularity of the along-shore dispersal in this region (section 4.3.1).

5.3.1.3 Reef meta-clusters

An alternative approach to identifying populations which may be associated with less genetic differentiation involves identifying clusters of reefs that tend to retain larvae, which we find using Infomap (Edler et al., 2023). This is shown in figure 5.6 and figure 5.7, where the closeness between reef groups in PC1-PC2-PC3 space (hereon PC space, respectively represented with values of red, green and blue) represents how consistently the reef groups are assigned to the same cluster across oceanographic variability (overlaid on in figure 5.7 biogeographical ecoregions from Obura (2012)). Reefs that consistently appear in similar clusters form *meta-clusters*, represented qualitatively by circles in figure 5.6. Strong differences in colour between reef groups indicates the presence of a consistent barrier to larval exchange. These barriers are not impermeable (indeed, a glance at figure 5.3 demonstrates that significant larval transport is possible across most of the SWIO), but simply indicate that exchange is consistently weak compared to exchange within meta-clusters.

We identify eight major meta-clusters in figure 5.6, where the dispersal barriers between meta-clusters are a function of geography and oceanography. The Inner Islands, Amirantes, and Southern Coral Group of Seychelles form a distinct meta-cluster from the Aldabra and Farquhar Groups, albeit positioned relatively close in PC space due to strong dispersal throughout the archipelago. East Madagascar and the Mascarene Islands (Réunion and Mauritius) form another meta-cluster, albeit with some separation between the islands and Madagascar. These reefs are connected through the SEC and, along the coast of Madagascar, the SEMC. The landmass of Madagascar physically separates reefs along the east coast from the reefs of north and west Madagascar, which form a large meta-cluster with the Comoro Islands, and remote reefs in the southern Mozambique Channel. The eddy-rich flow of the Mozambique Channel results in strong cross-basin connectivity but still acts as a leaky barrier to dispersal, resulting in a distinct meta-cluster in the northwest, occupying the coast of North Mozambique. The strong westward flow of the NEMC acts as a dispersal barrier separating Seychelles in the north, from Madagascar and the Mozambique Channel in the south. The Chagos Archipelago occupies an

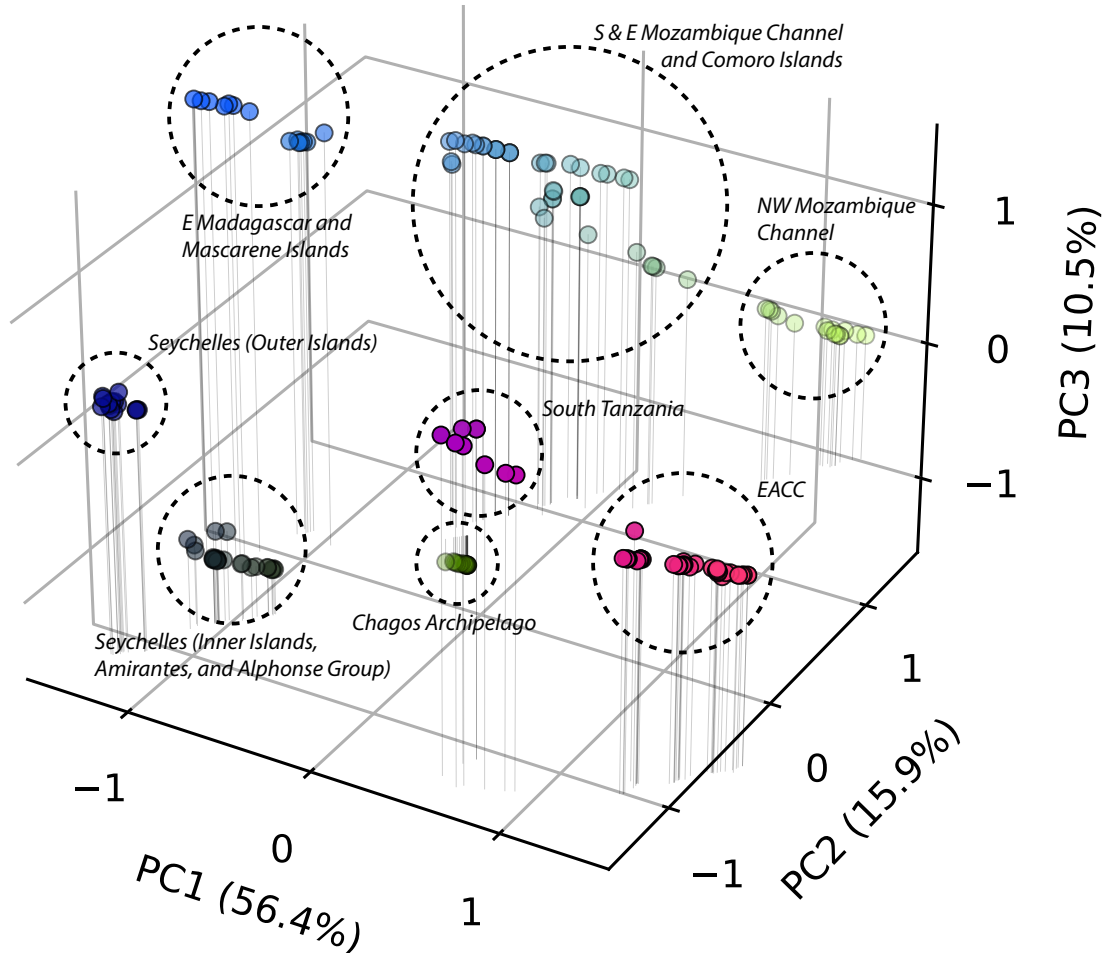


Figure 5.6: The 180 reef groups plotted according to their first three principal components. The normalised values of PC1, PC2, and PC3 respectively also determine the red, green, and blue values of each group.

intermediate position in PC space between the Mozambique Channel meta-clusters, and the Inner Islands of Seychelles. There are two distinct meta-clusters along the path of the EACC. A small meta-cluster occupies the southern coast of Tanzania, isolated from the Mozambique Channel through the bifurcation of the NEMC into the northward EACC and southward eddying flow. In the north, the EACC is deflected around Mafia Island, shielding reefs in its wake from upstream larvae (see thesis front cover), generating an effective gap in the otherwise near-continuous reef along most of the EACC.

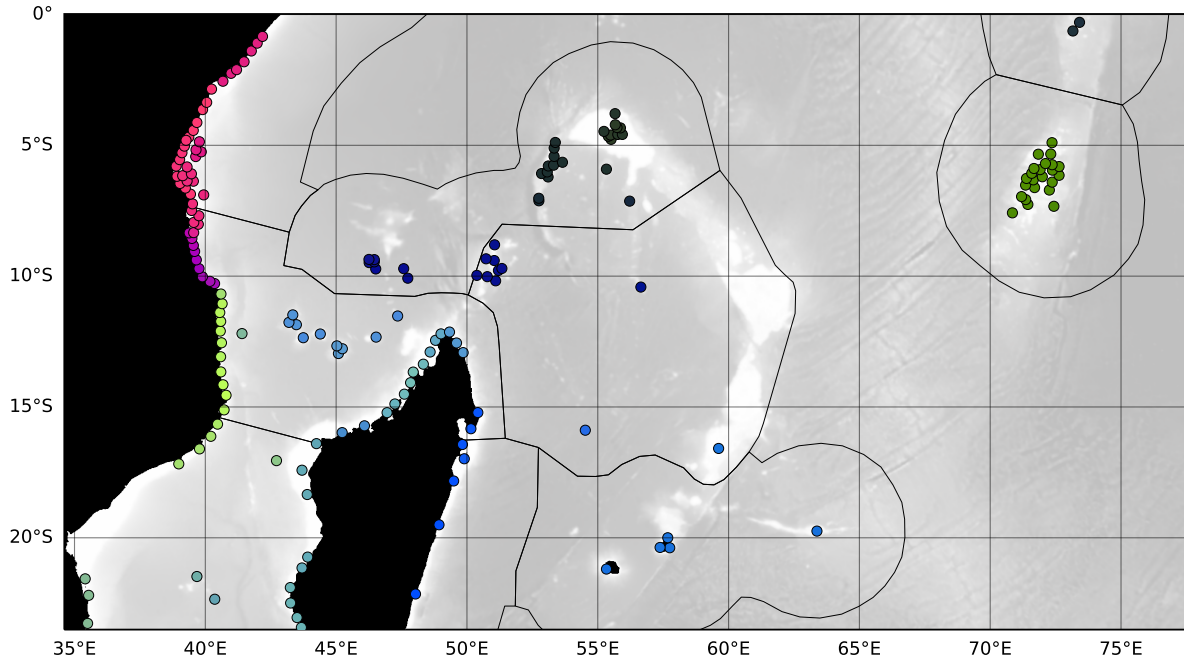


Figure 5.7: Decomposition of the reef network into meta-clusters that tend to retain coral larvae. Reef nodes with similar colours tend to be members of the same map equation cluster throughout oceanographic variability. White lines represent the boundaries of biogeographical ecoregions based on reef-building corals (Obura, 2012).

Crochelet et al. (2016) and Gamoyo et al. (2019) also extracted coral clusters, based on partitioning algorithms not specifically designed for flow networks. There are some significant similarities with these clusterings. For instance, Gamoyo et al. (2019) found a dispersal barrier at the bifurcation of the NEMC, in a similar position to ours, and also found a dispersal barrier across the NEMC, which is robust at all but the longest PLDs. In contrast, Crochelet et al. (2016) identified a cluster cutting across several of our major dispersal barriers for a PLD of 30 days and above, and allocated the Seychelles’ Inner Islands, Amirantes, and Farquhar and Aldabra Groups to separate clusters even at the longest PLD of 60 days. In general, our clustering agrees relatively well with Gamoyo et al. (2019), but has some significant disagreements with Crochelet et al. (2016). In addition to the good agreement with previous biogeographical and genetic studies, key advantages of our clustering analysis include (1) using an algorithm that specifically considers the retention of flow, (2) identifying meta-clusters that are persistent through time, rather than just considering time-mean connectivity, and (3) the ability to identify the strength

of dispersal barriers through their distance in RGB space (rather than reefs either being in the same cluster or not).

5.3.1.4 Comparison with regional biogeography and population genetics

In general, there is good agreement between our clustering analysis in section 5.3.1.3, and previous studies of biogeography and population genetics in the SWIO. This supports the hypothesis that ocean currents play a first-order role in setting large-scale genetic connectivity in the region.

Biogeography

Our clustering analysis is in broad agreement with the revised coral biogeographical ecoregions proposed for the SWIO by Obura (2012), with many ecoregion boundaries appearing as distinct meta-clusters in figure 5.7 (with arguably stronger agreement than with the general marine ecoregions proposed by Spalding et al. (2007)). Due to this agreement, we instead focus on how our meta-clusters diverge from regional biogeographical clusters identified by Obura (2012), and consider why this might be the case.

Obura (2012) identified a key ‘northern Mozambique Channel cluster’ (hereon NMC), typified by a rich biodiversity and a high level of similarity in coral fauna. Although our results support a strongly connected NMC, with reefs of the Comoro Islands and NE Mozambique Channel clustering closest to reefs in the W Mozambique Channel (figure 5.6, figure C.4), our clustering analysis nevertheless identifies a persistent, albeit leaky, dispersal barrier across the Mozambique Channel. Based on coral assemblages, Obura (2012) determined that the northern limit of the NMC is at Mafia Island in Tanzania. Although we identify a significant dispersal barrier at Mafia Island, we find a stronger barrier around the Mozambique-Tanzania border, coincident with the bifurcation of the NEMC. Obura (2012) also found greater similarity between fauna of the Chagos Archipelago and the NMC than with Inner Islands of Seychelles, the opposite to predictions from SECoW. Chagos-NMC connectivity in SECoW is proportionately greatest between February and May, which, interestingly, corresponds

with the timing of at least one observed spawning event in the Chagos Archipelago (Mangubhai et al., 2007). Obura (2012) interpreted this strong connectivity with the NMC as being due to the SEC and SECC. Due to the position of the northern boundary in our domain (figure 1.2), we have limited capacity to gauge the importance of eastward connectivity to the Chagos Archipelago from East Africa through the SECC using SECoW. However, no drifters from the Global Drifter Program (GDP) reached the Chagos Archipelago within 120 days of passing Mayotte (within the NMC) or even Zanzibar Island (figure 3.8), so we do not consider that this eastward dispersal pathway is significant. Importantly, eastward dispersal through the SECC from the Inner Islands of Seychelles is orders of magnitude more likely, with many GDP drifters from Seychelles reaching the Chagos Archipelago within 120 days (figure 3.8). In contrast, GDP drifters demonstrate that it *is* possible to reach the NMC from the Chagos Archipelago via the SEC within 120 days (figure 3.8), so this pathway is physically reasonable. As a result, connectivity between the NMC and the Chagos Archipelago is likely exclusively via the SEC, and therefore unidirectional.

Population genetics

There is strong support from coral population genetics for strong connectivity along the Kenya-Tanzanian coast (Montoya-Maya et al., 2016; Souter & Grahn, 2008; Souter et al., 2009; van der Ven et al., 2022; van der Ven et al., 2016, 2021). However, despite the relative lack of large-scale structure, local-scale genetic differentiation does occur. For instance, Souter et al. (2009) found significant differentiation between corals sampled in northeast and west Zanzibar with 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, previously noted in section 4.3.1 and also visible as very weak diversity across larval destinations in figure 5.13. This would result in larval retention and therefore self-recruitment. 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 with other reefs in the region (Souter et al., 2009).

There is equivocal evidence for the biogeographic barrier between Zanzibar and Mafia islands identified by Obura, Gudka, Porter, et al. (2021). Although this barrier is potentially supported by van der Ven et al. (2016) and appears weakly in our analyses, it does not clearly appear in the results of Souter and Grahm (2008), van der Ven et al. (2022), and van der Ven et al. (2021). For instance, Souter and Grahm (2008) found little differentiation across this hypothetical barrier, instead finding the most significant differences between corals sampled in lagoons, versus those in seaward-facing locations. 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 WINDS-M may play an (in some cases, more) important role at a local scale.

For the brooding coral *S. hystrix*, van der Ven et al. (2021) found evidence for connectivity between northern Mozambique and southwest Madagascar. This is supported by our analyses, with reefs in the NW and SE Mozambique Channel forming distinct but closely related meta-clusters (figure 5.6). van der Ven et al. (2021) also found strong differentiation between corals sampled in north Madagascar, and the rest of the SWIO. In their discriminant analysis, populations in southwest Madagascar plot between the north Mozambique and north Madagascar populations, which is reproduced in our meta-clustering analysis (figure 5.6), although we predict the greatest differentiation between north Mozambique and southwest Madagascar, whereas van der Ven et al. (2021) found generally strong differentiation between north Madagascar and all other sites. On the other hand, it is not clear how deeply we should be reading into these differences, since the methodologies of genetics-based clustering and our meta-clustering are very different. As a brooding coral, the PLD of *S. hystrix* is considerably lower than that of most broadcast spawning corals (Prasetia

et al., 2017) and certainly *P daedalea*, but the large-scale structure of our meta-clusters does not fundamentally change for parameters with a considerably shorter PLD.

Another large-scale population genetics study for the broadcasting coral *A tenuis* (van der Ven et al., 2022) identified four major clusters: a diverse east African cluster spanning the coast from north Mozambique to Kenya; south Mozambique (partially outside our model domain); north and northeast Madagascar; and southernmost Madagascar (outside of our model domain). van der Ven et al. (2022) interpreted these patterns as evidence for significant but infrequent dispersal between north Madagascar, southwest Madagascar, and the EACC region; strong (albeit spatially variable) connectivity along the EACC; and significant (but leaky) dispersal barriers isolating south Mozambique. These observations are, again, consistent with our larval dispersal simulations. The one exception is south Mozambique, which plots near southwest Mozambique in our meta-clustering analysis. However, these sites are small in number and highly marginal in SECoW, and it is therefore expected that they cluster with the nearest reefs due to the optimisation condition for the map question. As can be seen from figure 5.3, potential connectivity between south Mozambique (plotting on the border with Comoros) and all other sites is very low.

5.3.2 Potential connectivity and *P lutea* population structure in Seychelles

The two *P lutea* clades identified by the genetic analyses of Burt et al. (2022) exhibit different population structure (figure 5.8). Whereas the green clade shows a robust geographic structure with very strong differentiation between the Outer and Inner Islands, with little evidence for mixing between the island groups, the blue clade shows significantly greater mixing, with most corals showing evidence of mixed ancestry.

It is not clear what difference between the two clades would result in these different mixing patterns. However, this does suggest that there is a dispersal barrier between the Inner and Outer Islands of Seychelles (as evidenced by the very strong population structure of the green clade, and increase in the proportion of ancestry associated with the dark blue cluster for the blue clade), albeit a very leaky one. Blue clade corals

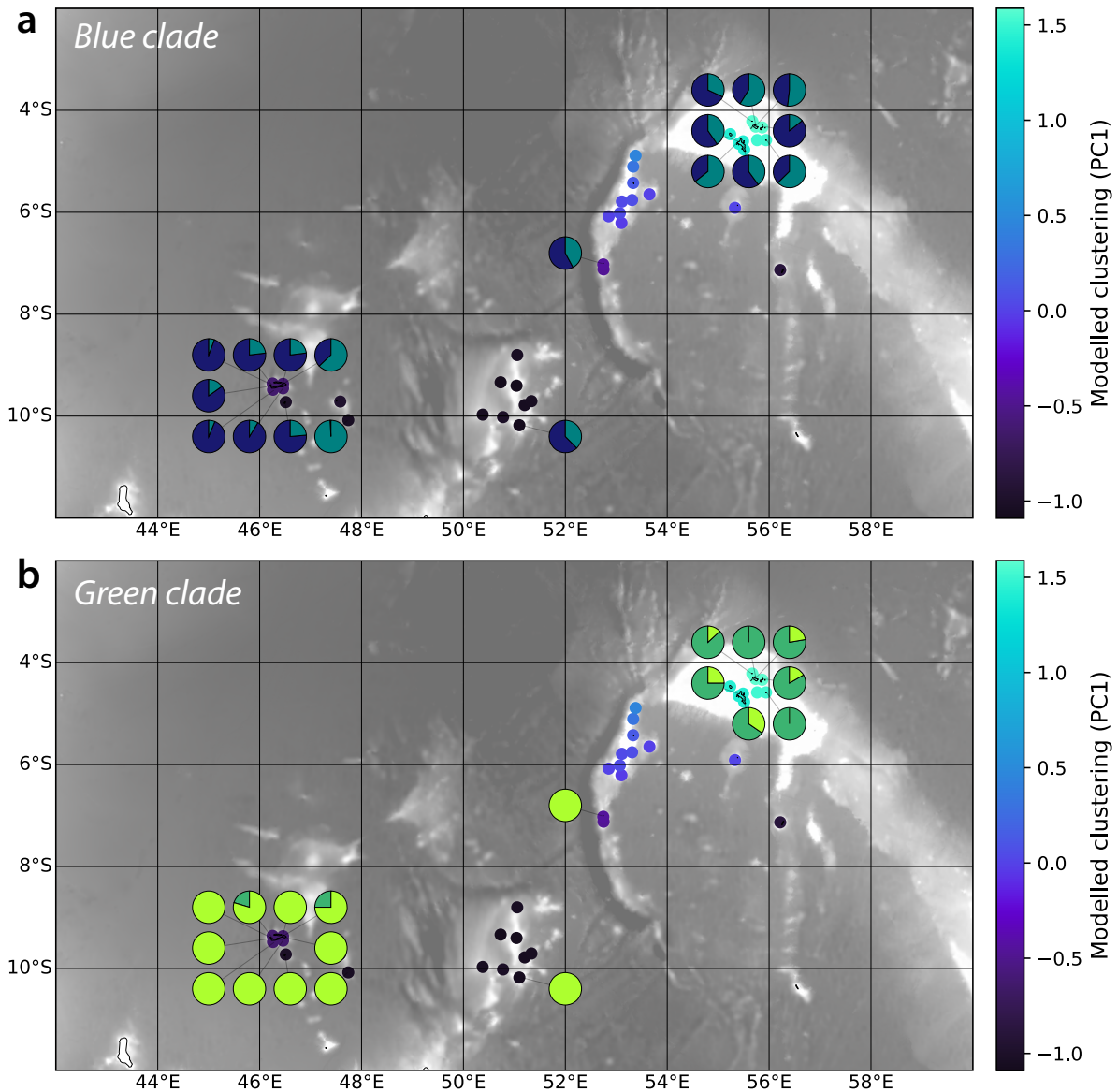


Figure 5.8: Comparison of the genetic ADMIXTURE analyses for the blue (a) and green (b) clades, averaged within sampling sites (pie charts). Also shown are simulated clusters of reefs consistently retaining larvae from the oceanographic model (coloured points, where points with similar colours are frequently members of the same simulated cluster)

from two sites within the Aldabra Group bear greater resemblance to populations in the Inner Islands than the rest of the Aldabra Group, indicative of just how leaky the dispersal barrier between the Inner and Outer Islands may be. This interpretation is generally consistent with the predictions from SECoW. The first principal component from a re-analysis of meta-clusters based on reef groups in Seychelles only (coloured points in figure 5.8) suggests that the Inner Islands and Aldabra and Farquhar groups

form opposite end-members, with the Alphonse Group, Amirantes, and Platte Island acting as intermediates. Dispersal is predicted to be more likely from the Inner Islands to the Outer Islands than vice versa (figure 5.3), potentially explaining why a couple of ‘Inner Islands-like’ sites are found in the Aldabra Group.

Meta-clusters based on the entire SWIO indicate that the most significant dispersal barrier is between the Aldabra and Farquhar Groups, and the rest of Seychelles. In contrast, meta-clusters based on Seychelles only suggests that the primary dispersal barrier is between the Inner Islands and the rest of Seychelles. The latter is more consistent with the population structure of the green clade (figure 5.8). However, the potential for significant genetic connectivity across Seychelles, as evidenced by the population structure of the blue clade, is supported by the relatively small number of generations separating all pairs of sites in Seychelles (tens, figure 5.5), and the closeness of all sites within Seychelles in figure 5.6 compared to the rest of the SWIO. As a result, there is broad consistency between the population structure of *P. lutea* inferred from genetics, and physical larval dispersal across Seychelles. This indicates that larval dispersal modelling, which is considerably less expensive than *in-situ* sampling and genetic analyses, can provide meaningful insights into population structure.

On the other hand, Bayesian inference of recent gene flow rates between sampled sites agrees poorly with potential connectivity computed from SECoW (figure 5.9). In general, there is reasonable agreement (within uncertainty due to oceanographic variability) for sites that are within around 200 km of one another, although the uncertainty is so large that it is not clear how meaningful this agreement is. For more distant pairs of sites, potential connectivity from SECoW is systematically orders of magnitude (typically by a factor of at least 10^6) lower than inferred gene flow. Even given the potential for stochastic oceanographic variability to generate rare, long-distance dispersal events, potential connectivity is still at least a factor of 10^3 too low to explain the magnitude of gene flow. Due to a lack of measurements, we assume in this analysis that *P. lutea* larvae have similar mortality and competency characteristics to *P. daedalea*. If *P. lutea* larvae instead have a considerably lower

mortality rate and longer competency window, such as for *A. valida* (Connolly & Baird, 2010), potential connectivity between distant sites is considerably higher. Nevertheless, even with the low mortality rates of *A. valida*, physical larval dispersal alone, as predicted by SECoW, cannot explain the rates of gene flow inferred between distant coral reefs in Seychelles.

For many reefs, the gene flow inferred from BayesAss is not significantly different from zero to the 95% confidence level (figure 5.9). As a result, it is possible that the genetic differentiation between sites is simply too low to accurately infer low rates of dispersal between the distant populations (Faubet et al., 2007; Samarasin et al., 2017). BayesAss also assumes that gene flow only occurs between sampled populations, but there are many islands across Seychelles that were not sampled in this study. In particular, no samples were obtained from the Amirantes and only a single site (with a small number of samples) was obtained from Alphonse (in the Alphonse Group). SECoW suggests that these sites act as intermediate stepping stones between the Inner Islands and Aldabra and Farquhar Groups figure 5.8, but BayesAss necessarily assumes that most gene flow between the Inner and Outer Islands is direct. As a result, it is possible that BayesAss is misinterpreting indirect gene flow as direct dispersal, and is therefore overestimating rates of gene flow between distant populations.

Finally, SECoW assumes constant coral fecundity, whereas fecundity can vary considerably in space and time (Hartmann et al., 2018; Leinbach et al., 2021; Pratchett et al., 2019). If fecundity were, for instance, (perhaps transiently) considerably higher within the Inner Islands than the Outer Islands, this could result in proportionately more larvae settling within the Outer Islands originating from long-distance dispersal, thereby resulting in greater (proportional) gene flow. However, the difference in fecundity required would be enormous, and there are no observations to support this hypothesis.

In summary, in contrast to genetic population structure analysis (figure 5.8) which reveals a geographic structure which is consistent with predictions from the larval dispersal model, attempts to quantitatively compare rates of gene flow inferred from genetic data to potential connectivity have been unsuccessful. The enormous

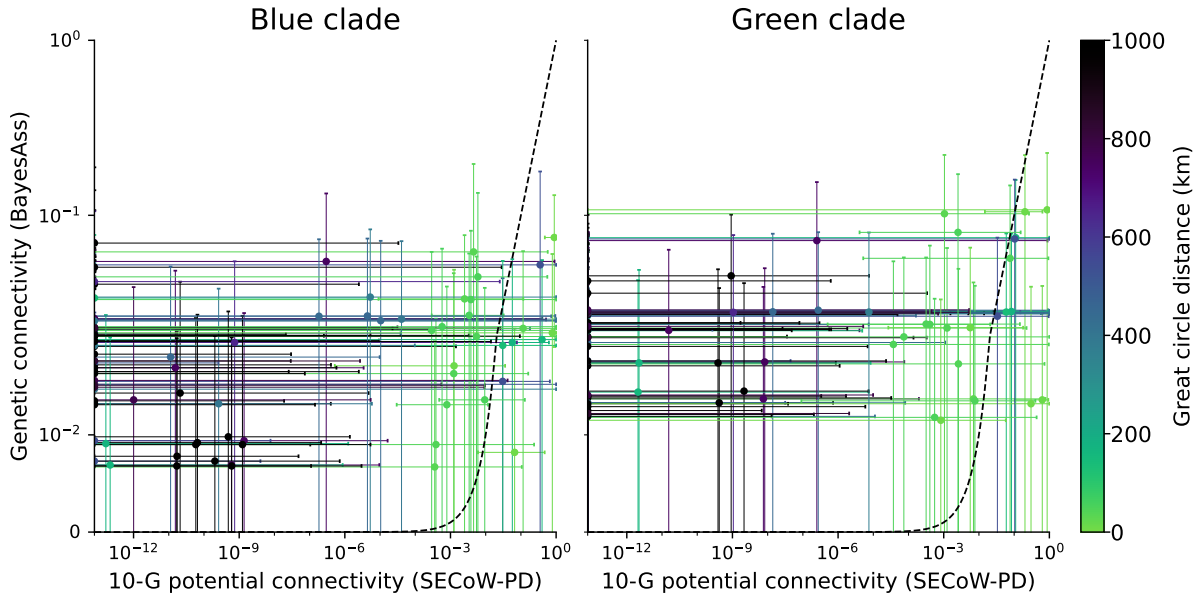


Figure 5.9: Gene flow inferred by BayesAss plotted against the mean larval flow between corresponding reef sites from SECoW across 10 generations, computed as the median across 1000 possible 10-year connectivity matrices. Error bars reflect the 95% confidence intervals. Note that gene flow is directional, so each pair of reefs is represented by two points. Points are coloured by their great-circle (shortest) distance. Self-recruitment is not plotted. The dotted line represents the 1:1 ratio between connectivity inferred from BayesAss, and potential connectivity computed from SECoW. Note that this line appears non-linear due to the *symlog* axes with different linear thresholds.

uncertainty introduced by both BayesAss (in fitting a gene flow matrix to coral genetic data with relatively little genetic differentiation) and the larval dispersal model (primarily due to stochastic oceanographic variability) suggests that this method of reconciling marine connectivity estimates from population genetics and numerical models may not be useful. This is not entirely surprising, since BayesAss attempts to compute rates from an integral measure (coral genomes) and may therefore be expected to amplify uncertainty, whereas our clustering approach is an integral measure based on rates (potential connectivity), thereby smoothing out variability. Even if it were possible to accurately infer recent gene flow through BayesAss, this may provide only very limited useful information about future or long-term connectivity (section 4.4.3), so future studies intending to quantify fine-scale marine connectivity may wish to avoid this approach.

5.3.2.1 Role of coral reefs in supporting network resilience

Given the potentially existential risk from climate change faced by tropical coral reefs globally under likely climate trajectories (Couce et al., 2023; Dixon et al., 2022; Frieler et al., 2013; Van Hooidonk et al., 2016), prioritisation is needed for reef conservation efforts. For instance, Beyer et al. (2018) identified optimal portfolios of reefs through a risk-management framework, to maximise the benefits of conservation investment. The authors considered a wide range of metrics to optimise, including present-day thermal stress, projected future conditions, exposure to cyclones, and connectivity (specifically, metrics from Wood et al. (2014) similar to *out-strength* used in this study).

In this study, we focus on connectivity and do not carry out a comprehensive portfolio assessment as in Beyer et al. (2018). Instead, we consider which reefs in the SWIO possess a range of connectivity characteristics which may maximise their importance in maintaining the resilience of the wider reef network, as described in section 5.2.2.

In general, reefs which consistently perform well in the six metrics considered are concentrated along the Tanzanian coast, NW Madagascar, and the Comoro Islands (figure 5.10), with some of the best performing reefs being found around Mafia Island in Tanzania.

Due to the almost continuous coral cover along the coast of East Africa, out-strength tends to be very high (figure 5.11), typically orders of magnitude greater than remote reefs (although we recognise that this may be an overestimate, see Dauhajre et al. (2019) and Grimaldi et al. (2022)). Larval retention along the coast is generally high in NW Madagascar during the northwest monsoon (section 4.3.2), explaining the high out-strength here. Out-strength is slightly lower in the Comoro Islands due to their relative remoteness, but currents converging with the coast and the enormous lagoon around Mayotte in particular still results in substantial retention. Along similar lines, out-consistency (the proportion of spawning events accounting for half of settling larvae, figure 5.12) is high along the coast of East Africa due to the EACC causing consistent along-shore transport, and high in NW Madagascar

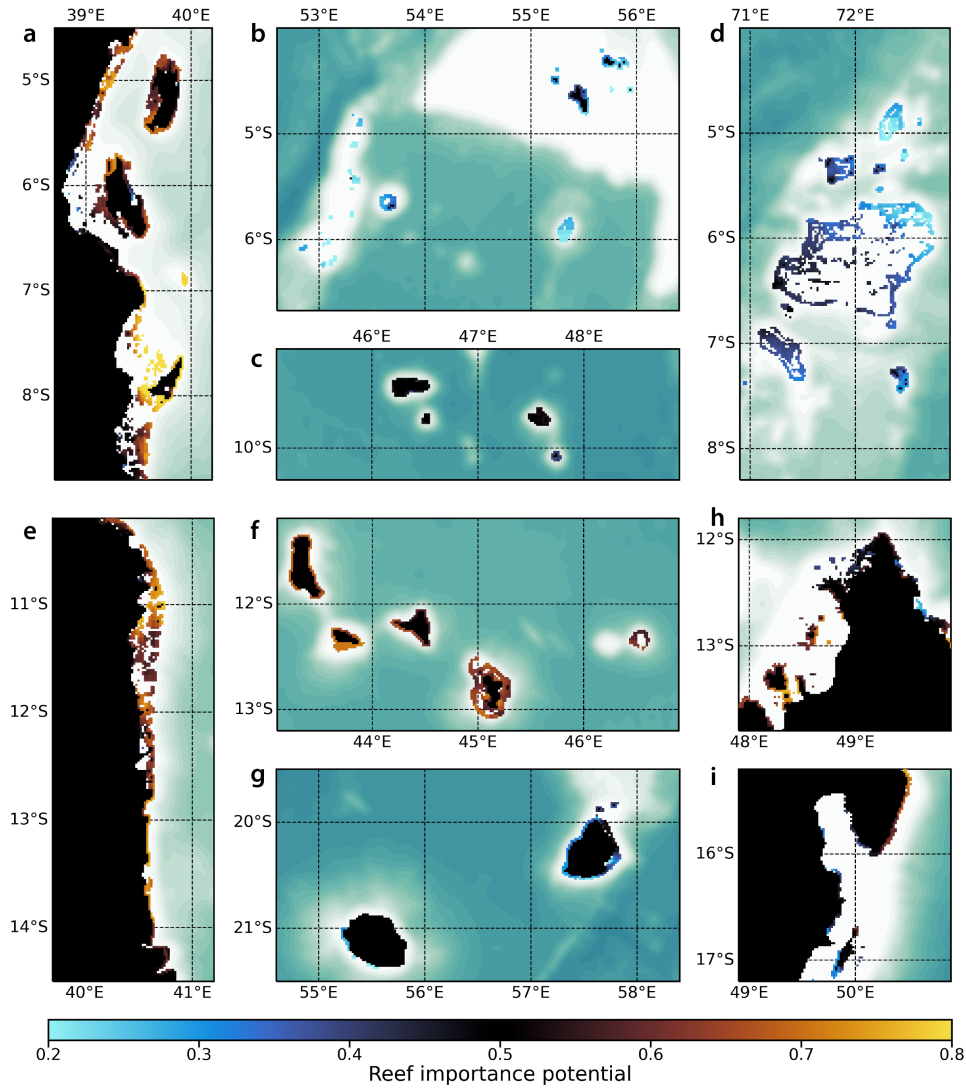


Figure 5.10: Median reef importance (section 5.2.2) across daily potential connectivity matrices for 9 regions within SECoW: (a) along the path of the ACC with (south to north) Mafia, Zanzibar and Pemba Islands; (b) the Inner Islands of Seychelles and Amirantes; (c) the Aldabra Group; (d) the Chagos Archipelago; (e) Quirimbas Archipelago; (f) Comoros and Mayotte; (g) Réunion and Mauritius; (h) North Madagascar; and (i) Northeast Madagascar.

due to strong larval retention. Again, out-consistency is lower at the Comoro Islands (aside from coastlines facing major currents and the inner lagoon of Mayotte).

In contrast, out-entropy (figure 5.13) is extremely high within the Comoro Islands, indicating that larvae here are dispersed in similar numbers across a large number of different destination reefs. The median daily out-entropy in parts of Mayotte and Mwali exceeds 6b, suggesting that a typical spawning event at a reef here may

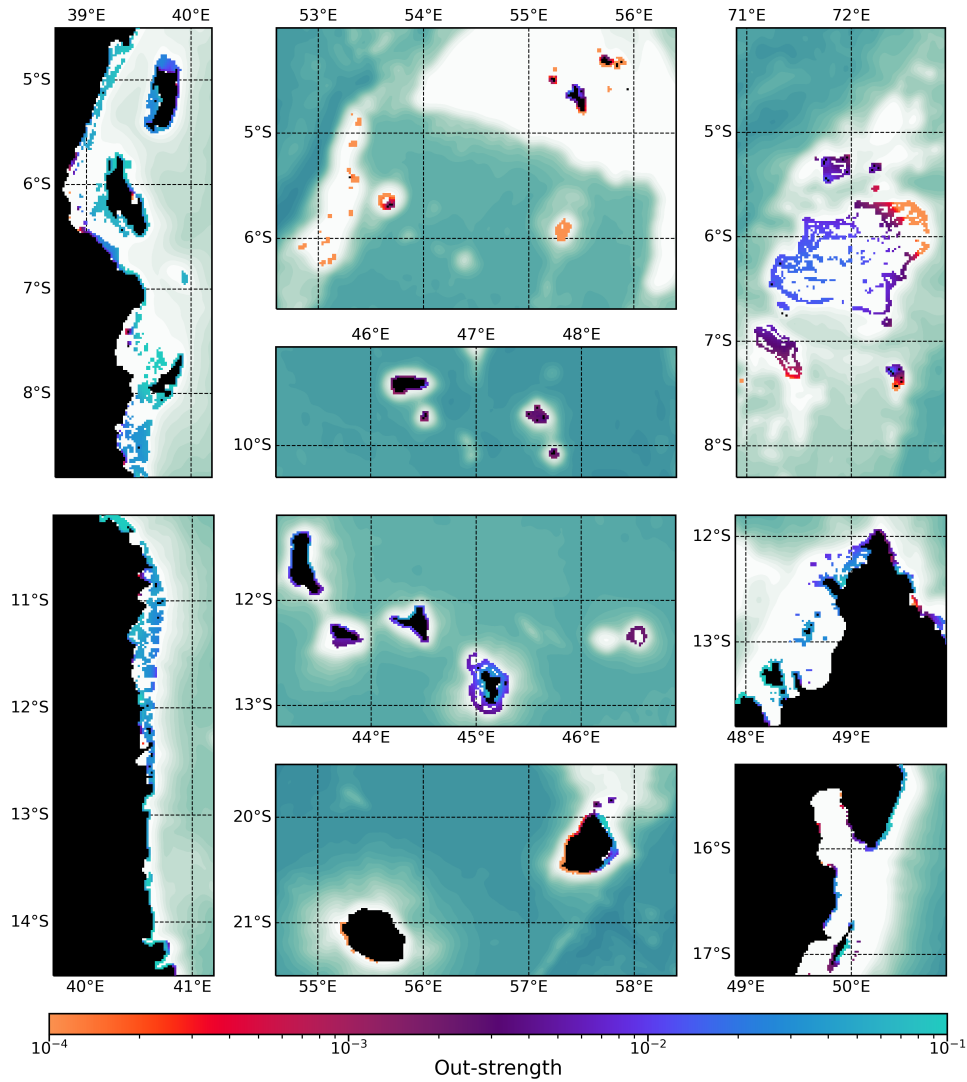


Figure 5.11: Median out-strength across daily potential connectivity matrices.

disperse larvae in similar numbers to over 64 different reef cells. Although the larval supply here may be lower and less regular than along the path of the EACC, the diversity of reef connections is very high. Within East Africa, out-entropy is highly variable, following similar trends to the high-frequency potential connectivity variability in section 4.3.1. For instance, out-entropy is low along the northeast coast of Zanzibar Island due to the trapping of larvae against the coast, resulting in a relatively low diversity of destination reefs for these larvae. Conversely, out-entropy is high in west Pemba, due to divergent ocean currents resulting in rapid larval transport into the EACC, facilitating a higher diversity of destination reefs.

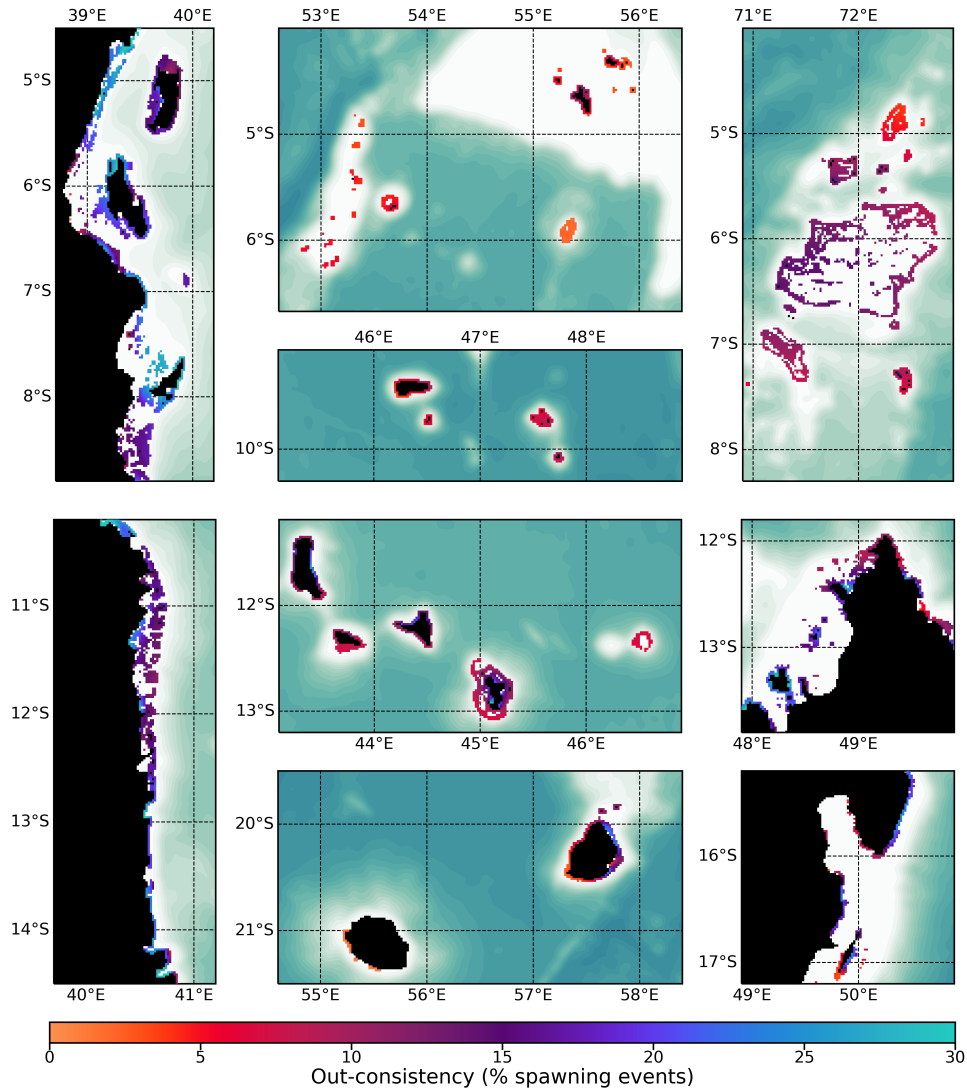


Figure 5.12: Out-consistency across daily potential connectivity matrices.

The out-BAD (bleaching alert dissimilarity) metric is generally low in magnitude ($<1\%$) as reefs currently only spend a minority of their time in bleaching alert conditions. Nevertheless, in general, sites with high out-BAD tend to be those with disproportionately important long-distance connectivity, thereby connecting reefs with hydrodynamic regimes with less correlation in marine heatwave occurrence (figure 5.14). Despite the EACC facilitating long-distance dispersal, the high level of continuous reef cover still results in a dominance of short-distance dispersal, so the out-BAD metric is generally quite low here (aside from certain sites with low retention such as west Pemba. In the Comoro Islands, out-BAD is highest

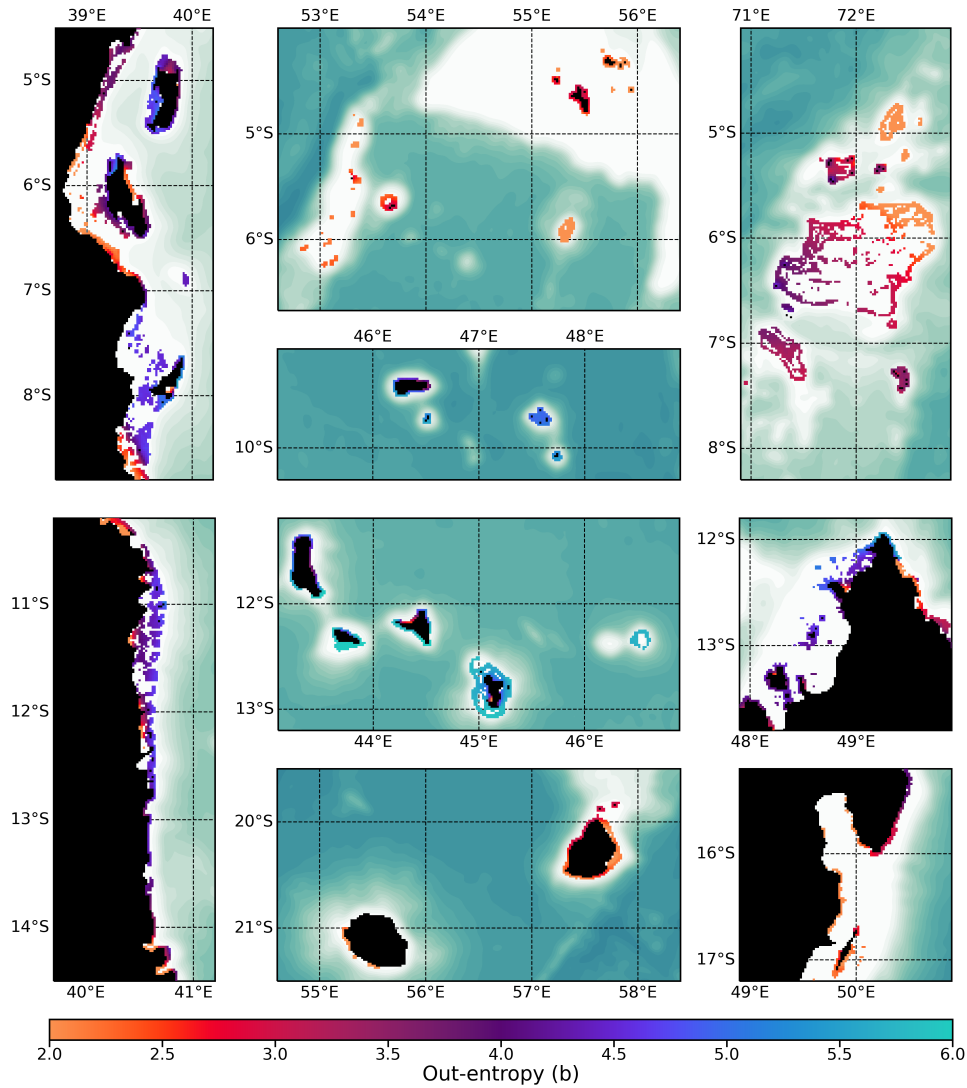


Figure 5.13: Median out-entropy across daily potential connectivity matrices.

in peripheral regions with low retention, such as south Mwali and some of the outermost parts of Mayotte’s barrier reef.

The out- Δ TST metric is also generally low in magnitude, within $\pm 0.2K$ for practically all sites (figure 5.15). Notably, our values are often considerably lower than those computed for the Coral Triangle by Kleypas et al. (2016), who found values in excess of 1K in some cases. The definition of the TST in Kleypas et al. (2016) is different to ours (the mean monthly maximum (MMM) SST + 2.5 times the standard deviation of the MMM, rather than the MMM + 1K as used in this study), so it is possible that the spatial variability in TST was greater in their study. Kleypas

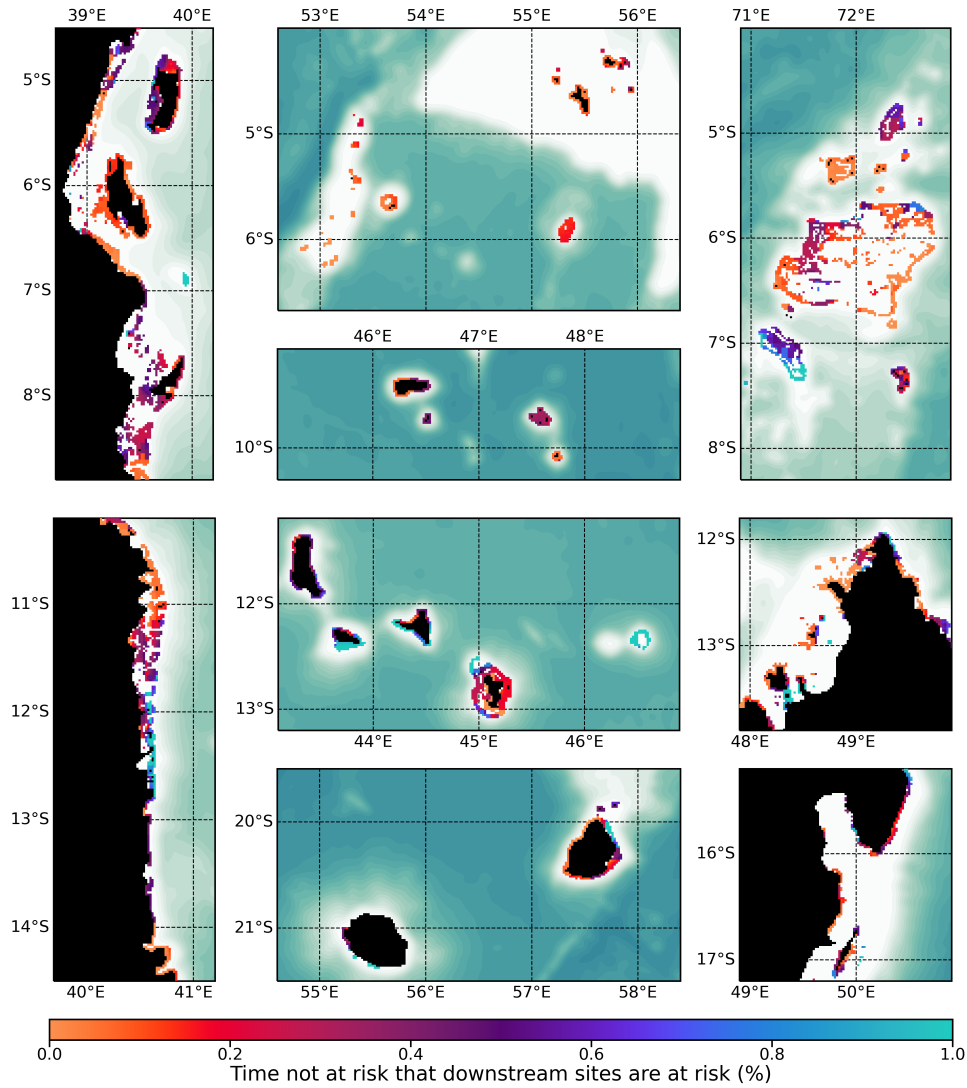


Figure 5.14: Mean out-BAD across daily potential connectivity matrices.

et al. (2016) also computed potential connectivity using the Lagrangian PDF method (Mitarai et al., 2009) which does not consider en-route settling, and is therefore more likely to overestimate long-distance dispersal. Long-distance dispersal may therefore be proportionately more important in the potential connectivity matrices considered by Kleypas et al. (2016), perhaps inflating the Δ TST metric. On the other hand, local (reef-scale) thermal regimes likely exist, which would not be resolved in the 5 km resolution TST product used in this study. Given the considerable range of mean temperature and, in particular, temperature variability found within individual reef systems (e.g. Green, Lowe, Buckley, et al., 2019), it is quite possible

that unresolved ΔTST due to local thermal regimes is greater than ΔTST introduced by long-distance larval dispersal. As a result, and due to findings in section 5.3.3, it is not clear how useful this metric is within the scope of this study.

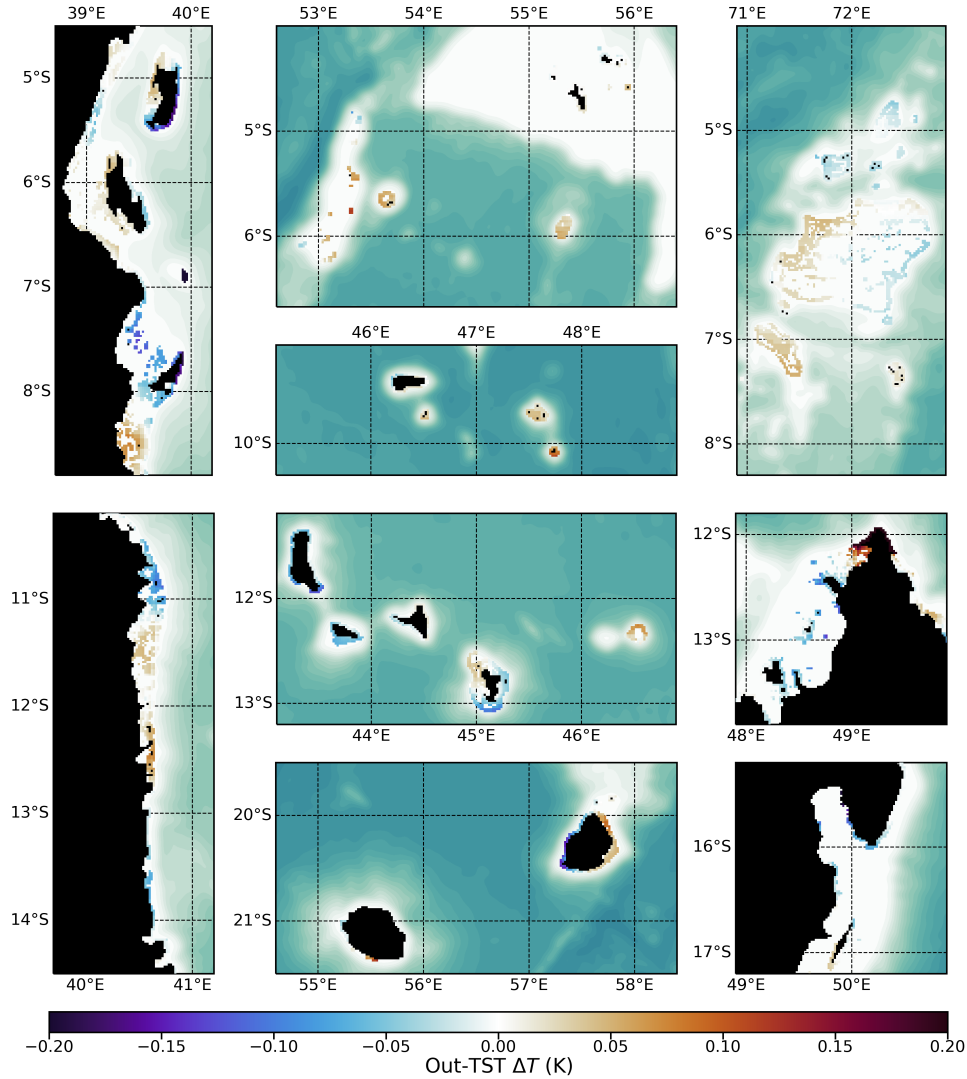


Figure 5.15: Median out- ΔTST across daily potential connectivity matrices.

Betweenness centrality is highly spatially variable, although is generally low for peripheral remote islands (which are too poorly connected to act as important stepping stones) and the Chagos Archipelago, where the high connectivity reduces the importance of any one particular dispersal route (figure 5.16). The betweenness centrality metric is generally highest for reef groups that act as the only dispersal pathway along a linear route. For example, the north tip of Madagascar has high

betweenness centrality as it acts as a ‘springboard’ to catapult larvae into the NEMC and towards downstream reefs in the Comoro Islands and beyond. Islands in the Quirimbas Archipelago of Mozambique also have high betweenness centrality, as the coral groups extend from the coast to the open ocean, so the most efficient dispersal pathway along the coast of Mozambique is through these groups. However, it is possible that the betweenness centrality metric could be quite sensitive to the grouping of reefs used. Both Crochelet et al. (2016) and Gamoyo et al. (2019) also computed betweenness centrality for the SWIO, although it is not clear whether they computed multiplicative betweenness centrality, as should be applied to dispersal networks (Costa et al., 2017). There is limited agreement in betweenness centrality for the SWIO for any of these studies so, due to a lack of spatial coherence and an unclear theoretical basis for why betweenness centrality should be important in the first place for a relatively well-connected region such as the SWIO, we suggest that this metric should not be a priority for evaluating coral reefs in this region. The betweenness centrality metric may be more useful for very sparse dispersal networks such as hydrothermal vents (e.g. Brunner et al., 2022), where the role of individual sites in preventing network fragmentation is clearer.

Empirical evidence for the importance of the above metrics is lacking. However, the consistently strong performance of regions such as the Comoro Islands, NW Madagascar, and the coast of Tanzania across a range of connectivity metrics suggests that these reefs may be particularly important for maintaining the resilience of the regional coral reef network. We also note that these are precisely the same reefs identified by Beyer et al. (2018) as high-priority conservation targets in the SWIO, supporting previous evidence from Wood et al. (2014) that these reefs are very well-connected.

5.3.3 Reef eco-evolutionary resilience

Although temperature rise is not the only stressor affecting corals, marine heatwaves are strongly associated with severe coral bleaching (e.g. Kumagai et al., 2018). Almost 100% of reefs are expected to regularly experience significant bleaching under 1.5 °C

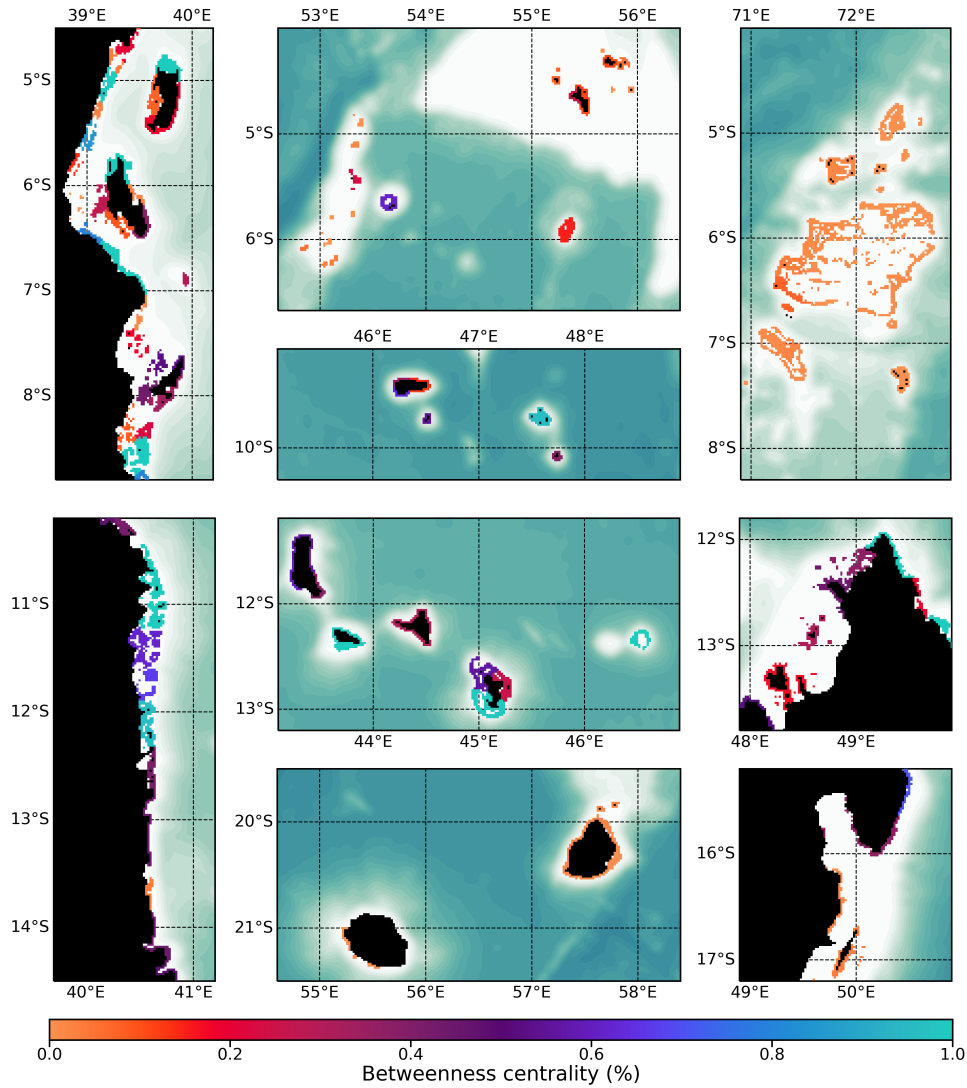


Figure 5.16: Median betweenness centrality across daily potential connectivity matrices.

warming (Dixon et al., 2022), a highly optimistic prediction for future climate change. As a result, in the absence of adaptation, the prognosis for tropical coral reefs is extremely poor. However, given that thermal tolerance does appear to be somewhat heritable (Dixon et al., 2015), the assumption of no adaptation potential may be inappropriate for tropical corals. To test whether adaptation (driven by selection and the exchange of genes between populations adapted to different temperatures) could prevent coral reef collapse in the SWIO, we investigate the response of virtual reefs from 1850-2300 under RCP4.5 (Giorgetta et al., 2013) using an eco-evolutionary model (McManus, Forrest, et al., 2021).

In the absence of adaptation, hard coral cover collapses to zero across the entire SWIO (not shown). With moderate heritable genetic variance in heat tolerance, predicted relative hard coral cover decline over the 21st Century is still considerable, with an average decline of over 80% across reef cells (figure 5.17). However, across the SWIO, this figure varies from over 90% across much of the Inner Islands of Seychelles and parts of Tanzania, to less than 50% in parts of Mauritius and east Madagascar. Although the magnitude of hard coral cover decline over the 21st Century is sensitive to poorly constrained parameters, particularly the additive genetic variance and effective fecundity, the patterns between reefs are fairly robust within the range of reasonable parameters (figure 5.1).

These patterns may be surprising as, although the Inner Islands of Seychelles are remote and relatively poorly connected, Mauritius is also very remote, yet fares (comparatively) well in our eco-evolutionary simulation. The coasts of Tanzania and Kenya are very well-connected due to the near-continuous coral cover along the coast and influence of the EACC, yet predictions of coral cover decline for many of these reefs are dire.

Instead, the response of coral cover is dominated by the local rate of warming (figure 5.18). The mean rate of SST rise over the 21st Century varies between 0.1 and 0.15 K decade⁻¹ across the tropical SW Indian Ocean. Under the MPI-ESM-LR RCP4.5 scenario considered in this study, warming rates are lowest in the southeast of the WINDS domain, around east Madagascar, Réunion, and Mauritius, which is also the case in the CMIP6 ensemble mean (IPCC, 2021b; Iturbide et al., 2020). The mean rate of SST rise alone explains around 71% of the variance in hard coral cover over the 21st Century in our simulations but, as can be seen in figure 5.18, some reefs experience only moderate decline despite a relatively high warming rate. These anomalous reefs tend to have extremely high in-strength, and are usually in regions of convergence where larvae are trapped against the coast, such as coastal reefs in north Mozambique and the northeast coast of Zanzibar Island in Tanzania (figure 5.17). Together, mean SST rise rate and in-strength almost entirely explain the variance in hard coral cover decline in our simulations.

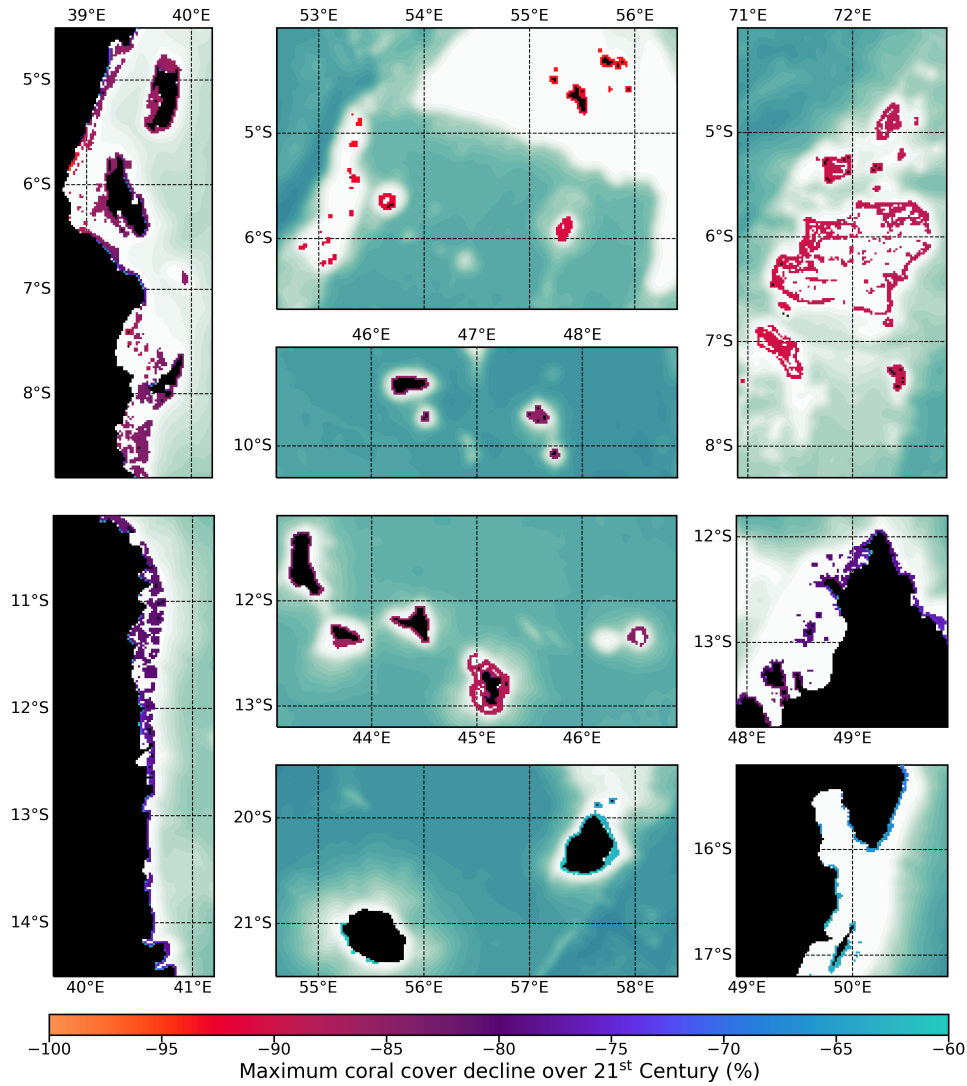


Figure 5.17: Decline in reef cover throughout the 21st Century under RCP4.5 relative to the 1875-1974 average (%).

Contrary to in-strength, the Δ SST metric does not appear to have any significant effect on reef resilience in our simulations. This suggests that the benefit of high in-strength to reefs is *not* the introduction of genotypes adapted to warmer temperature, but rather the pure mass effect of a constant, significant supply of coral larvae to compensate for the deleterious effects of warming. Based on figure 5.18, the threshold at which in-strength can begin to significantly affect the population growth rate is around 0.1, i.e. 0.1 larvae attempting to settle for every larva generated in that same reef. Given the inability of a 2 km resolution model to reproduce fine scale coastal processes (e.g. Dauhajre et al., 2019), it is not clear to what extent these predictions

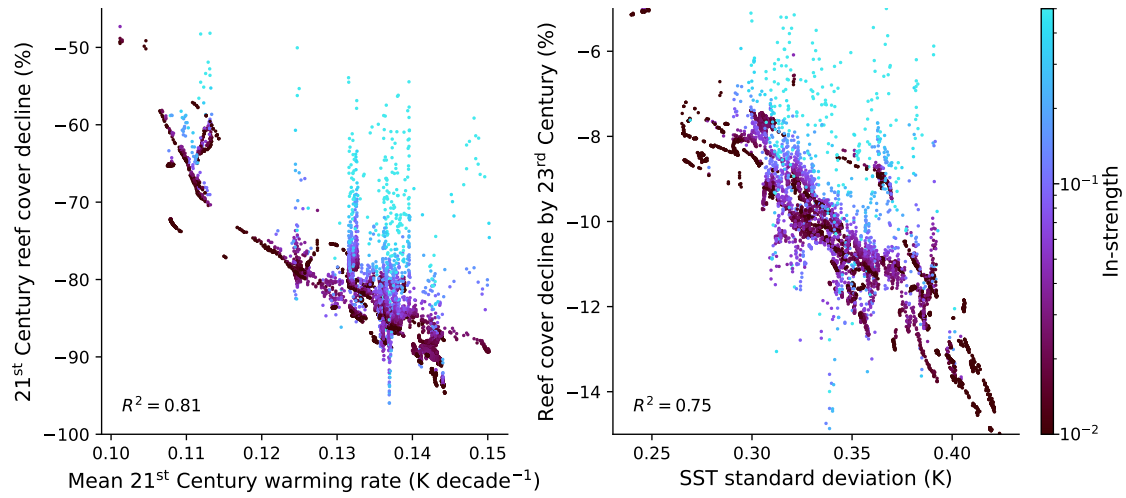


Figure 5.18: *Left:* Decline in reef cover throughout the 21st Century under RCP4.5 relative to the 1875-1974 average (%), as a function of average warming rate (x axis) and in-strength (colours). *Right:* Change in coral cover from 1875-1974 to 2200-2299 (%) as a function of SST standard deviation after low-frequency variability is removed (x axis) and in-strength (colours).

of exceptionally high in-strength are reasonable, as opposed to a modelling artefact.

Although defined slightly differently, McManus, Forrest, et al. (2021) found that the analogous *destination strength* metric tended to reduce coral cover decline across the Caribbean, Southwest Pacific, and Coral Triangle regions in their simulations. Interestingly, the change in SST (broadly proportional to the rate of SST rise considered in our study) was only found by McManus, Forrest, et al. (2021) to be a significant driver of coral cover decline at low values of effective fecundity for the Southwest Pacific and Coral Triangle, and never for the Caribbean. Matz et al. (2020) similarly found little correlation between warming rate and reef decline in their eco-evolutionary simulations. The proportion of reef cells with a high in-strength is considerably higher for all the connectivity matrices considered in McManus, Forrest, et al. (2021) (figure C.3). It is therefore possible that the greater inferred influence of connectivity on resilience found by McManus, Forrest, et al. (2021) for similar values of effective fecundity to our study is due to generally higher in-strength (or destination strength) in the underlying connectivity matrices. On the other hand, our sensitivity analysis (figure 5.1) demonstrates that similar spatial patterns of reef decline persist even at higher values of effective fecundity, so the importance

of the rate of temperature rise as a driver of reef decline in the SWIO appears to be a robust feature of our simulations.

As a result, evolution through local selection rather than connectivity appears to be key for coral resilience in the SWIO in the face of anthropogenic warming. Although we found that a mass effect allowed comparatively high reef cover to persist at some rapidly warming sites, there is insufficient evidence for whether the coral recruitment required for this is reasonable. In reality, there is only finite additive genetic variance within a population (in the absence of mutation), and selection will therefore tend to reduce genetic variance in this model for a truly isolated population. However, even if larval fluxes between populations are insufficient to *drive* evolution, they are probably high enough to maintain a significant exchange of genotypes between populations and maintain genetic variation (Lowe & Allendorf, 2010).

Finally, we note that we only attempt to model hard coral cover, rather than diversity. Coral species richness is generally lower in more marginal environments, despite relatively high coral cover (Harriott & Banks, 2002; Ministry of the Environment & Japanese Coral Reef Society, 2004). The reefs with the least coral decline in our model tended to be towards the margins of the biodiversity hotspot in the SWIO (Obura (2012), although see Kusumoto et al. (2020)) and are therefore unlikely to preserve much of the coral diversity in the region.

5.4 Conclusions

Despite the presence of a large number of remote islands, no coral reef in the tropical SWIO is truly isolated over evolutionary timescales, with practically all pairs of reefs physically connected within a couple of hundred generations. This is the first study to quantify multiple-generational coral connectivity in the southwest Indian Ocean.

Our larval dispersal simulations suggest that the NEMC acts as a leaky dispersal barrier, separating the Seychelles Archipelago 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 EACC, fed by the NEMC, results in strong and consistent connectivity along the coasts of

Tanzania, Kenya, and southern Somalia, 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 SECC, and broadcasts larvae to the Mozambique Channel through the SEC.

These findings suggest that the large-scale coral population structure of the tropical SWIO can be explained reasonably well through physical larval dispersal. Although the flow of larvae between distant populations is generally unlikely to be high enough to be ecologically significant (figure 5.3, section 5.3.3), it is certainly strong enough to establish long-distance genetic connectivity. Evidence for a well-connected ecosystem within the north Mozambique Channel, as proposed by Obura (2012), is robust, even if the Mozambique Channel does physically impair larval dispersal between Madagascar and East Africa. The northern boundary of this region is uncertain. As far as connectivity is concerned, there is a (weak) physical basis for expecting a dispersal barrier north of Mafia Island, as described in section 5.3.1.3 and supported by Obura (2012) and van der Ven et al. (2016). More robust in our simulations (and supported by previous modelling by Gamoyo et al. (2019)) is the existence of a dispersal barrier due to the bifurcation of the NEMC around the Mozambique-Tanzania border but, despite some support from a brooding coral (van der Ven et al., 2021), empirical evidence for significant differentiation here is lacking (Obura, 2012; van der Ven et al., 2022). Setting the question of the northern limit of the north Mozambique Channel system aside, there is a strong consensus from population genetics, biogeography, and numerical models, for strong connectivity along the path of the EACC, albeit with small scale exceptions due to local flow regimes.

Regional biogeography demonstrates the existence of connectivity between the isolated Chagos Archipelago and the SWIO (Obura, 2012), even though the absolute number of larvae traversing this distance is likely small (Montoya-Maya et al., 2016). Our simulations suggest that dispersal to the Chagos Archipelago from the Inner Islands of Seychelles through the SECC is greater than dispersal from the

Chagos Archipelago to the north Mozambique Channel region through the SEC, indicating that the greater similarity in fauna between the Chagos Archipelago and north Mozambique Channel region than with Seychelles (Obura, 2012) cannot be explained through larval dispersal alone.

Identifying clusters of reefs that tend to retain coral larvae using Infomap has a stronger theoretical basis than alternative metrics such as modularity, and our results suggest this approach is useful for comparing modelled potential connectivity to results from population genetics and biogeography. We also find that our meta-clustering approach is an excellent data visualisation tool. Based on figure 5.7, it is possible to immediately identify not only major dispersal barriers, but the relative persistence of these barriers. This is not possible when the network is divided into one discrete set of partitions, which can be compounded by unclear colour choice (Gamoyo et al., 2019). Limitations of our approach are that (1) the resulting 3D colour map in RGB space is not perceptually uniform (e.g. Thyng et al., 2016), and (2) that it exaggerates the importance of principal components 2 and 3 for the sake of clarity. As a result, figure 5.7 should be used in conjunction with the full principal component plot and Euclidean distances (figure 5.6 and figure C.4) for in-depth analyses.

Although there is good evidence that larval supply (from nearby reefs) supports coral reef resilience (Edmunds, 2022; Gouezo et al., 2020; Lukoschek et al., 2013; Thomson et al., 2021), there is limited empirical evidence for the importance of large-scale connectivity from long-distance dispersal for resilience. Connectivity also appears to have only a minor effect on coral cover decline in our eco-evolutionary simulations. Nevertheless, reefs along the east African coast from northern Mozambique to Tanzania, in addition to the Comoro Islands, perform consistently strongly across a range of connectivity metrics quantifying their ability to supply the wider reef network with coral larvae. Due to the lack of evidence for their utility, we would caution relying too heavily on large-scale connectivity metrics (as derived from our simulations, or existing coarser-scale dispersal models) for marine management. However, the strong similarity between our results and the resilient reefs identified

by Beyer et al. (2018) indicates that, in addition to strong connectivity, these reefs perform strongly across a range of climate-based resilience indicators.

On the other hand, our eco-evolutionary simulations suggest that selection, not connectivity, drives the adaptation potential of corals in the SWIO to climate change over the 21st Century. Our results, which are robust across a considerable range of parameter space, predict that the local rate of temperature rise is the dominant environmental control on coral reef decline in the region and that, rather than the well-connected reefs along the EACC, it will be the more marginal reefs of East Madagascar and Mascarene Islands which experience the least catastrophic decline in coral cover over the coming century. These conclusions differ from previous studies which find a greater role for connectivity (Matz et al., 2020; McManus, Forrest, et al., 2021), but this difference may in part be due to the generally lower potential connectivity we compute for the SWIO. The overestimation of dispersal distances through larval dispersal simulations is well-known (Shanks, 2009) and is likely driven by insufficient model resolution to reasonably represent hydrodynamics around coral reefs and in the near-shore environment (e.g. Grimaldi et al., 2022; Monismith, 2007; Monismith et al., 2018). Our oceanographic model resolution is an improvement over those used as the basis for Matz et al. (2020) and McManus, Forrest, et al. (2021), and larval settling is arguably parameterised more realistically, which may be a factor in explaining the generally lower potential connectivity we predict for the SWIO, although we emphasise that it is still incapable of reasonably representing circulation below a horizontal scale of around 10 km. As a result, although the reefs of north Mozambique, Kenya and Comoros are strongly connected over many generations, it is not clear to what extent this will actually translate into resilience in the face of the warming of the ocean.

6

Conclusions

6.1 Summary

In this thesis, we set out to investigate the transport of MPP and coral larvae in the WIO, with the aims of building physical understanding behind the resulting patterns of marine connectivity, and generating data products that will be useful and actionable for practitioners working on conservation in the region.

In chapter 2, we found that, whilst the smallest MPP fragments beaching at remote WIO islands (with a short residence time at the ocean surface and not experiencing a push from the winds) originate from within the WIO, more buoyant fragments of terrestrial origin are overwhelmingly transported from the north and east of the Indian Ocean due to the large rate of MPP production, and westward transport by winds and the SEC. Source regions for MPP from fisheries are largely controlled by the distribution of fishing effort. Monsoonal winds play an important role in determining the seasonality of MPP beaching rates at these remote islands. This is particularly the case for the Outer Islands of Seychelles, where local winds block MPP from arriving from most of the Indian Ocean during the southeast monsoon. Arguably the most important finding in chapter 2 is how our simulation results *differed* from observations of MPP sources. MPP manufactured in countries associated with maritime trade through the Indian Ocean (such as China, Malaysia,

and Singapore) were systematically over-represented in observations relative to model predictions. This suggests that, for many remote islands, MPP being discarded at sea - in likely contravention of MARPOL Annex V - is comparable in significance to terrestrial sources of MPP.

To generate the higher-resolution surface current predictions required for our coral larval dispersal simulations, in chapter 3 we presented WINDS, a configuration of the CROCO ocean model for the tropical SWIO. We validated WINDS and demonstrated that, although high-frequency current variability may be overestimated in certain regions and the position of the northern boundary causes some problems for equatorial dispersal predictions, WINDS generally agrees very well with observations and is appropriate for use in chapters 4-5.

With surface current predictions for the tropical SWIO spanning almost three decades, we then simulated the potential connectivity between all known shallow-water coral reefs in the region using SECoW. We found that, although potential connectivity experiences interannual and seasonal variability, connectivity is generally dominated by stochastic, day-to-day variability, introduced by eddies and fronts. This variability is enormous, and introduces a fundamental level of uncertainty associated with short-term (tens of spawning events) potential connectivity between coral reefs. We showed how, for many remote islands, a tiny proportion of spawning events may be responsible for the majority of successfully settling coral larvae, and that extended spawning durations of just a few days can considerably increase the stability of reefs as larval sources. We also demonstrated some potential risks associated with using the time-mean potential connectivity to infer short-term connectivity between reefs, and urge future larval dispersal studies to make more data available rather than (usually at best) a single time-mean matrix.

Finally, having established the importance of connectivity *variability*, we concluded the main body of this thesis with an investigation into SWIO reef connectivity itself. Although there are discrepancies at a local scale, our modelled predictions of coral reef connectivity generally agree well with previous data from coral biogeography and population genetics, as well as other larval dispersal models that have been

run in the region. We predicted that all coral reefs in the SWIO are at least physically connected within ~ 200 generations of larval dispersal, and developed a novel ‘meta-clustering’ and data visualisation technique using the Infomap algorithm, to identify groups of reefs that consistently retain coral larvae. By combining our potential connectivity matrices with an eco-evolutionary model that considers the ability for corals to adapt to warming temperatures, we predicted that coral cover decline will nevertheless be considerable (although potentially not terminal) across the SWIO. Our simulations predicted that coral cover decline is largely set by the local warming rate, rather than reef connectivity.

Although we investigated two rather different environmental problems in this thesis (marine plastic pollution and coral reef ecology), as described in chapter 1, physical similarities between the dispersal of MPP and coral larvae mean that we can apply similar research methods to both. Indeed, many of the techniques used in the coral connectivity analyses in chapters 4-5 were originally developed for use in the MPP dispersal model in chapter 2.

An innovation in this thesis is the selective use of output from the Lagrangian model to minimise the storage requirements to reproduce fluxes associated with beaching/settling events. Although there are limitations to this approach (e.g. interpreting results is difficult without trajectories), this is compensated by the ability to comprehensively capture all beaching/settling events and efficiently explore parameter space, neither of which are practical with conventional methods. The latter is particularly important for our applications of MPP and coral larval dispersal, where key parameters are poorly constrained, and the ability to investigate the sensitivity to these parameters is therefore essential. Combined with the fact that we have made all raw output available on public repositories, this means that the results of this thesis will remain useful even if future research establishes that our parameter choices are not optimal.

The input distributions of MPP and coral larvae are very different and, aside from the smallest plastic fragments, the residence time of MPP at the ocean surface is generally greater. However, one important similarity in the physical behaviour of both

is the intensely pulsed nature of beaching and settling, driven by the filamentation of buoyant material around eddies and fronts (Harrison et al., 2013). This introduces considerable stochastic variability to MPP accumulation and coral reef connectivity although, in the case of MPP, this is somewhat modulated by the direct and regular push of the monsoonal winds. Furthermore, although we do not directly investigate the density of MPP or larvae at sea, we would expect smaller MPP classes and larvae to accumulate in similar marine environments due to their similar physical behaviour. This is confirmed by observations finding high concentrations of both plastics and neuston/larvae within accumulation zones in subtropical gyres (Chong et al., 2023) and, at a much smaller scale, surface slicks (Gove et al., 2019).

Predicting the dispersal and connectivity of MPP and marine larvae is difficult. Both problems span orders of magnitude in scale (both spatially and temporally), are a function of many physical and biological processes (most of which are poorly constrained by observations), and are often extremely difficult to validate directly, particularly in the case of larval dispersal. Despite these difficulties, as long as questions are well posed given model limitations, it is possible to obtain substantial scientific value from numerical modelling approaches.

6.2 Outstanding questions

6.2.1 Unresolved scales

Variability - physical and biological - occurs across a range of spatial and temporal scales. Even for our studies based on WINDS, with a horizontal resolution of ~ 2 km, we cannot adequately represent the hydrodynamics that dominate flow in the near-coastal or reef environment (Lowe & Falter, 2015; Monismith, 2007; van Sebille et al., 2020) such as wave-driven flows over reefs, Langmuir circulation, and rip currents. Inadequately resolving these processes limits the capacity of large-scale dispersal models to quantify connectivity between distant reefs. For instance, Grimaldi et al. (2022) found that a $1/10^\circ$ ocean model overestimated dispersal distance from an atoll by more than an order of magnitude compared to a reef-scale hydrodynamic

model, with Monismith et al. (2018) also finding that a $1/12^\circ$ model overestimated connectivity between islands with coral reefs compared to drifters.

Reasonably representing sub-mesoscale coastal circulation in large-scale, regional ocean models is a significant technical challenge, both in terms of computational expense and storage. Nested grids are often used to locally improve the resolution of an ocean model, but dispersal modelling is rarely carried out *between* nested subdomains. Although this has been attempted by a small number of studies (e.g. Wang et al., 2019), we are not aware of any investigations into whether particle tracking across domain boundaries in nested grids introduces artefacts due to the change in resolution. Alternatively, unstructured meshes allow the horizontal resolution to be varied within a single grid. For modelling the dispersal of larvae and MPP, unstructured meshes have generally only been used for relatively small domains compared to the regions we consider in this thesis. One exception is the Great Barrier Reef, where hydrodynamic computation has been simplified by using 2D (as opposed to 3D) unstructured meshes, justified by the shallow water and well-mixed water column (e.g. Critchell et al., 2015). However, ocean models using unstructured meshes have been run on a larger scale, such as the ocean component of the ICON ESM, which has been used to locally resolve sub-kilometre scales within a global grid (Hohenegger et al., 2023). The use of regional-scale unstructured grids represents an excellent opportunity to improve the representation of long-distance connectivity between coastlines in ocean models. One barrier to widespread use is the lack of offline Lagrangian particle tracking codes that can process unstructured grids (van Sebille et al., 2018). Hopefully, if support for unstructured grids is implemented in widely-used particle tracking software, this may lead to significant improvements in predictions of long-range marine dispersal and connectivity.

Another option worth exploring is larval retention parameterisations around coral reefs. Using idealised models, Cetina-Heredia and Connolly (2011) found that larval retention around shallow submerged reefs is sensitive to the formation of wake eddies, and can be approximated using an ‘Island Wake Parameter’ (analogous to the Reynolds number). It would be interesting to test whether this parameterisation also

holds for deep-water coral islands (abundant throughout the SWIO), which we expect would be the case for tropical reefs based on Heywood et al. (1996). Testing whether these parameterisations remain robust in a realistic model (with complicating factors such as tides, complex coastlines, etc) would also be insightful.

For coral connectivity, fine-scale biological variability adds another layer of complexity. Within each $\sim 4 \text{ km}^2$ coral reef grid cell we considered in chapter 5, there likely exists a wide range of local thermal environments (or microclimates) within different reef zones (e.g. Falter et al., 2014; Green, Lowe, Buckley, et al., 2019), hosting locally-adapted corals. Variability in thermal tolerance is not wholly genetic in origin (for instance, the symbiotic dinoflagellates within corals play a significant role in adaptation, which may not be heritable), but there is nevertheless increasing evidence for genetic variance across reef microclimates (e.g. Bay & Palumbi, 2014; Cerutti et al., 2019; Thomas et al., 2022). Our study assumed that the additive genetic variance in thermal tolerance is constant in both time and space, but more thermally heterogeneous reefs may host greater genetic variance, improving local adaptive capacity. Given that gene flow within individual reefs tends to be very strong (Thomas et al., 2022), we can hypothesise that local, hot reef microclimates could play an important role in facilitating rapid coral evolution.

It would therefore be interesting to test the relative importance of within-reef versus between-reef connectivity in coral adaptation to environmental change, for instance within a nested ocean model. If within-reef connectivity dominates (as our results in chapter 5 hint might be the case, since the additive genetic variance we use is relatively small compared to the thermal variability within many reefs), it may be useful to develop parameterisations for the base genetic variance present within reef nodes. For example, reef heterogeneity could be used as a proxy for thermal heterogeneity, estimated using the geomorphological classifications provided by the Allen Coral Atlas (Lyons et al., 2022). Understanding the importance of within-reef versus between-reef connectivity is also critical given the potential for local coral refugia, for instance mesophotic reefs (e.g. Holstein et al., 2016; Takeyasu et al., 2023) or shallow-water reefs cooled by upwelled water from internal tides (e.g.

Green, Lowe, Buckley, et al., 2019; Wyatt et al., 2020). However, even if within-reef connectivity drives rapid evolution, the genetic variance within an individual reef is finite, and could be reduced under intense selection (Klausmeier et al., 2020), throttling adaptation. As a result, even if long-distance larval fluxes are too small to directly drive evolution, between-reef connectivity may still be important in terms of maintaining genetic variance within populations.

6.2.2 Hydrodynamics around Aldabra Atoll, Seychelles

A particular site of interest throughout this thesis is Aldabra Atoll, Seychelles. In the aftermath of the 2015-2016 El-Niño event, Cerutti et al. (2019) found that, despite experiencing greater thermal stress, hard corals within Aldabra’s lagoon experienced less decline compared to corals in the seaward reefs. The authors suggest this may be due to local adaptation to the high temperature variability within Aldabra’s tidal lagoon, which experiences a (semi)diurnal tidal elevation and SST range of up to 3 m and 5.6 °C (Cerutti et al., 2019; Farrow & Brander, 1971). It is therefore, in theory, possible that the resilient corals within Aldabra’s lagoon could act as a source of thermally tolerant larvae for Aldabra’s seaward-facing reefs and, perhaps, other distant downstream reefs. The exchange of larvae between Aldabra’s lagoon and the ocean will depend on the residence time of water within the lagoon. A back-of-the-envelope calculation¹ suggests that the average residence time of water in the lagoon is about 4 days, comparable to another tidally forced atoll (Green et al., 2018). This is short compared to the competency period and lifespan of many coral larvae, suggesting that there may well be strong potential connectivity between corals in Aldabra’s seaward reefs, and those within the lagoon

¹The lagoon has a volume of $\sim 2 \text{ km}^3$ assuming an average depth of 10 m and surface area of 203 km^2 (Hamylton et al., 2018), and we assume all exchange with the ocean is tidal, and through the Grande Passe, Passe Gionnet, and Passe Hoareau channels (ignoring the very shallow channels in the west). We take an average tidal current speed of 0.5 m s^{-1} (active half the time, since flow reverses over the tidal cycle), and use channel widths of 500 m, 50 m, and 50 m; and average channel depths of 20 m, 10 m, and 15 m for Grande Passe, Passe Gionnet, and Passe Hoareau respectively. We have coarsely estimated these figures from Admiralty Chart 718, Farrow and Brander (1971) and Hamylton et al. (2018).

- certainly those near the tidal channels, which is where most of the corals in the lagoon are anyway (Hamylton et al., 2018).

However, due to its large size, and interactions between strong tidal currents and very shallow and variable bathymetry, tides are highly heterogeneous within the lagoon (Farrow & Brander, 1971), which likely extends to the water residence time. A hydrodynamic model for the tidal flushing of Aldabra's lagoon (constrained by *in-situ* observations, with open boundaries in the tidal channels) would be useful for quantifying connectivity within Aldabra's lagoon, as well as with Aldabra's seaward reefs. Most of the lagoon is shallow enough to construct high-resolution bathymetry from optical satellite imagery (Hamylton et al., 2018) and point-observations for tides are available around Aldabra (Farrow & Brander, 1971), so this would be feasible without extensive further fieldwork.

There is also interest in modelling the flow around Aldabra Atoll. Aldabra is influenced by the SEC and NEMC (figure 1.2), and flow past the island is sufficient to generate a range of wake eddy behaviour (Heywood et al., 1996) and upwelling (Heywood et al., 1990). Recent studies have revealed the importance of upwelling for remote coral reefs, by cooling reefs during marine heatwaves and acting as a nutrient source, promoting plankton growth and allowing corals to shift towards heterotrophy (Fox et al., 2023; Green, Jones, et al., 2019; Spring & Williams, 2023). The Thermal Stratification Index (TSI, Guillaume-Castel et al. (2021)) is a metric used to quantify upwelling into tropical shallow waters, computed as the first vertical moment of temperature anomalies above a certain depth (which we set to 30 m, the zone most shallow-water tropical corals occupy). Stronger upwelling is characterised by a more negative TSI. Although 3D output from WINDS is only available as 5-day averages (section 3.3) and therefore has limited capacity to identify upwelling associated with tidal bores (e.g. Green, Jones, et al., 2019), WINDS nevertheless suggests that upwelling does occur around Aldabra figure 6.1.

The TSI suggests that upwelling is pronounced along the south coast of Aldabra (figure 6.2), particularly during the southeast monsoon, when coastal Ekman-induced upwelling is expected (figure 1.4). Upwelling, potentially associated with island

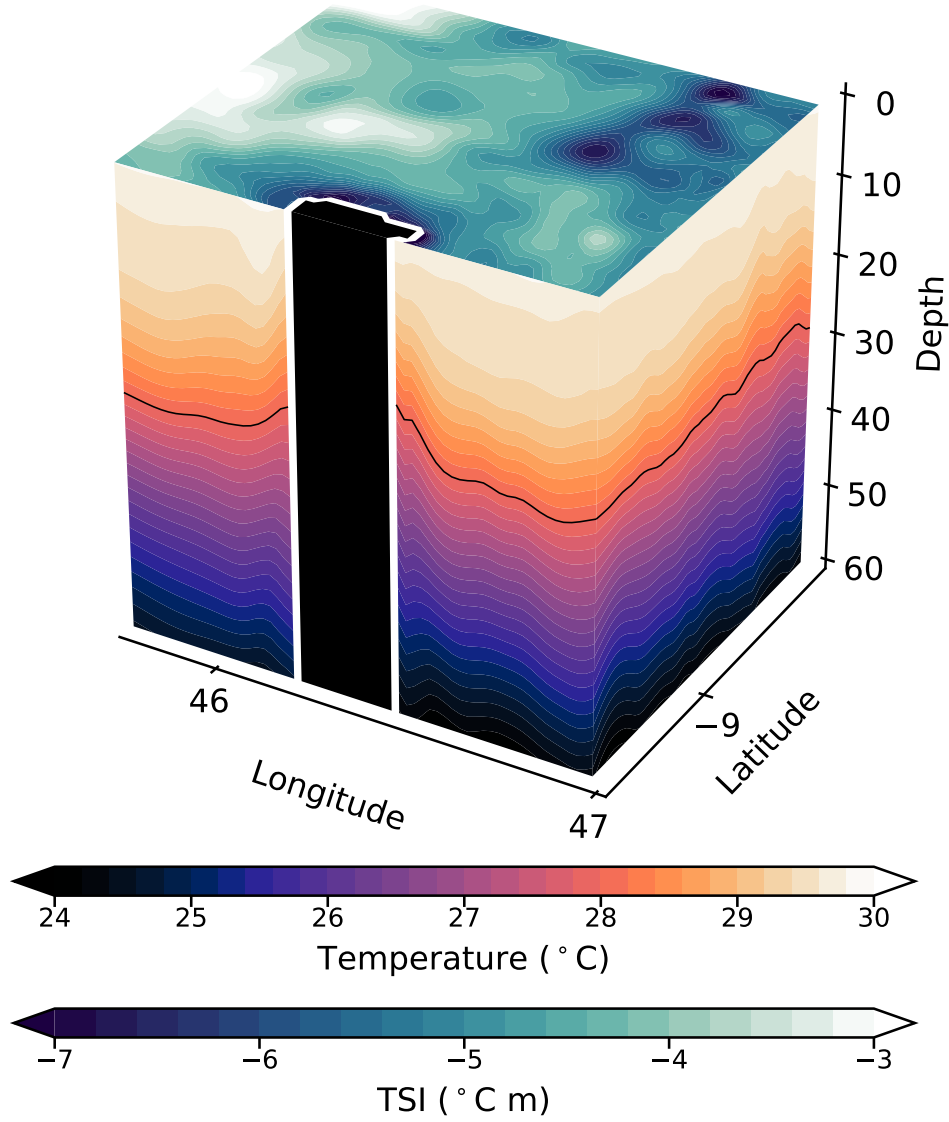


Figure 6.1: (*lateral view*) 5-day average temperature in the upper 60 m of the water column around Aldabra (early March 2010 from WINDS-M) and (*plan view*) TSI (Guillaume-Castel et al., 2021) computed from temperature in the upper 30 m of the water column.

wakes, is also visible during the southwest monsoon to the west of Aldabra and Assomption, due to the greater current speed around the islands during this season (figure 3.3). Satellite-derived chlorophyll-a concentration confirms the existence of upwelling around Aldabra (Garnesson et al., 2021), although the seasonal cycle appears to be dominated by the mixed layer depth rather than fine-scale upwelling sites as indicated in figure 6.2.

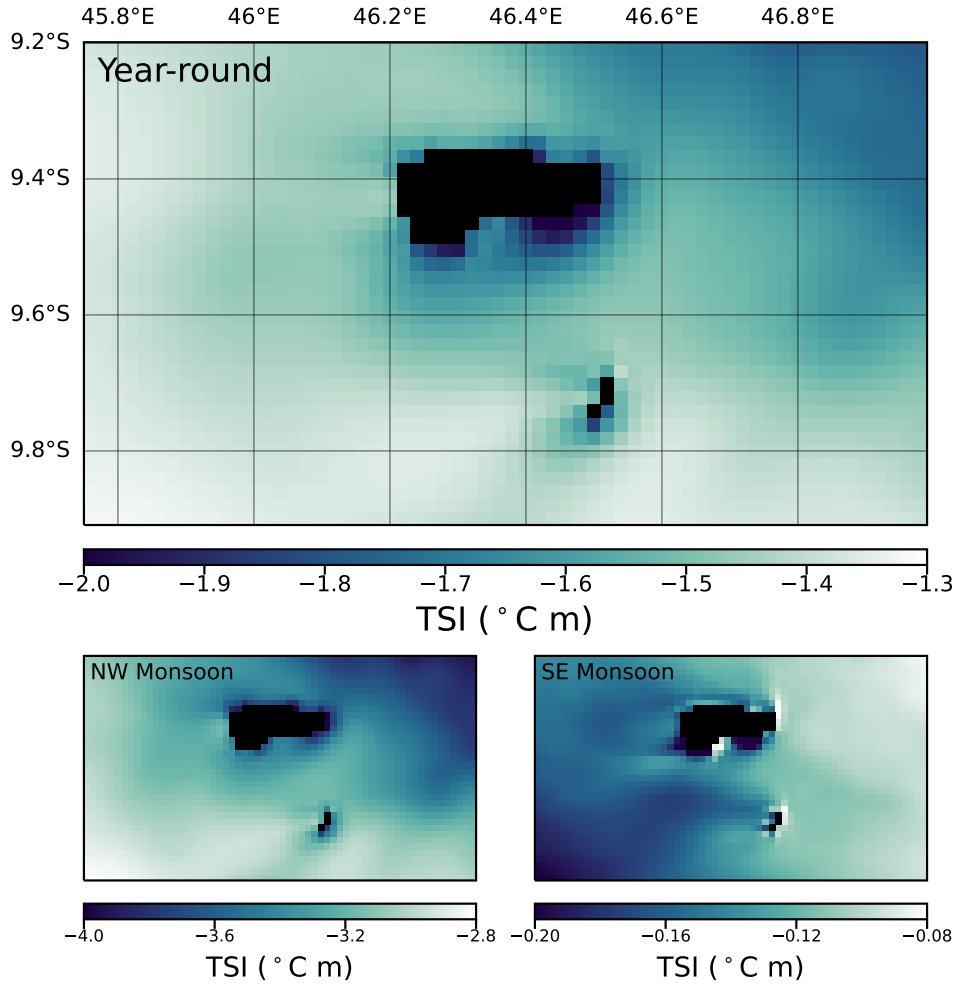


Figure 6.2: Mean TSI across 5-day average temperature profiles around Aldabra and Assumption for the entire year, northwest monsoon (DJF), and southeast monsoon (JJA). Note that the magnitude of TSI is much lower during the SE monsoon, as the mixed layer is deeper and stratification within the top 30 m of the water column is low.

Although the 2 km resolution of WINDS is sufficient to resolve wake eddies behind relatively large islands such as Aldabra (Heywood et al., 1996), it is insufficient to reasonably represent the hydrodynamics around Aldabra’s reefs. A hydrodynamic model for Aldabra with a resolution of order 100 m (perhaps nested within WINDS) could be useful for assessing reef-scale connectivity, as described in section 6.2.1, as well as predicting the nutrient supply to the lagoon (Green, Jones, et al., 2019) and improving estimates of interisland connectivity. Unfortunately, multibeam bathymetry only exists for a very small fraction of the ocean immediately around Aldabra (Swanborn et al., 2022), and comparison of the most recent GEBCO grid

(GEBCO Compilation Group, 2022) with point soundings from Admiralty charts reveals that there are vertical errors in excess of 1 km for the gravimetry-derived bathymetry in the region. Although we used these soundings to improve the representation of bathymetry around Aldabra in chapter 3, we are not aware of publicly available data at sufficient resolution to generate reasonable bathymetry around Aldabra appropriate for a reef-scale hydrodynamic model. This highlights the urgent need for improved multibeam bathymetry coverage in the ocean (e.g. The Nippon Foundation-GEBCO Seabed 2030 Project), particularly around atolls and seamounts, which are often subject to significant errors in gravimetry-derived bathymetry.

6.2.3 Poorly-constrained behaviour

Parameterising behaviour (where here ‘behaviour’ broadly refers to anything deviating from passive, conservative advection) is a recurring challenge in predicting marine dispersal and connectivity. In this thesis, we take the approach of minimising the computational expense associated with changing non-physical behaviour (e.g. beaching/settling rates). Another approach, which is possible for MPP in less data-sparse regions than the SWIO (but probably not coral larval dispersal), is inferring probability density functions for parameters through inverse modelling (Kaandorp et al., 2020).

Fundamentally, more empirical data is needed for the behaviour of both MPP and (coral) larvae. For instance, despite the enormous impact of wind on buoyant debris trajectories, there is very little publicly available empirical data for parameterising windage coefficients for different types of MPP (e.g. Domon et al., 2012). We suspect that more data exists in the grey literature, for instance from search and rescue organisations, so it could be useful to liaise with regional and national coastguards to ensure their findings are being communicated to the scientific community.

The lack of empirical data is arguably even more concerning for larval dispersal. The vertical position of larvae in the water column can significantly affect dispersal pathways (e.g. Dauhajre et al., 2019; Paris et al., 2007), yet there are limited observational constraints to inform modelling strategies. Eggs and young larvae of

broadcasting corals tend to be positively buoyant, but buoyancy decreases with age and larvae tend to be found at the bottom of water tanks within days to weeks of spawning (Hariri et al., 2007; Szmant & Meadows, 2006; Tay et al., 2011). On the other hand, the vertical swimming speed of coral larvae is significant, and at least some coral larvae exhibit phototaxis, actively swimming towards the ocean surface (Mulla et al., 2021; Szmant & Meadows, 2006). However, these experiments are generally carried out in controlled laboratory environments (although see Mulla et al. (2021)), and it is unclear what the real vertical distribution of coral larvae would be in the open ocean, and how much this varies between (or even within) species. Further empirical data on the behaviour of coral larvae in realistic marine settings (e.g. in marine mesocosms) would therefore be very useful for improving their representation in dispersal models.

In this thesis, we assume that larval biology is independent of the environment. However, mortality and competency acquisition rates increase with higher temperature (Figueiredo et al. (2014) and O'Connor et al. (2007), but see Kitchen et al. (2020)). The effects of large-scale warming on connectivity (through mortality and competency) have been tested and, unsurprisingly, increases larval retention and reduces connectivity (Figueiredo et al., 2022). However, what has not yet been investigated is the role fine-scale temperature variability (in space and time) could have in determining connectivity variability. Aside from temperature variability associated with the seasonal cycle and weather, larvae could be exposed to prolonged thermal stress (or relief) if they become entrained into a larval filament associated with an SST front (Harrison et al., 2013).

Temperature-dependent mortality could be simplistically incorporated into SECoW using SST output from WINDS, by assuming that the instantaneous mortality rate depends on temperature only, and linearising $\mu_m(T)$ around $T = T_0$. In that case, the only additional information needed to evaluate the larval settling flux within a settling event is the integral $I_T(t) = \int_0^t (T - T_0) dt$, which could be approximated through interpolation by recording the integral value at the start and end of each event.

6.2.4 Larval dispersal and eco-evolutionary model validation

Validating models of macroplastic MPP beaching is, in principle, relatively straightforward because of the abundance of MPP on most beaches, and the availability of provenance indicators (such as labels), albeit with the limitations described in chapter 2 of this thesis. However, due to the impracticality of directly tracking individuals over large distances and the lack of any provenance indicators that have been shown to work in realistic marine environments, validating coral larval dispersal models is, at present, only possible through indirect methods. Although population genetics and biogeography are useful for comparison against potential connectivity predictions, they have limited capacity to act as ‘validation’ since they are not measuring the same thing (genetic connectivity, demographic connectivity, and potential connectivity are fundamentally different).

For example, the observation of similar coral fauna between sites and generally low genetic differentiation is *proof* of genetic connectivity, so these observations can ‘validate’ the larval dispersal model insofar that the model predicts that significant dispersal pathways exist between reefs. However, when assessing an apparent difference between a SECoW prediction and observation (such as the greater similarity identified by Obura (2012) between coral assemblages in the Chagos Archipelago and north Mozambique Channel versus Seychelles), it is very difficult to tell whether this is due to the poor accuracy of modelled potential connectivity, sampling limitations in the observations, or the many other confounding ecological factors that could cause biogeography to diverge from potential connectivity. There is therefore a real danger of potential connectivity predictions becoming non-falsifiable, since there is no way of telling whether a discrepancy between model predictions and observations of proxies such as biogeography is due to an incorrect model prediction (of potential connectivity), or a limitation of the proxy as validation for potential connectivity.

Given that eco-evolutionary models predict that rapid evolution could prevent complete coral cover collapse (e.g. McManus, Forrest, et al., 2021), validation of these models is particularly important. Kleypas et al. (2016) and Matz et al. (2020) both found that accounting for the thermal environment of upstream reefs improved

predictions of short-term bleaching and coral cover in the Coral Triangle (broadly corresponding to maritime SE Asia). However, these statistical relationships are weak, likely because short-term variability in coral cover also depends on many confounding factors such as disease (e.g. Cramer et al., 2020), local and/or subsurface thermal environments that would not be captured by relatively coarse satellite-derived SST (e.g. Green, Lowe, Buckley, et al., 2019; Wyatt et al., 2020), and genetic variability (Humanes et al., 2022). Indeed, our eco-evolutionary model was also unable to reproduce observed short-term coral cover variability (figure 5.2).

With coral cover compilations that now span multiple decades, we can also consider whether decadal trends in coral cover are significantly different from what would be expected in the absence of adaptation. Observations indicate that there has so far been no sustained large-scale collapse in coral cover in the SWIO (Souter et al., 2021). This is more consistent with our simulations incorporating adaptation than those without (figure 6.3). On the other hand, given the enormous amount of variability in observed coral cover records, it is very difficult to tell whether this is genuinely an effect of adaptation, as opposed to model limitations and/or sampling biases.

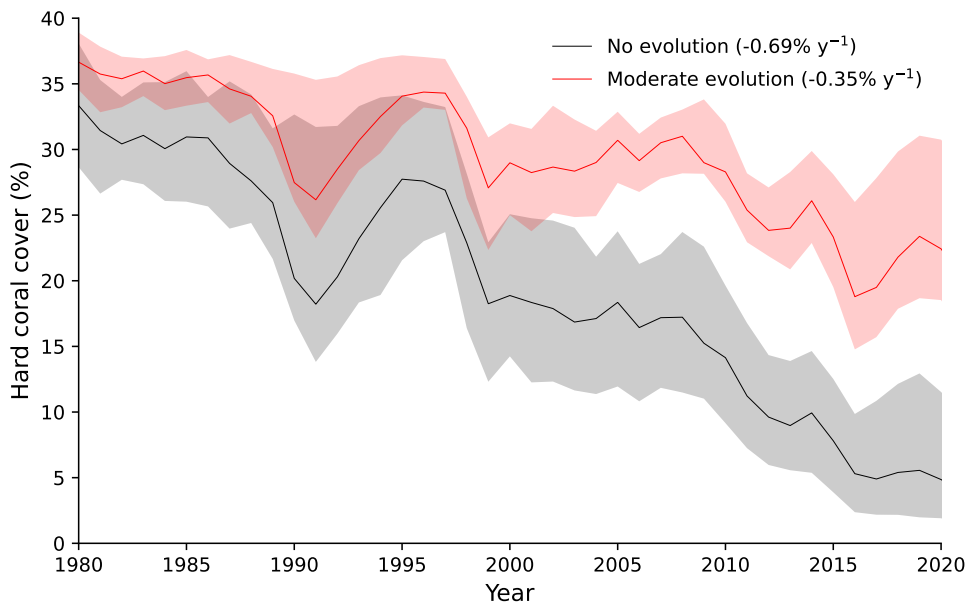


Figure 6.3: Mean modelled hard coral cover within SECoW with moderate (red, additive genetic variance of 0.03 K^2) and no (black) evolution. Numbers in brackets refer to the average loss of hard coral cover per year over the plotted period. Parameters are otherwise identical to those used in chapter 5.

The extraordinary complexity of coral reef systems means that it is unlikely we will be able to precisely predict the role of adaptation in the macroecological response of corals to ocean warming before irreversible changes (within this century, at least) have already occurred. However, testing eco-evolutionary models at a finer (reef) scale, where it may genuinely be possible to observe and model the spatial biophysical variability present on reefs, could be a useful step towards improving our confidence in these models. Another potentially useful large-scale test case for eco-evolutionary models is the tropicalisation of subtropical and temperate reefs. Contrary to established tropical coral reefs, where we are trying to observe changes against a very noisy coral cover signal, tropical corals have been observed colonising subtropical environments (e.g. Beger et al., 2014; Yamano et al., 2011), where they were previously entirely absent. It would be interesting to investigate whether eco-evolutionary models are capable of reproducing this observed range expansion, and whether this places any further constraints on model parameters.

The difficulty associated with comparing model output to observations does not in any way diminish the importance of model validation. Generating *testable* predictions is fundamental to the scientific method, and although we do not have all the solutions in this thesis, this should be a priority for future research, and will require greater collaboration between marine biologists, ecologists, and modellers. In particular, experiments should be *designed* with validation in mind, rather than including a model-data comparison as an afterthought.

6.2.5 The role of palaeoceanography in setting contemporary biogeography

Another possible explanation for mismatch between observed biogeography and contemporary potential connectivity is changes in surface currents over geological time (Barber et al., 2000; Obura, 2016). The last glacial was accompanied by a fall in eustatic sea level, reaching its lowest point at -135 m relative to the present at the last glacial maximum (LGM, Lambeck et al. (2014)). Within the SWIO, this would have resulted in the exposure of much of the Seychelles and Mascarene Plateaus

(the latter potentially providing an enhanced stepping stone along the path of the SEC between the Chagos Archipelago and the north Mozambique Channel), as well as shallow shelf seas within the Mozambique Channel.

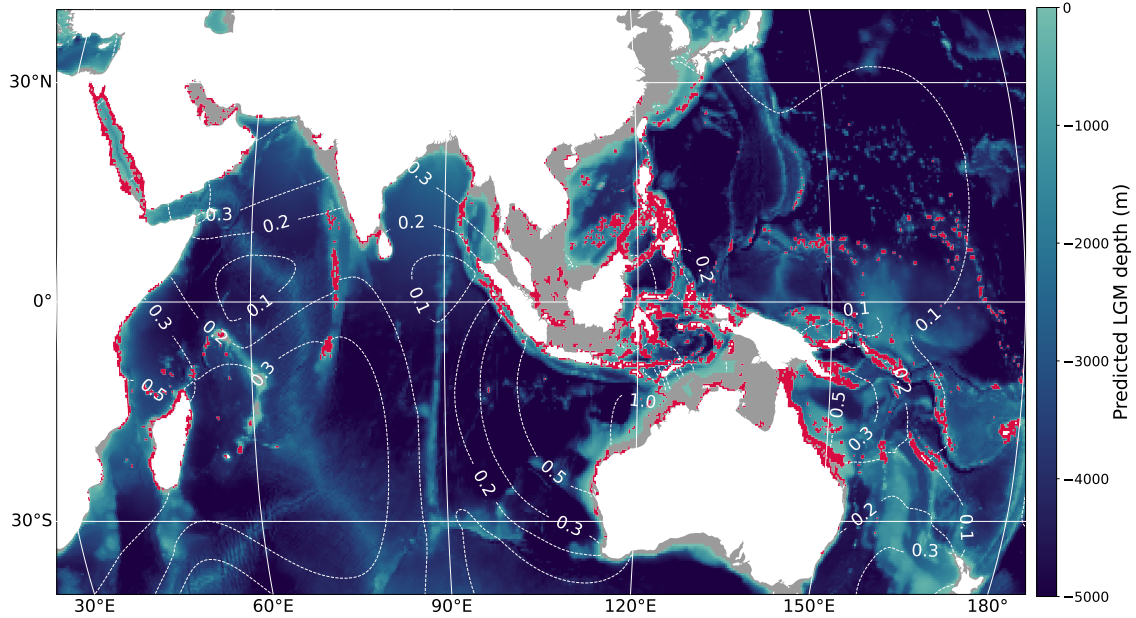


Figure 6.4: Modern coastline (white) overlaid on predicted LGM bathymetry based on GEBCO Compilation Group (2022) and Roy and Peltier (2018). Modern ocean that was subaerially exposed under LGM sea-level change is shaded in grey. Notice the dramatic coastline changes in the central Indo-Pacific. Dotted contours represent the amplitude of the M_2 tidal constituent (m) under LGM bathymetry from a preliminary experiment using the OTIS model (Egbert & Erofeeva, 2002). Red polygons represent the present-day distribution of (sub)tropical coral reefs (UNEP-WCMC, 2018).

These changes are, however, minor compared to the major rearrangement of surface currents that must have occurred within the Coral Triangle (Kuhnt et al., 2004), as can clearly be seen in figure 6.4. Uncertainty in reconstructing palaeoshorelines and atmospheric forcing propagates into uncertainty in simulating surface currents in the geological past. As a result, any ‘palaeodispersal’ model (for instance, based on dynamically downscaling PMIP output (e.g. Vogt-Vincent & Mitarai, 2020)) would be limited to inferring only the coarsest changes in past potential connectivity, and research questions would have to be carefully designed with these limitations in mind. However, if large-scale and robust changes in connectivity were predicted, it would be interesting to assess these changes in the context of contemporary biogeography. Palaeo-eco-evolutionary models could also be tested

by predicting the locations of observed reef formation at the LGM and subsequent deglaciation (e.g. Hongo, 2012; Sasaki et al., 2006; Yamano et al., 2012), the last period of major global environmental change before the Anthropocene. There is therefore potential to use palaeontological records of past reef formation to assess the long-term response of eco-evolutionary models for corals, although this would require considerably more sampling of LGM reefs.

6.2.6 Identifying local MPP accumulation hotspots in the SWIO

In chapter 2, we investigated the sources of MPP for Seychelles using a relatively coarse ($1/12^\circ$) global ocean reanalysis (and even coarser forcing for waves and wind). We did not use WINDS for this study since the domain does not include all sources of interest, and we avoided using nested particle tracking as this is largely untested (section 6.2.1), and there would be a significant velocity discontinuity at the domain boundary due to tides. Although our approach in chapter 2 was useful for identifying the sources of MPP for remote islands, the resolution limits its usefulness for predicting finer scale spatial and temporal patterns in MPP accumulation.

For instance, figure 6.5 shows the divergence of surface currents averaged over one month in WINDS. Superimposed on large-scale (100s km) variability are local regions of consistently high (magnitude) surface current divergence, associated with island wakes, transient fronts, and the surface expression of internal waves around sudden changes in bathymetry (e.g. the margins of the Seychelles Plateau, Amirantes, and Farquhar Group). The divergence associated with these structures is significant. If ϕ is the concentration of MPP at the surface, $\frac{\Delta\phi}{\phi} \sim -(\nabla \cdot \mathbf{u}) \Delta t$ for initially homogeneous ϕ . Surface current divergence of order 10^{-5} s^{-1} is therefore sufficient to result in very significant changes in the local concentration of MPP over timescales of a day or longer. This is consistent with previous studies on passive tracers in the wake of islands (Hasegawa et al., 2009).

With the long-distance sources of MPP reasonably well established, it would be interesting to carry out MPP dispersal experiments using output from WINDS to

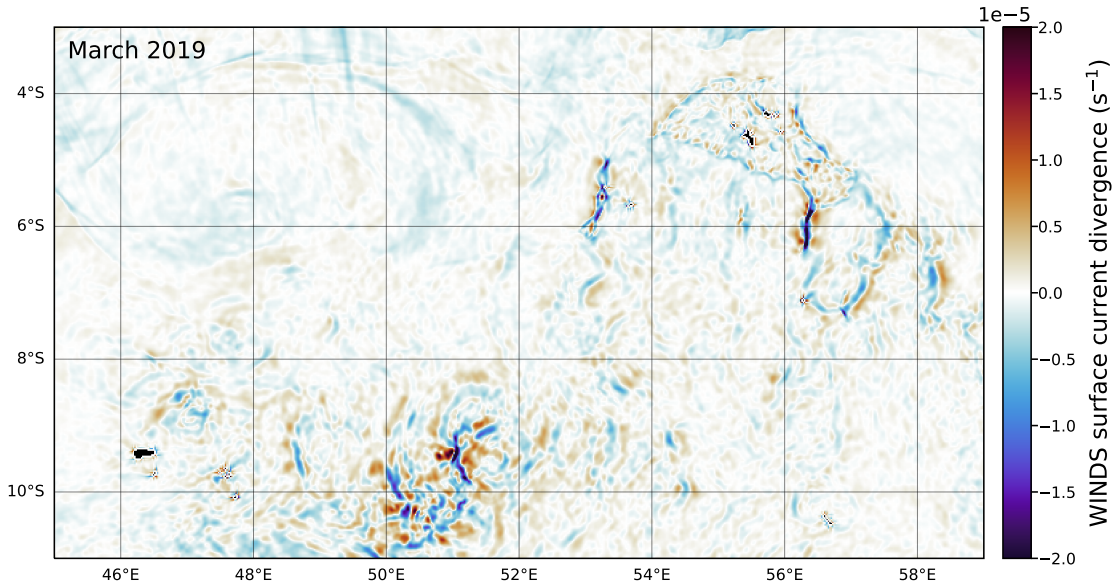


Figure 6.5: Surface current divergence (mean across August 2019) taken from WINDS-M.

investigate the effect of finer-scale oceanographic variability on MPP accumulation, on beaches and at the ocean surface (albeit with the caveats outlined in section 6.2.1). For instance, A. Burt (*personal communication*) observed that MPP accumulation was significantly greater on the south coast of Aldabra compared to the north. Since WINDS resolves some of the submesoscale disturbances of the SEC/NEMC due to the island of Aldabra (and upstream islands), it is worth investigating whether an MPP dispersal model using WINDS output could reproduce this observation. This would not be possible using the coarser reanalysis data used in chapter 2, since Aldabra was only around 2 grid cells wide. Since some of the major shipping corridors and purse seine fishing effort is within the WINDS domain (figure 2.2 and figure 2.5), it may also be possible to refine estimates of where the highest risk marine sources of MPP are for Seychelles. As a demonstration, in figure 6.6 we continuously seed buoyant particles (advected by surface currents from WINDS-M only) around the Aldabra Group, during the northwest monsoon when we expect beaching rates to peak (section 2.3.2.1) and wind is weak (figure 1.4). Convergence and shear deforms surface MPP into filaments, with MPP concentration varying by orders of magnitude over distances of only a few kilometres. The snapshot in figure 6.6 shows how the south

coast of Aldabra appears to block debris from reaching the north coast, but further analyses are required to test whether this snapshot represents long-term patterns.

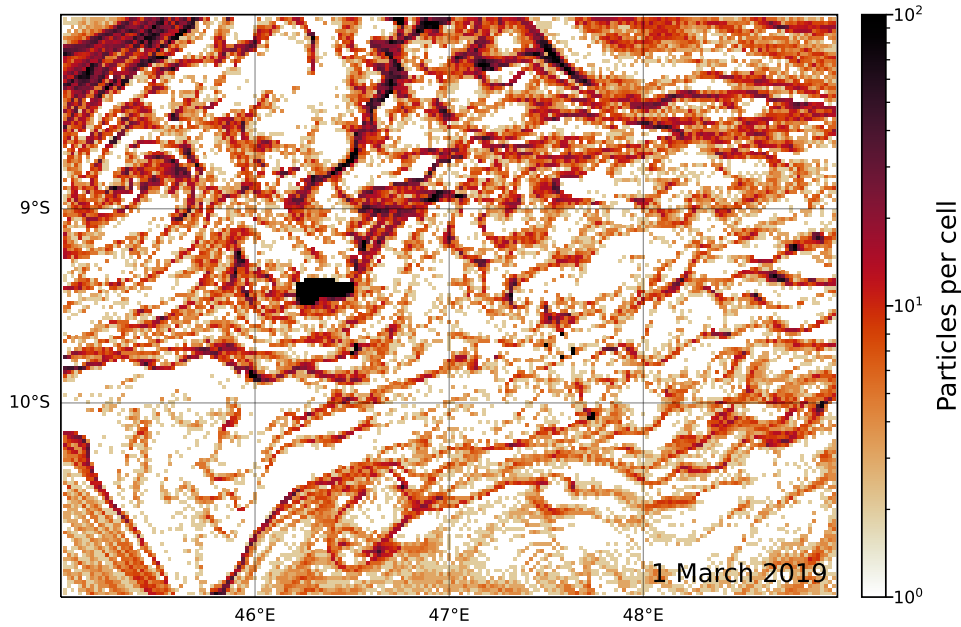


Figure 6.6: Instantaneous density of buoyant MPP (affected by ocean currents only) around the Aldabra Group, with particles seeded hourly outside of the visible domain.

6.3 Concluding remarks

As we began by stating in chapter 1, the ocean is dynamic, connected through a complex and multiscale network of currents and eddies. How important is this connectivity for our dual problems of MPP and coral reef decline?

Connectivity is obviously important for the impacts of MPP, certainly for vulnerable small island states in the western Indian Ocean. We do not need numerical models to tell us that the hundreds of tonnes of debris accumulating on the shores of uninhabited islands have remote origins, but the ability to determine sources more precisely is a first step towards accountability.

For coral connectivity, the case is less clear. There appears to be a significant (albeit complex) imprint of large-scale potential connectivity on coral biogeography and population genetics in the southwest Indian Ocean, mirroring findings from the Coral Triangle (Thompson et al., 2018). Potential connectivity at a reef scale

(up to tens of kilometres) appears to significantly affect the larval supply to a reef, thereby influencing coral recruitment and resilience (e.g. Gouezo et al., 2020; Lukoschek et al., 2013; Thomson et al., 2021). There is also considerable evidence that connectivity maintains resilience and diversity amongst coral reef fauna more broadly (e.g. Fontoura et al., 2022; Goetze et al., 2021; Harrison et al., 2020). However, aside from suggestions with low statistical power from Kleypas et al. (2016) and Matz et al. (2020), there is little evidence for the importance of long-distance connectivity for coral resilience, and it is certainly not essential in itself for coral recovery (Gilmour et al., 2013). There is no strong empirical evidence for the specific role of connectivity in introducing genotypes adapted to thermal stress, and our results hint that long-distance dispersal may not be a driving factor in this respect. The role of *intra*-reef connectivity in supporting rapid evolutionary adaptation may be important, but this has not yet been robustly investigated.

As a result, there is arguably a disconnect between the increasing number of studies aiming to map long-distance larval dispersal (including this thesis), motivated by the importance of coral connectivity in reef resilience, and the available empirical evidence that large-scale potential connectivity genuinely drives resilience. No coral reef is truly isolated, but the degree to which connectivity matters for a coral appears to be highly question-dependent. This is not to imply that coral larval dispersal modelling is pointless, simply that there is a need for greater collaboration between modellers and ecologists to address the knowledge gaps described above.

Finally, despite the potential usefulness of connectivity in urging action against MPP and optimising conservation strategies for coral reefs, no amount of research in this area is going to save the ocean (and by extension, humans) from pollution, or coral reefs from decline. The root causes for both of these problems have been clear for decades. As scientists, we can do our best to improve and communicate our understanding of the natural world, but the only *solution* will come from an educated and engaged society (particularly the sectors of society most responsible for historical and ongoing environmental harm) realising that the status quo is not sustainable, and taking the actions required to make a difference.

Appendices



Supplementary Methods and Data for Chapter 2

A.1 Backward experiments to constrain potential sources

We carried out computationally inexpensive backtracking experiments to identify which countries could potentially act as sources of MPP for Seychelles. We released approximately 5.1×10^7 particles from islands across Seychelles (spread across monthly releases), and backtracked them for up to 27 years following surface currents and Stokes drift (no windage), regularly outputting each particle position $\mathbf{x}$, age t , and the time spent in coastal grid cells t_b , i.e. an observation i is given by the set (x, t, t_b) . From these data, for every particle position, we then calculated the proportion of mass $f_M^i(t, t_b)$ that would remain once the particle reached Seychelles, using the following equation:

$$f_M^i(t, t_b) = \exp(-\mu_s t - \mu_b t_b),$$

For $\mu_s = 1/30$ y, and $\mu_b = 1/20$ d as a pessimistic estimate. We then gridded all $f_M^i(t, t_b)$ to a regular grid, resulting in a list of $f_M(t, t_b)$ associated with each grid cell. To obtain a reasonable worst-case estimate, we then took the 90th percentile (highest) $f_M(t, t_b)$ for each grid cell. The result is Figure A.1. In short, the colour of each grid

cell in Figure A.1 gives the (90th percentile of the) proportion of MPP passing through that cell that reaches Seychelles. However, it is important to remember that since this preliminary analysis is based on a backtracking experiment, all trajectories necessarily end at Seychelles. Figure A.1 is therefore an absolute worst-case estimate. For instance, Figure A.1 shows that particles leaving the coast of Angola in southwestern Africa only lost a small proportion of their mass through beaching and sinking before arriving at Seychelles. However, the full forward experiments demonstrate that only an extremely small proportion of trajectories originating from Angola reached Seychelles, so Angola is not a significant source of MPP for Seychelles.

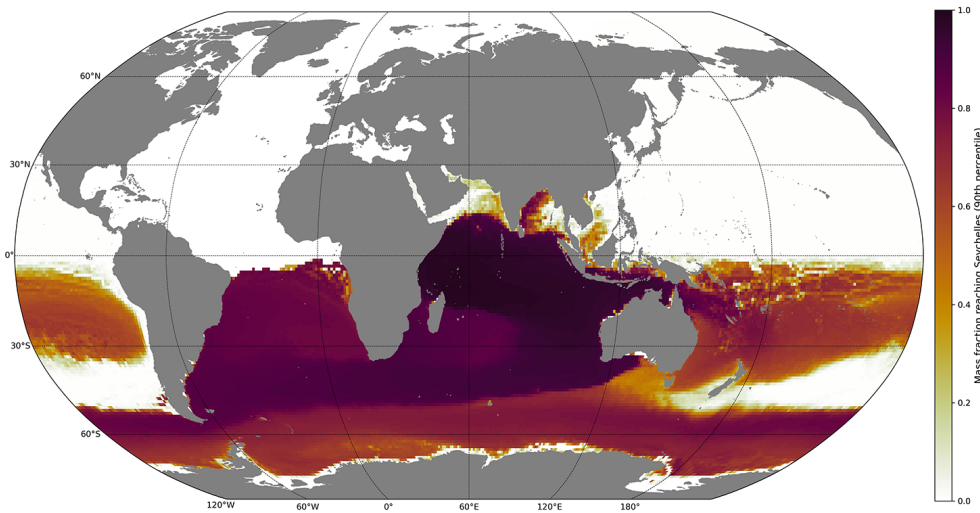


Figure A.1: Mass fraction of MPP from each grid cell remaining available for beaching upon arrival at Seychelles, based on backtracking experiments from Seychelles ($\mu_b^* = 1/20d$, $\mu_s = 1/30y$, scenario CS0). This experiment does not take into account sources of MPP so high values do not necessarily indicate that a significant quantity of MPP arrives at Seychelles from a location, it simply means that of the trajectories that reached Seychelles from that location, losses from beaching and sinking were minor. In other words, cells appearing as white are very unlikely to be sources of MPP for Seychelles, but coloured cells are not necessarily sources of MPP for Seychelles. This, combined with a very conservative value for μ_s , provides us with a list of most countries that could feasibly be sources of MPP for Seychelles.

Winds were not included in this preliminary experiment. Based on climatological wind patterns, this preliminary experiment may underestimate the likelihood of MPP reaching Seychelles from the western coast of the Americas and Brazil. However, the

enormous size of the Pacific and relatively small sources of MPP along the western coast of the Americas makes this an unlikely source of MPP for most of the WIO, and based on our full forward model, if Brazil is a significant source for any WIO islands, it likely only affects Réunion and Mauritius.

A.2 Constraints on μ_b^* from the Global Drifter Program drifters and drifting Fish Aggregating Devices

Based on a dataset of (1) drifters from the Global Drifter Program (GDP) and (2) dFADs, we estimated the model parameter μ_b^* , i.e. the probability per unit time that MPP beaches, given that it is within $1/12^\circ$ of the coast. To do this, we evaluated whether a drifter was within $1/12^\circ$ of the coast every time it reported its position, and then calculated the total time spent within $1/12^\circ$ of the coast by the time it beached.

Evaluating whether a drifter has beached is not straightforward. For GDP drifters, we assessed this through four methods:

1. A GDP drifter has beached if its last reported position is less than 500 m from the coastline (using the GSHHG shorelines database, Wessel and Smith, 1996).
2. A GDP drifter has beached if its last reported position is in less than 30 m water depth (the typical length of a GDP drogue), based on the GEBCO2021 dataset.
3. A GDP drifter has beached if its death code assesses that it had a $>90\%$ chance of being beached (Lumpkin et al., 2012).
4. A GDP drifter has beached if the elevation 1 km to the N/E/S/W of the last reported drifter location has an elevation of >0 m (the criterion used in Kaandorp et al., 2020).

We can extract the parameter μ_b^* by (1) calculating the proportion of drifters still afloat that beach per day spent within $1/12^\circ$ of the coast, or (2) finding a

least-squares best fit of a curve in the form $\exp(-\mu_b^* t)$ to the proportion of drifters still afloat after spending time t within $1/12^\circ$ of the coast. The results are shown in Figure A.2. The proximity criterion appears to be the most conservative method, returning $\mu_b^* \approx 1/45 \text{ d}^{-1}$. The GDP death code criteria was the least conservative, returning $\mu_b^* \approx 1/10 \text{ d}^{-1}$. All methods returned a roughly uniform μ_b^* , apart from the GDP death code criterion.

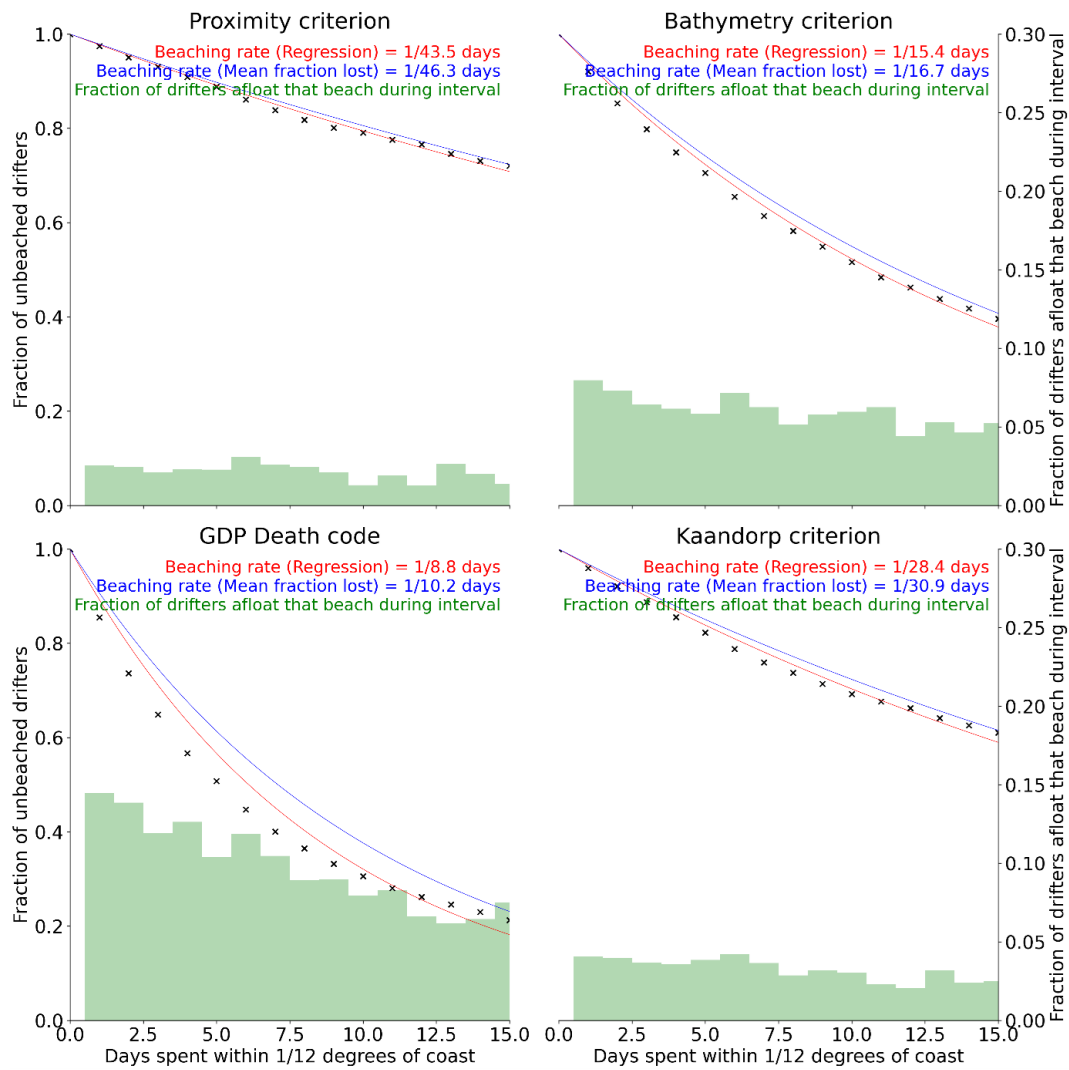


Figure A.2: Estimates of μ_b^* inferred from observations of drifters from the Global Drifter Program based on four different methodologies to assess whether a drifter has beached: (i) a trajectory terminating within 500 m of the coast based on GSHHG, (ii) a trajectory terminating in less than 30 m water depth based on GEBCO2021, (iii) a death code of ‘beached’ GDP drifter using a 90% likelihood threshold (Lumpkin et al., 2012), (iv) the beaching criterion used in Kaandorp et al., 2020, i.e. based on whether at least one point 1 km to the N/E/S/W has an elevation >0 m.

We assessed whether dFADs had beached using the following four methods:

1. A dFAD has beached if its last reported position is less than 500 m from the coastline (using the GSHHG shorelines database, Wessel and Smith, 1996)
2. A dFAD has beached if its last reported position is in less than 30 m water depth (the typical length of a GDP drogue), based on the GEBCO2021 dataset.
3. A dFAD has beached if its death code assesses that it had a >90% chance of being beached (Lumpkin et al., 2012).
4. A dFAD has beached based on beaching events detected through a stagnation threshold in Imzilen et al., 2021.

Many dFADs beached and subsequently unbeached according to the analysis by (Imzilen et al., 2021) so, as we are primarily concerned with ‘terminal’ beaching events in this study, we only considered ‘final’ beachings as true beachings for the evaluation of μ_b^* . All of the above methods produced time-varying estimates of μ_b^* apart from the criterion used by (Imzilen et al., 2021), which was approximately constant for $t > 3$ d (not shown). The estimate for μ_b^* based on the Imzilen et al., 2021 criterion was $\mu_b^* \approx 1/20$ d.

On the basis of these analyses, we suggest that $1/45 \text{ d}^{-1} < \mu_b^* < 1/20 \text{ d}^{-1}$. Drifters and dFADs have long drogues which may get tangled in shallow water, potentially resulting in them being more likely to beach than undrogued MPP. However, we note that Kaandorp et al., 2020 obtained an estimate of $\mu_b^* = 1/24$ d, based on their $1/16^\circ$ resolution grid. Scaling this up to our $1/12^\circ$ resolution grid, this results in an expected value of $\mu_b^* = 1/32 \text{ d}^{-1}$. This is within the range of reasonable values inferred from our analysis of GDP and dFAD beaching rates, so we have used a value of $\mu_b^* = 1/30 \text{ d}^{-1}$ in this study. However, we note that our results generally have low sensitivity to the value of μ_b^* (figure 2.10), although certain source attributions do show a dependency on μ_b^* (Figure A.3).

A.3 Supplementary Figures

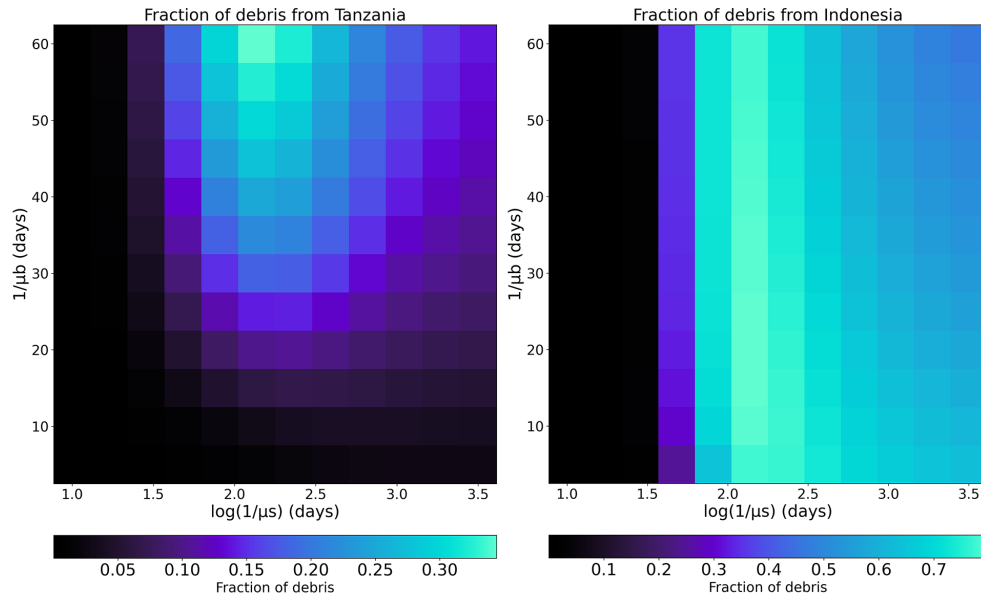


Figure A.3: Fraction of MPP arriving at Aldabra originating from Tanzania (*left*) and Indonesia (*right*) for physical scenario CS0, as a function of the sinking and beaching rates. Note that whereas the fraction of MPP originating from Indonesia is largely independent of the beaching rate, this is not the case for MPP originating from Tanzania.

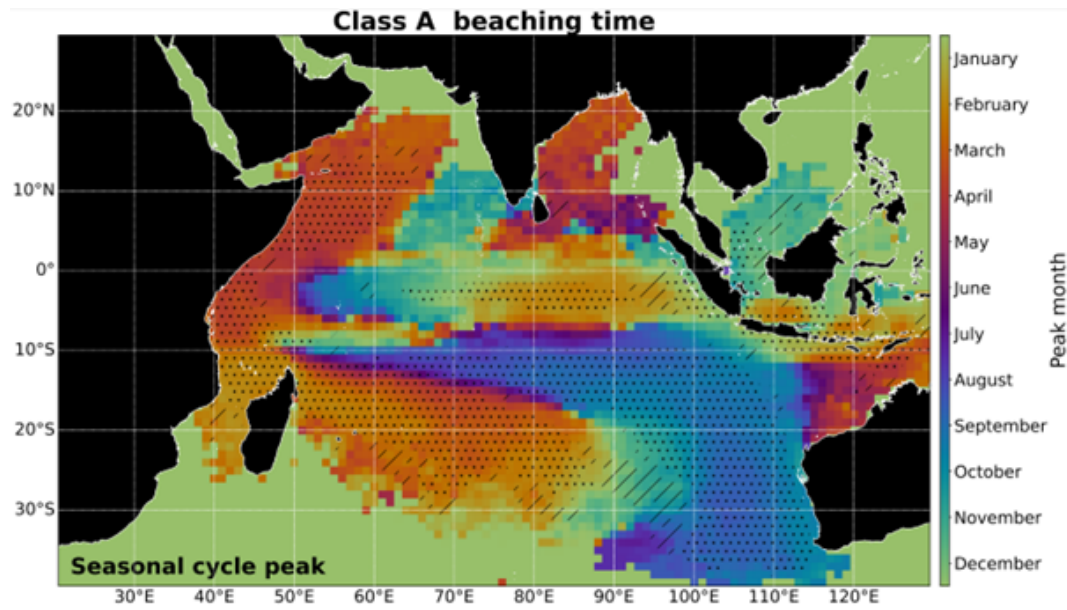


Figure A.4: Phase of the seasonal cycle for Class A MPP beaching at the Aldabra Group, i.e. when MPP is most likely to beach at the Aldabra Group for a uniform seeding rate.

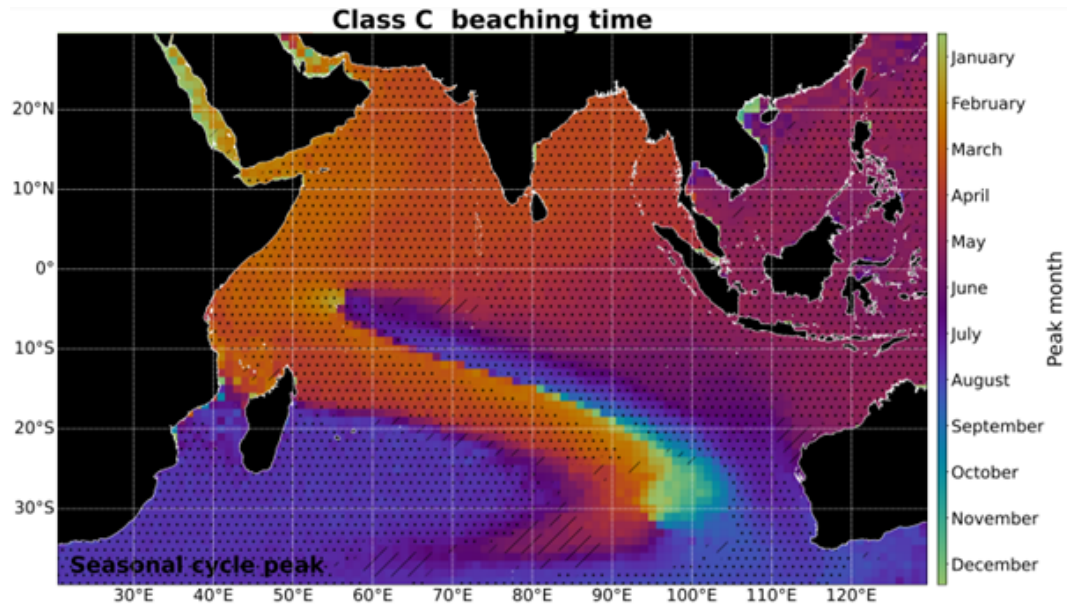


Figure A.5: Phase of the seasonal cycle for Class C MPP beaching at the Seychelles Plateau. Note how the phase for Indonesia (May-June) contradicts the September-October ‘peak’ attributed to Indonesia in Figure 2.6(d). This is because, as described in the main text, the September-October ‘peak’ is driven by a small number of beaching pulses and is not consistent. This spectral analysis suggests that the Class C pathway from Indonesia to the Seychelles Plateau most consistently terminates in May-June, not September-October.

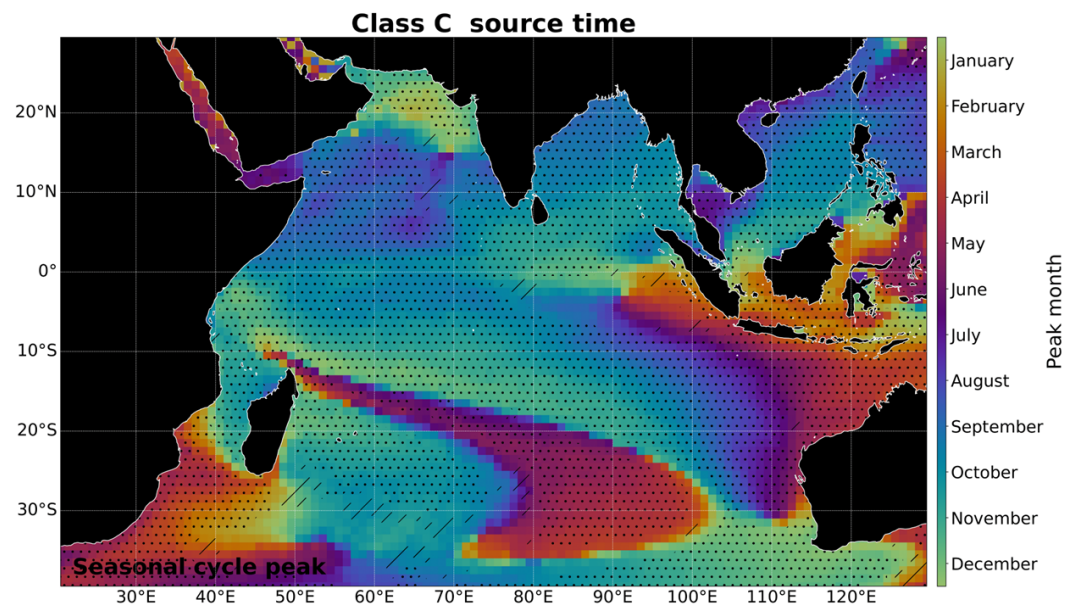


Figure A.6: Phase of the seasonal cycle of risk (source time) for Class C MPP eventually beaching at the Aldabra Group, i.e. during which month Class C MPP has the highest chance of beaching at the Aldabra Group.

B

Supplementary Methods and Data for Chapter 4

B.1 Offline computation of coral larval fluxes

We could solve equations equation (4.1) and equation (4.2) directly by numerically integrating them, either ‘online’ during particle tracking, or ‘offline’ after regularly saving particle positions. However, these methods have some significant disadvantages. Integrating these quantities online would require all parameters in equations equation (4.1) and equation (4.2) to be set before particle tracking. This would limit the applicability of simulation results, since they would have to be rerun for any new sets of parameters. Regularly saving particle positions would require a very high output frequency to integrate equations equation (4.1) and equation (4.2) without considerable error, which would involve enormous storage requirements. Instead, we can reconstruct the number of larvae settling within a ‘settlement event’ (defined as a larval particle remaining within a single cell with nonzero F_r^j) by storing only three parameters per event:

- The cell ID (a 16-bit unsigned integer in our configuration, which is used as a key for dictionaries containing the reef area and other parameters)
- The event start time-step (a 16-bit unsigned integer in our configuration)

- The event duration (a 16-bit unsigned integer in our configuration)

Integrating equation (4.1) with respect to t' , letting $L_1(t' = 0) = L_0^i$, and defining the survival function $s(t') = e^{-\int_0^{t'} \mu_m(\tau) d\tau}$, we obtain

$$L_1(t') = \begin{cases} L_0^i s(t') & t' < t_c, \\ L_0^i s(t') e^{-\alpha(t' - t_c)} & t' \geq t_c. \end{cases}$$

$L_2(t')$ is only nonzero for $t' > t_c$ and no settlement event can occur for $t' \leq t_c$. We therefore define $t = t' - t_c$ (i.e. the time since the minimum competency period t_c), and set $t \geq 0$. Therefore:

$$L_1(t) = L_0^i s(t + t_c) e^{-\alpha t}. \quad (\text{B.1})$$

Substituting equation (B.1) into equation (4.2) and solving the resulting differential equation, we obtain the following:

$$L_2(t) = \alpha L_0^i s(t + t_c) e^{-\beta t} e^{-\mu_s \int_0^t F_r(t^*) dt^*} \cdot \int_0^t e^{t^*(\beta - \alpha)} e^{\mu_s \int_0^{t^*} F_r(t^{**}) dt^{**}} dt^*. \quad (\text{B.2})$$

We now need to consider the fact that, within a particular settling event $j = 1, 2, \dots, N$ lasting from τ_0^j to $\tau_0^j + \Delta\tau^j$, $F_r(t) = F_r^j$ is a constant. Therefore, for $\tau_0^j \leq t \leq \tau_0^j + \Delta\tau^j$:

$$\begin{aligned} \int_0^t F_r(t^*) dt^* &= \int_0^{\tau_0^j} F_r(t^*) dt^* + \int_{\tau_0^j}^t F_r^j dt^* \\ &= \phi_0^j + F_r^j (t - \tau_0^j), \end{aligned} \quad (\text{B.3})$$

where $\phi_0^j = \int_0^{\tau_0^j} F_r(t^*) dt^*$ and $\phi_0^{j=1} = 0$. We will now define the outermost integral in equation (B.2) as $I_j(t)$, i.e.

$$I_j(t) = \int_0^t e^{t^*(\beta - \alpha)} e^{\mu_s \int_0^{t^*} F_r(t^{**}) dt^{**}} dt^*. \quad (\text{B.4})$$

For $\tau_0^j \leq t \leq \tau_0^j + \Delta\tau^j$, we will split this integral into three sections: $[0, \tau_0^{j-1} + \Delta\tau^{j-1}]$ (i.e. up until the end of the last settlement event), $[\tau_0^{j-1} + \Delta\tau^{j-1}, \tau_0^j]$ (i.e. from the end of the last settlement event to the start of the current settlement event), and $[\tau_0^j, t]$:

$$\begin{aligned} I_j(t) &= \int_0^{\tau_0^{j-1} + \Delta\tau^{j-1}} e^{t^*(\beta - \alpha)} e^{\mu_s \int_0^{t^*} F_r(t^{**}) dt^{**}} dt^* \\ &\quad + \int_{\tau_0^{j-1} + \Delta\tau^{j-1}}^{\tau_0^j} e^{t^*(\beta - \alpha)} e^{\mu_s \int_0^{t^*} F_r(t^{**}) dt^{**}} dt^* \\ &\quad + \int_{\tau_0^j}^t e^{t^*(\beta - \alpha)} e^{\mu_s \int_0^{t^*} F_r(t^{**}) dt^{**}} dt^*. \end{aligned} \quad (\text{B.5})$$

For $\tau_0^j \leq t \leq \tau_0^j + \Delta\tau^j$, we firstly recognise that the first term is equal to $I_{j-1}^{\tau_0^{j-1} + \Delta\tau^{j-1}}$. For the second term, the larval particle is by definition not within a reef cell during the time bounds, i.e. $F_r = 0$, so $\int_0^{t^*} F_r(t^{**}) dt^* = \phi_0^j$. Therefore, equation (B.5) evaluates to:

$$\begin{aligned} I_j(t) &= I_{j-1}^{\tau_0^{j-1} + \Delta\tau^{j-1}} + \int_{\tau_0^{j-1} + \Delta\tau^{j-1}}^{\tau_0^j} e^{t^*(\beta-\alpha)} e^{\mu_s \phi_0^j} dt^* + \int_{\tau_0^j}^t e^{t^*(\beta-\alpha)} e^{\mu_s(\phi_0^j + F_r^j(t^* - \tau_0^j))} dt^* \\ &= I_{j-1}^{\tau_0^{j-1} + \Delta\tau^{j-1}} + \frac{e^{\mu_s \phi_0^j}}{\beta - \alpha} \left[e^{t(\beta-\alpha)} \right]_{\tau_0^{j-1} + \Delta\tau^{j-1}}^{\tau_0^j} + \frac{e^{\mu_s \phi_0^j - \mu_s F_r^j \tau_0^j}}{\beta - \alpha + \mu_s F_r^j} \left[e^{t(\beta-\alpha + \mu_s F_r^j)} \right]_{\tau_0^j}^t. \end{aligned} \quad (\text{B.6})$$

Whilst algebraically long-winded, $I_j(t)$ is nevertheless now defined analytically. Therefore, substituting equation (B.3) and equation (B.4) into equation (B.2):

$$L_2(t) = \alpha L_0^i s(t + t_c) e^{-\beta t} e^{-\mu_s(\phi_0^j + F_r^j(t - \tau_0^j))} \cdot I_j(t). \quad (\text{B.7})$$

Finally, from equation (4.2) the number of larvae settling during event j , N_s^j , is given by:

$$\frac{dN_s^j}{dt} = \mu_s F_r^j L_2(t), \quad (\text{B.8})$$

$$N_s^j = \mu_s F_r^j \int_{\tau_0^j}^{\tau_0^j + \Delta\tau^j} L_2(t) dt. \quad (\text{B.9})$$

Therefore, to compute N_s^j , we will use the following steps:

1. Retrieve ϕ_0^j and $I_{j-1}^{\tau_0^{j-1} + \Delta\tau^{j-1}}$, both of which were computed in the previous step.
Note that both are 0 for $j = 1$.
2. Retrieve F_r^j from the stored cell ID.
3. Integrate equation (B.9) numerically.
4. Store $I_j(\tau_0^j + \Delta\tau^j)$ for the next computation.
5. Store $\phi_0^{j+1} = \phi_0^j + F_r^j \Delta\tau^j$ for the next computation.

B.2 Supplementary Figures

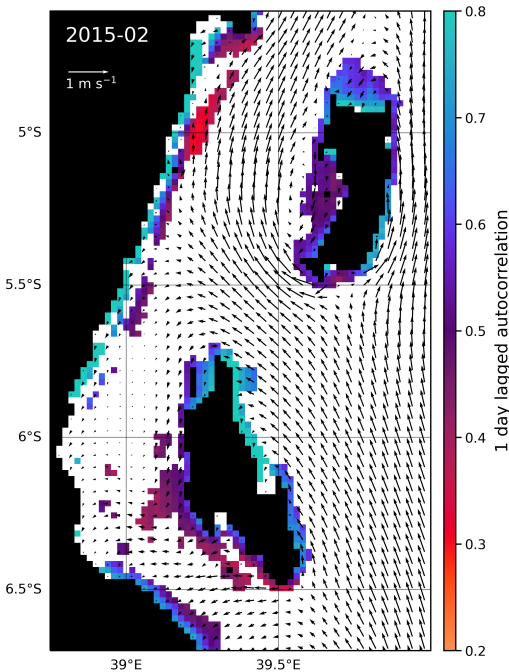


Figure B.1: Example of flow around Zanzibar and Pemba (February 2015), showing a flow reversals and deflections around capes and headlands, and out-strength autocorrelation.

B.3 Supplementary Tables

Species	Code	α^* (d ⁻¹)	β (d ⁻¹)	t_c (d)	λ (d ⁻¹)	ν	σ	μ_s (d ⁻¹)
<i>A millepora</i>	AM	0.18	0.050	3.239	0.043	0.57	0.0	1.0
<i>A valida</i>	AV	0.22	0.031	1.0	0.019	0.46	0.0	1.0
<i>A gemmifera</i>	AG	0.39	0.145	3.471	0.067	1.0	0.0	1.0
<i>G retiformis</i>	GR	0.58	0.096	1.0	0.087	1.0	0.0	1.0
<i>P daedalea</i>	PD	0.39	0.099	2.937	0.060	0.72	0.0	1.0
<i>P daedalea</i> (fast)	PDf	0.39	0.099	2.937	0.060	0.72	0.0	2.0
<i>P daedalea</i> (slow)	PDs	0.39	0.099	2.937	0.060	0.72	0.0	0.5

Table B.1: Biological parameters used for larval competency, mortality and settling in this study (Connolly & Baird, 2010).

C

Supplementary Methods and Data for Chapter 5

C.1 The map equation

Consider a random walk through the coral reef network, where the probability of the walk transiting from node i to node j is proportional to F_{ij} (section 4.2.2). A simple approach to describing this random walk would involve assigning a unique code to each node, and representing the random walk as a list of codes. We have 180 reef nodes in our network, so $\lceil \log_2 180 \rceil = 8$ bits of information are required to describe every node visited.

This strategy is inefficient, since some nodes are more likely to be visited than other nodes. An alternative approach might involve simulating large numbers of random walks, observing how many times each node is visited, and assigning Huffman codes based on these visitation probabilities. This involves assigning shorter codes to frequently visited nodes, and longer codes to rarely visited nodes, resulting in an overall reduction in the information required to describe a random sequence of nodes (Huffman, 1952). However, this approach is still not optimal for describing a random walk through most realistic networks. This is because many networks are partitioned into clusters that tend to retain a random walk (or flow) for an extended period of time, so the likelihood of the random walk transitioning to node j is strongly

dependent on the identity of node i . As an example, whilst a reef along the coast of Tanzania may appear many times in an arbitrarily long random walk, a random walker that is currently in the Chagos Archipelago is extremely likely to remain within the Chagos Archipelago across a large number of steps.

Instead, we could partition the network into clusters that tend to retain random walks, and assign Huffman codes to nodes based on visitation frequency within the cluster (Rosvall et al., 2009). Since codes are now no longer unique to individual nodes (only being unique within the scope of a cluster), the number of bits required to describe a node is reduced. To deal with this non-uniqueness, codes are assigned to clusters, and the cluster code is reported when the random walker moves between clusters. However, as long as these clusters represent collections of nodes that tend to retain random walks, random walks will only rarely move between clusters, and the information required to describe a random walk is reduced (due to the reduction in information required to describe a random walk within clusters). The more clusters there are, the fewer nodes there are per cluster (and therefore the shorter node codes are). However, more clusters also increase the length of cluster codes, and the frequency at which they have to be used. The map equation (Rosvall et al., 2009) and Infomap algorithm (Edler et al., 2023) identifies this optimal partitioning of the network. Note that partitioning can also be hierarchical (i.e. partitioning clusters into sub-clusters, and so on).

Since we can model the movement of genes as a random walk through the network (for now neglecting complications such as effects of selection), this optimisation problem identifies clusters of reefs that would be expected to retain larvae and gene flow over a significant number of generations and spawning events, based on potential connectivity.

A widely used algorithm to partition ecological networks is *modularity* (e.g. Brunner et al., 2022; Frys et al., 2020; Gabriela Mayorga-Adame et al., 2022; Gamoyo et al., 2019; Lequeux et al., 2018; Trembl & Halpin, 2012), which maximises the total weight of links within a cluster minus the weight of links with nodes outside the cluster (identifying clusters with strong intraconnectivity and weak

interconnectivity). Intuitively, this sounds as if this algorithm would be very well suited to identify clusters of reefs that tend to retain larvae. However, consider figure C.1 (Rosvall et al., 2009). Figure C.1(a,b) show two possible partitions of a flow network. Through inspection of this flow network, it is obvious that flow will tend to be retained within the cycles in each corner, since leaving a cycle is only possible within a quarter of nodes. We may therefore expect that this network would be partitioned into four clusters, one for each cycle (figure C.1(a)), and indeed this is the optimal clustering identified by both the map equation and modularity, versus one single cluster for the entire network (figure C.1(b)).

For the networks represented by figure C.1(c,d), flow through the network is no longer possible: the longest random walk has length 2. There is no partitioning of the network that retains flow because a random walk will immediately enter a sink node, regardless of where it is within the network. This is recognised by the map equation, but modularity identifies the same partition as in figure C.1(a), since the total weight of links within clusters versus between clusters is unchanged.

C.2 Supplementary Figures

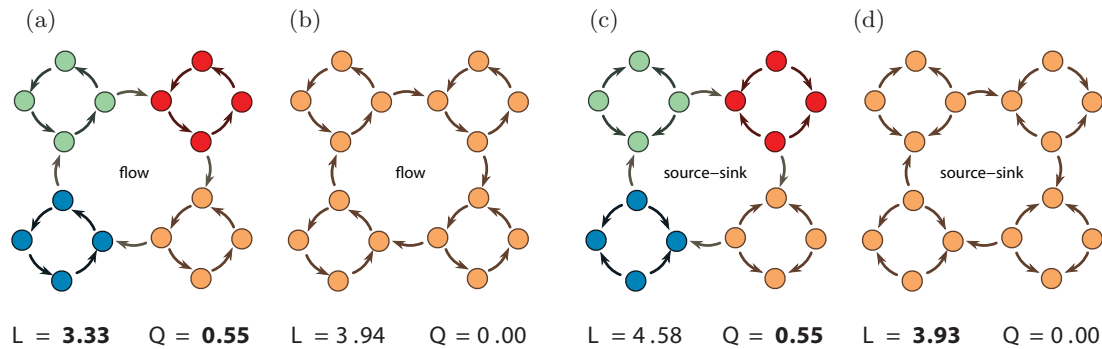


Figure C.1: (a, b) Two possible partitions of network A, and the minimum average code length L (minimised by the map equation) and modularity Q (maximised by modularity). Partition (a) is identified as optimal by both algorithms. (c, d) Two possible partitions of network B, and the minimum average code length L and modularity Q . Partition (c) is identified as optimal by modularity, whereas partition (d) is identified as optimal by the map equation. This figure is reproduced with permission from Rosvall et al. (2009).

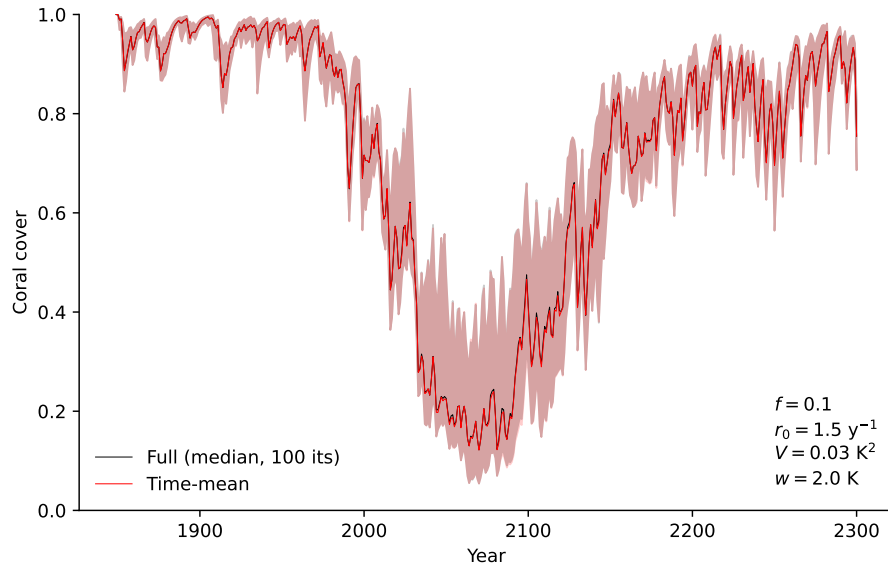


Figure C.2: Mean (line) and 5th-95th range for coral cover across all groups using the time-varying matrix (red, median across 100 iterations) and time-mean matrix (black) for the parameters used in this study.

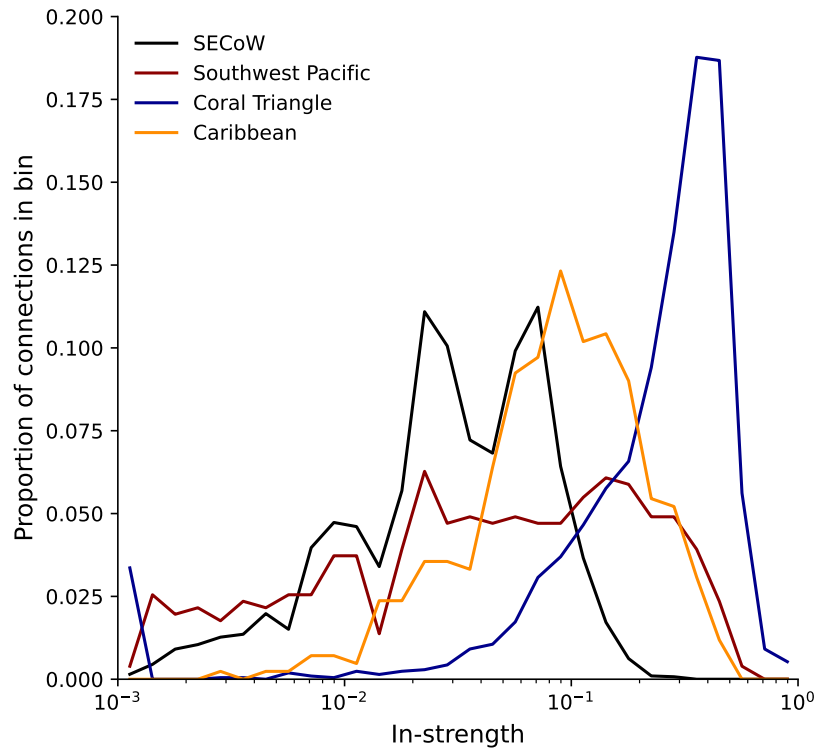


Figure C.3: Comparison of in-strength distribution in SECoW (black) with pseudo in-strength (sum of the connectivity matrix over all source sites, equivalent to ‘destination strength’ in McManus, Forrest, et al., 2021) for the three regions considered (Schill et al., 2015; Thompson et al., 2018; Treml et al., 2008)

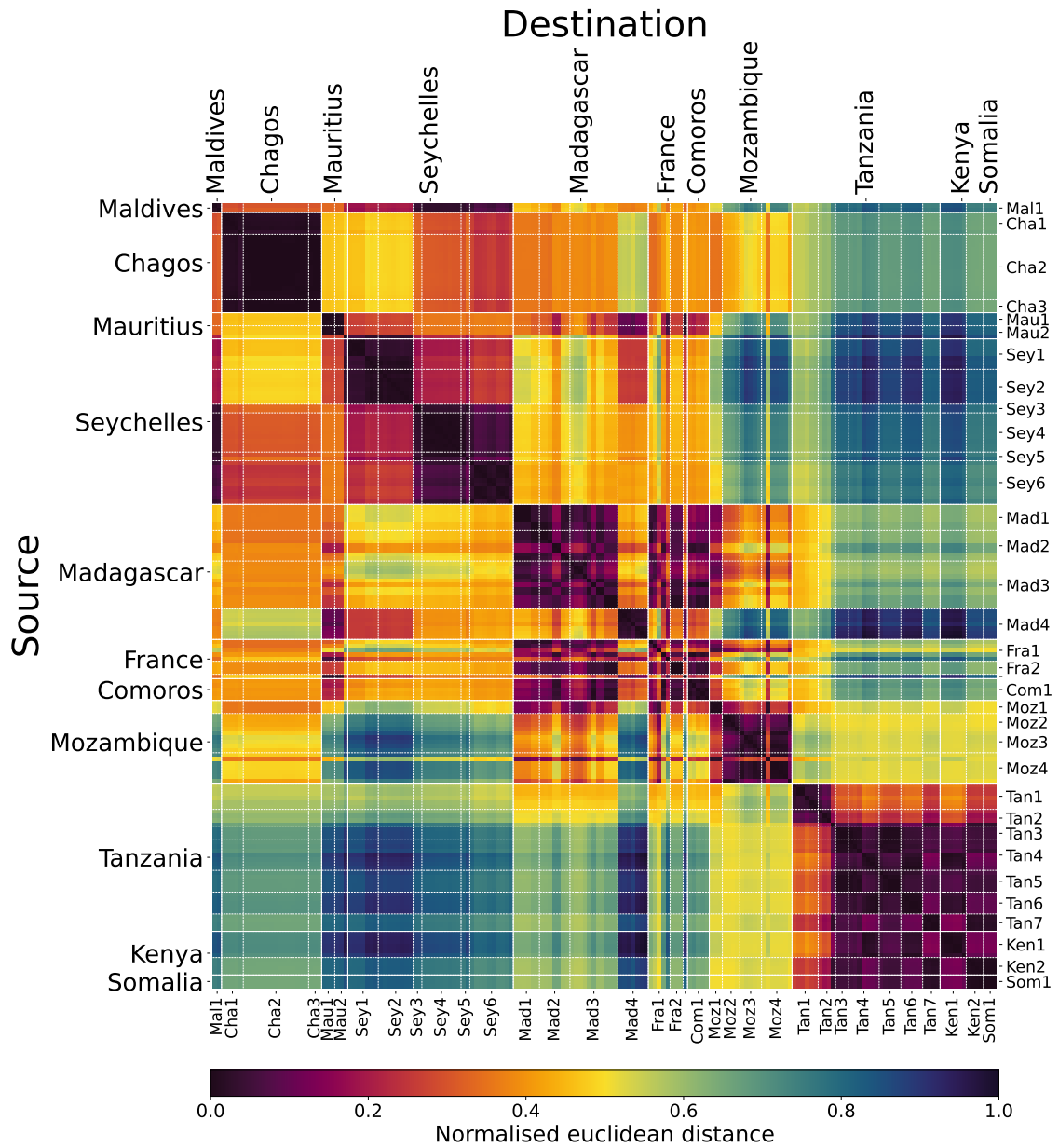


Figure C.4: Euclidean distance between coral reef groups embedded in PC1-PC2-PC3 space (figure 5.6). Note that principal components are normalised for clarity to zero mean and unity standard deviation in figure 5.6 and figure 5.7, but the distances in this figure are based on the true Euclidean distance.

References

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