

Setting priorities for conservation at the interface between ocean circulation, connectivity, and population dynamics

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Abstract

Population persistence in the marine environment is driven by patterns of ocean circulation, larval dispersal, ecological interactions, and demographic rates. For habitat forming organisms in particular, understanding the relationship between larval connectivity and meta-population dynamics aids in planning for marine spatial management. Here, we estimate networks of connectivity between fringing coral reefs in the North West Shelf of Australia by combining a particle tracking model based on shelf circulation with models of sub-population dynamics of individual reefs. Coral cover data were used as a proxy for overall habitat quality, which can change as a result of natural processes, human-driven impacts, and management initiatives.

We obtain three major results of conservation significance. First, the dynamics of the ecological network result from the interplay between network connectivity and ecological processes on individual reefs. The maximum coral cover a zone can sustain imposes a significant non-linearity on the role an individual reef plays within the dynamics of the network, and thus on the impact of conservation interventions on specific reefs. Second, the role of an individual reef within these network dynamics changes considerably depending on the overall state of the system: a reef's role in sustaining the system's state can be different from the same reef's role in helping the system recover following major disturbance. Third, patterns of network connectivity change significantly as a function of yearly shelf circulation trends, and non-linearity in network dynamics make mean connectivity a poor representation of yearly variations.

From a management perspective, the priority list of reefs that are targets for management interventions depends crucially on what type of stressors (system-wide vs localised) need addressing. This choice also depends not only on the ultimate purpose of management, but also on future oceanographic, climate change and development scenarios that will determine the network connectivity and habitat quality.

Key-words: ecological modelling, meta-population, dispersal, network analysis, ecological uncertainty, resilience, persistence, coral reef

Introduction

Connectivity has major consequences for the ability of populations to persist and sustain themselves as a network, or regional meta-population. A network's ability to maintain its functioning under variable local conditions and to contribute to larger scale recovery from occasional network-wide regional disturbances, both key components of resilience, relies on the input and exchange of new individuals from remnant neighbouring populations (Cowen et al. 2006, Treml et al. 2008). Connectivity is particularly important for marine organisms that generally display bipartite life histories, with a dispersive larval phase following reproduction before transitioning to a more sedentary benthic phase. Ocean currents are a major driver of larval transport, and larvae can disperse distances ranging from meters to thousands of kilometres from their natal reef (Cowen and Sponaugle 2009, Jones et al. 2009). Thus, understanding connectivity is a particularly important consideration in the management of marine natural resources (Gaines et al. 2010).

The consideration of connectivity in management is especially prominent in the conservation of coral reefs and marine reserves (e.g. Almany et al. 2009, Krueck et al. 2016). Both are usually somewhat isolated and discrete areas of habitat that are connected by larval transport over ecological and evolutionary timescales. Coral reefs are subject to a number of threats from anthropogenic sources, both local and global. These include but are not limited to overfishing, habitat destruction, coastal development, sedimentation, eutrophication and tropical storms, as well as the global impacts of climate change (Harborne et al. 2017). Given this array of disturbances and the fragmented geography of coral reef habitats there is a clear need for active efforts to ensure the persistence of coral reef ecosystems.

Spatial management approaches are a common tool employed to protect the resilience and persistence of coral reefs at a regional scale, and the idea of networks of marine reserves is being applied globally (Mora et al. 2006). Yet,

because coral reefs support the livelihoods of millions, decisions regarding which reefs to protect and how to balance conservation with more immediate human needs, are difficult (Klein et al. 2008, Halpern et al. 2013). Consequently, connectivity based approaches to prioritising reefs and optimising conservation outcomes are increasingly common and include studies of larval behaviour, genetics and numerical hydrodynamic modelling (Ovaskainen and Hanski 2003, Werner et al. 2007a, Figueira 2009, Jones et al. 2009, Jacobi and Jonsson 2011a). To understand the implications of this knowledge however, they should also be combined and viewed in a network or meta-population context.

Modelling approaches including the use of connectivity matrices and network analysis have increasingly been used for conservation prioritization (e.g. Ovaskainen and Hanski 2003, Figueira 2009, Jacobi and Jonsson 2011a, Kininmonth et al. 2011, Treml and Halpin 2012, Hock et al. 2014). These uses include marine reserves, but network analysis can also be used to prioritize reefs for the eradication of undesirable species such as crown-of-thorns starfish (Hock et al. 2014). While consideration of single reefs would suggest that larval retention is key to their persistence, there is a further need to include networks of populations in order to manage marine populations at appropriate scales. Such analyses have highlighted that prioritising areas on the basis of either sink or source characteristics alone is relatively ineffective (Jacobi and Jonsson 2011b) and that the key components of a network, in terms of its ability to recover from disturbances and ultimately to persist, include those nodes of the network that both supply and receive substantial numbers of larvae. Such nodes have been variously termed gateway reefs (Bode et al. 2006) or superspreaders (Hock et al. 2014).

Representations of connectivity such as 'betweenness centrality' (Holstein et al. 2014) have been used to rank habitat components in terms of their input to persistence, and it is increasingly recognised that such prioritizations need to incorporate

multigenerational and dynamic aspects of populations at each node in order to include realistic representations of habitat quality. Variations in habitat quality or population parameters have been shown to have strong influences on the relative ranking of high priority sites, potentially altering priorities that might be made based on connectivity alone. For example, local demography becomes increasingly important under conditions of high larval retention where demographic variability can turn sources into sinks (Figueira 2009), and spatial variations in habitat quality can change network dynamics (Watson et al. 2011). These variations find their fullest expressions in the contrasting network characteristics of different species within the same region (Watson et al. 2011, Holstein et al. 2014). Hydrodynamic variability can potentially also have important influences on network properties (Bode et al. 2006, Golbuu et al. 2012).

Here we focus on a regional network of coastal reefs on the Pilbara Coast of north-west Australia with a view to informing management approaches in the region to address multiple stake-holder use. The region is the focus of significant industrial activity (oil, gas) and major port developments (Hanley 2011), well-established conservation initiatives including several large multiple-use marine parks and a World Heritage Area at Ningaloo Reef (CALM and MPRA 2005), as well as recreational and commercial fishing (Fletcher and Santoro 2009). Using a 6-year time series of hydrodynamic models we have estimated connectivity among coral reefs in the region. We then used a meta-population model, based on regional measurements of coral populations, to study the interplay between local population dynamics and regional connectivity.

In setting up a regional management plan for the conservation of marine resources, a manager needs to address a number of stakeholder aspirations, but also to ensure that the system is resilient to three types of disturbances: i) local, relatively frequent natural and anthropogenic disturbances leading to variable local conditions which can

be balanced by larvae supplied from other areas (we term this ‘system maintenance’ from hereon); ii) occasional major and potentially catastrophic regional disturbances affecting a significant section of the region (we term this ‘system recovery’) and iii) larger scale biophysical processes or climate change, which may lead to yearly or decadal variability in climatic and ecological regimes. The main result of this study is to show that zones which offer larger contributions to system maintenance do not necessarily have the same level of importance for system recovery or under different disturbance regimes. This finding is of both regional importance and general significance and represents robust advice across a range of management sectors.

Materials and methods

Methodological overview

We firstly describe the study region, data collection, and analysis which provide the estimated current coral cover and maximum sustainable coral cover used in the meta-population model. We then describe the hydrodynamic model which provides the connectivity data and meta-population model used to study changes in coral cover as a function of both connectivity and local population dynamics. Next, we describe the modelling approach used to study the three types of disturbances. First, we employ an impact analysis to assess how much each zone contributes to system maintenance – i.e., preserving coral biomass in the overall region. Second, we explore the role each zone plays in system recovery following regional system collapse. Finally, we describe how yearly variability in network connectivity is analysed and its role on impact and recovery.

Study area

The Pilbara consists of over 300 low islands (<6m above sea-level) with most having well developed fringing coral reefs. The region is characterised by a large tidal range (3m spring tides) and a wide, gently sloping continental shelf, resulting in strong tidal flows throughout the region (0.4knts). Average annual rainfall is low (mean = 306 mm), however during the austral summer months

(November to March) cyclones are common (mean 0.6 per year; BOM <http://www.bom.gov.au/climate/maps/average/s/tropical-cyclones/>) and have resulted in large declines of coral cover within *Acropora* dominated assemblages (Marsh and Marsh 2000). Most fringing coral reefs in the region are dominated by macroalgae (*Sargassum*, *Turbinaria*, *Padina*), however diverse assemblages of hard corals and invertebrates are common throughout (Richards and Rosser 2012, Pitcher et al. 2016).

Benthic communities were surveyed using 50m photo-transects (English et al. 1997). A total of over 1200 transects, distributed evenly throughout the model sub-regions, were completed between November 2013 and May 2015. Sub-regions were defined based on clusters of adjacent and geomorphologically similar reefs. To quantify the current coral cover and the maximum sustainable coral cover for each sub-region, the mean percent cover of live and recently dead (Ridgway et al. 2016, Lafratta et al. 2017) coral were obtained from photo-transects. Photos were captured at 0.5m intervals along the transect and randomly selected for analysis with the genus of any scleractinian corals recorded for 6 fixed points per photograph using Transect Measure™ (i.e.180 pts per 50m transect). The coral cover was calculated as the mean coral cover of transects within that sub region (Figure 1). Estimated maximum sustainable coral cover was based on observed coral cover and recently dead coral cover, adjusted where data from other sources showed higher maximum cover, and where necessary by referring to estimates in adjacent zones. Recently dead coral cover is represented by dead coral colonies covered in sediment or early successional taxa such as turf algae. Patches of dead coral can be up to approximately 3 years old, after which time early successional taxa are replaced by late successional stage taxa including macroalgae, crustose coralline algae and/or new hard coral. As such, the sum of the observed coral cover and recently dead coral cover reliably represents the maximum coral cover at a location within the last approximately 3 years.

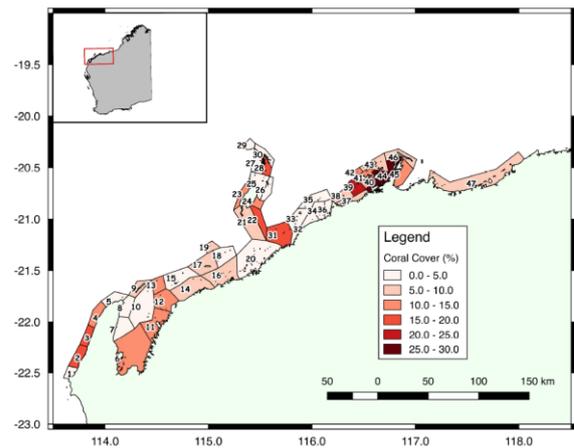


Figure 1. West Pilbara model domain, zone locations and labels (as in Feng *et al.* 2016). Colours map coral cover, calculated as the mean coral cover of transects within each zone. The 10 zones with highest coral cover in decreasing order = 44, 40, 39, 3, 22, 31, 2, 28, 41, 12

Connectivity data

Connectivity data were obtained by simulating larval release and diffusion by tracking particle movement on the studied area forced by oceanic data recorded in the years 2004 to 2009. The full parameterisation and simulation of the larval connectivity model is described in Feng *et al.* (2016).

In brief, the particle tracking is based on hydrodynamic model outputs from model simulations using Rutgers version of the Regional Ocean Modelling System (Feng et al. 2016) and was run with ~1 km horizontal resolution. The bottom topography was taken from a collection of sources including GA2009, industry provided LIDAR and MNF multi beam data. Reef distribution was summarised by compiling benthic habitat maps from CSIRO, Western Australia Department of Parks and Wildlife, Western Australia Museum, and environmental impact statement documents from industrial developments in the region. Reefs were used as the seeding locations of coral larvae in the particle tracking model, and as settlement sites when evaluating retention and connectivity. A total of 3430 reef release sites were modelled within the domain, divided among 47 sub-regions to facilitate summation of the results (as shown in Figure 1). The dominant austral summer-autumn coral mass spawning event was modelled by

releasing particles 7-9 days after the full moon in March (Gilmour et al. 2016) for the 6 years (Feng et al. 2016). Once released, a larval competence ratio is derived from the product of larval mortality and competency functions (Feng et al. 2016), based on parameters published in (Connolly and Baird 2010). Larval competence relative to initial release takes the form of a log-normal function (Fig. 6 in (Feng et al. 2016)), with a minimum competency period of 3.2 days and a peak competency period occurring at 8-12 days. Larvae are tracked for a total of 60 days, by which time no live and competent larvae remain. Competent particles located within a 0.3 km radius of suitable reef habitat were regarded as settled on that reef to incorporate coral larvae sensory behaviour.

Meta-population model

The ecological model consists of a network of 47 zones, each hosting a separate coral population and interacting with other populations via a connectivity matrix C . For two zones, $zone_i$ and $zone_j$, C_{ij} represents the ratio of larvae originating from $zone_i$ which settles on $zone_j$. The coral population state is here represented as percentage coral cover. The dynamical evolution of the percentage coral cover of $zone_i$ is modelled as:

$$b_{i,t+1} = b_{i,t} + r b_{i,t} \left(1 - \frac{b_{i,t}}{K_{i,t}}\right) - db_{i,t} + \sum_j C_{ji} b_{j,t} f + e_{i,t} \quad (1)$$

where $b_{i,t}$ is the percentage coral cover in $zone_i$ at time t , r is intrinsic growth rate, d is mortality rate and f is fecundity, understood as the number of visible recruits per unit cover. $K_{i,t}$ is the maximum sustainable coral cover (see below for a description of this term) in $zone_i$ at time t , C_{ji} is the probability that a juvenile released at $zone_j$ may recruit at $zone_i$ and $e_{i,t}$ is a process error term. In all simulations described below, Eq. 1 is iterated for 50 years with a time-step of one year.

This is a simple model since it does not explicitly account for interactions between corals and other species. Nevertheless, it allows us to analyse the interplay between three processes: i) the population dynamics acting locally at each zone, as represented by

the second and third terms on the right-hand side on Eq 1, ii) maximum sustainable coral cover, as represented by the term $\left(1 - \frac{b_{i,t}}{K_{i,t}}\right)$ and iii) the network dynamics as a function of the connectivity matrix C . A discussion about this and alternative model formulations can be found in (Berryman et al. 1995). Values assigned to starting percentage coral cover ($b_{i,t=0}$) and K are explained in *Study area*. Model parameterisation, example runs, sensitivity analysis, and model uncertainty and limitations are presented in Appendix S1. Notice that because b represents *percentage* coral cover it does not depend on zone size, while the connectivity matrix C , which represents the probability that a juvenile released at one zone may recruit at another zone, depends on the relative size of the originating and settling zones in addition to oceanic circulation.

Uncertainty and yearly variability for these parameters is accounted for indirectly in the simulations via the process error term e_i^t which follows a normal distribution with zero mean and standard deviation = 1.5 % cover. This value was chosen so that the error term has an impact on the model result comparable to ~10% variation on the intrinsic growth r . To account for stochastic variability, all model results are obtained by performing ensemble runs of 500 independent model simulations, with random error terms, and averaging the results.

Particularly relevant for our analysis is the role of the maximum sustainable coral cover $K_{i,t}$ in Eq 1. Commonly, in logistic equations like Eq 1, in place of $K_{i,t}$ we would find a maximum sustainable coral cover K , interpreted as an intrinsic property of a region, and thus a constant across all zones and over time. Here, as in (Sainsbury 1991, Thébaud et al. 2015, Britten et al. 2017), $K_{i,t}$ is interpreted as a proxy for the quality of the habitat supporting the coral community, which determines the maximum coral cover the zone can sustain. As such, values of K can change across individual zones. In addition, K can change with time since it may be negatively impacted by development projects that can induce excess

sedimentation and water turbidity (Pollock et al. 2014), or natural disturbance such as coral bleaching (Lukoschek et al. 2013), or may be positively impacted by habitat restoration initiatives or natural recovery (Depczynski et al. 2013). In this work, variations in $K_{i,t}$ are used to model events that completely destroy the coral supporting habitat in a zone, to mimic the effects of climate change or local development (see section ‘Impact analysis’ below).

Whether K is interpreted as a constant or variable maximum sustainable coral cover, the role of $K_{i,t}$ is the same. When the coral cover is below the maximum sustainable ($b_{i,t} < K_{i,t}$), the growth term $rb_{i,t} \left(1 - \frac{b_{i,t}}{K_{i,t}}\right) > 0$ and the coral cover increases. When the coral cover is above the maximum sustainable ($b_{i,t} > K_{i,t}$), the growth term $rb_{i,t} \left(1 - \frac{b_{i,t}}{K_{i,t}}\right) < 0$ effectively turning into an additional mortality term due to competition for space, and the coral cover decreases.

Yearly variations in connectivity

Yearly variations in connectivity are analysed using three approaches. First, changes in the betweenness centrality of the different yearly connectivity networks are assessed. Second, we check how changes in connectivity affect the system maintenance and recovery analysis. Both analyses assume that a yearly connectivity matrix applies to each of the 50 years of the simulation run. A third approach is designed to account for year to year variability in the simulation run itself.

‘Betweenness centrality’ (BC) is commonly used in network theory to quantify the relative importance of a node in the overall network connectivity (Holstein et al. 2014). BC measures the number of shortest paths between any two zones in the ecological network that go through a specific zone. For example, a larva released from a zone can recruit into a different zone, grow into a full colony, and subsequently release new larvae that recruit into a third zone. Over several years, or model time-steps, zones are thus connected directly via a specific yearly connectivity matrix and

indirectly via multi-step temporal transitions between multiple zones. BC represents the extent to which a zone is likely to be visited by these indirect links and how likely it is over a large number of generations that coral offspring transit through that specific zone.

Accounting for year to year variability in the simulation run itself is complicated by the inherent stochasticity of simulation runs, a lack of knowledge of the probability distribution of connectivity patterns, and uncertainty relating to future oceanographic conditions under climate change. To address this challenge, we ran 500 simulations of the model in Eq 1, using the *mean* connectivity matrix. This procedure results in 500 coral cover values for each zone one for each of the simulation runs. We then repeated this process, only using a connectivity matrix for each year that was chosen at random among the years 2004-2009. For each zone, we determined p -values for Kolmogorov-Smirnov tests of differences between distributions of simulated coral cover created assuming mean and randomly assigned connectivity matrices. This analysis indicates, for each zone, the degree to which the simulated distributions of coral cover are affected by annual variability in connectivity.

Impact analysis

The role a zone plays in system maintenance is the regional impact of perturbing that zone’s percentage coral cover and maximum sustainable coral cover. Impact is defined as the difference between the system in its baseline state and what the system *would* be had a specific perturbation occurred in a specific zone. This estimated impact constitutes a reasonable hypothesis of the effects of climate change and development on regional coral extent that is consistent with current understanding and which can be compared to future observations. Impact as described is an effective proxy for the analysis of system maintenance since the larger the number of zones with high global impact, the more the system may withstand minor local stressors and ecological variability.

The overall regional impact of an event that completely destroys the coral supporting habitat in zone_{*i*} is computed via the following steps. We first calculated the projected overall coral cover after 50 years in the case of no perturbation. This value is defined as *baseline*. Then, for each zone_{*i*} we modelled how the complete destruction of coral-supporting habitat from that zone influenced maximum sustainable coral cover all other zones. The change in coral cover over the regions (*B_i*) after 50 years in the case of $K_i \rightarrow 0$, is

$$impact_i = (baseline - Eq 2 \\ b_i - B_i)$$

Where the notation ‘-*i*’ refers to all zones except for *i* (1, 2, 3, ..., *i*-1, *i*+1, *i*+2 ...). Notice that because the coral cover of zone_{*i*} (*b_i*) is subtracted from the baseline coral cover in Eq 2, *impact_i* represents the contribution of zone_{*i*} to the coral cover in all other zones, separate from the coral cover loss in zone_{*i*} itself.

Recovery analysis

While impact analysis simulates the regional impact of a perturbation in a single zone, recovery analysis addresses the opposite. All zones apart from zone_{*i*} have coral cover removed and the time it takes for the overall region to recover its original coral cover solely from the contribution from zone_{*i*} is quantified. Once again, projected overall coral cover after 50 years in the case of no perturbation is calculated and defined as *baseline* = $\sum_i b_i$. For each zone in succession, we presumed the destruction of coral cover in all other zones by setting $b_{-i} = 0$ (leaving K_{-i} unchanged to allow for recovery of coral cover. We then determined the projected overall coral cover at each subsequent time-step for each zone and summed these values across regions, $S^t = \sum_i b_{i,t}$. The *RecoverTime_i* was defined as the value of *t* at which $S^t \geq baseline$.

Sensitivity analysis

The model response to changes in a parameter is a function of the parameter itself, of all other parameters and of the state variables. A full sensitivity analysis is thus computationally unfeasible. An approximate understanding of model sensitivity can however be achieved by studying how the model responds to changes in

a few parameters at a time, using the simulations under standard conditions as baseline references. Some of these results are presented in Appendix S4 where the sensitivity of both the impact and recovery analyses to changes in intrinsic growth, mortality, fecundity and maximum sustainable coral cover are discussed.

We used the results from the impact and recovery analyses described above as baseline references, and compared these to results using three alternative model parameterisations. If C^0 and K^0 are the connectivity and maximum sustainable coral cover values in Eq 1 (as described in the Meta-population model section above), the three alternative parameterisations were as follows.

1. “Fixed K”; $K_i = mean(K_i^0)$ and $C = C^0$. In this parametrisation, the connectivity matrix is unchanged and the maximum sustainable coral cover is the same in all zones and equal to the mean of the maximum sustainable coral cover used in the baseline simulations.
2. “Fixed self-recruitment”; $K_i = K_i^0$ and $C = C^1$, where $C_{i \neq j}^1 = C_{i \neq j}^0$ and $C_{i=j}^1 = mean(C_{i=j}^0)$. In this parametrisation, the maximum sustainable coral cover and external recruitment are unchanged and the self-recruitment (diagonal entries in the connectivity matrix) is the same in all zones and equal to the mean of self-recruitment used in the baseline simulation.
3. “Fixed external recruitment”; “ $K_i = K_i^0$ and $C = C^2$, where $C_{i=j}^2 = C_{i=j}^0$ and $C_{i \neq j}^2 = f(distance)$. In this parametrisation, the maximum sustainable coral cover and self-recruitment are unchanged and the external recruitment (off-diagonal entries in the connectivity matrix) is an inverse square function of the distance between zones.

The comparison between the baseline, “Fixed K”, “Fixed self-recruitment” and “Fixed external recruitment” simulations gives an indication of how regional variability in maximum sustainable coral cover, self-recruitment and external recruitment affect the

sustainability of the reef system and thus the extent to which data collection to assess this variability can inform management as well as the extent to which focussing on the management of local variability vs regional averages can benefit long term conservation.

Joint assessment of impact and recovery under variable connectivity patterns

Finally, to account for variability in yearly connectivity patterns and to summarise our findings for decision making, we plot recovery time and impact analysis on the same figure under different types of connectivity matrices. Lacking information on the probability distribution of future ocean circulation patterns, and thus of future connectivity patterns, we represent yearly variability via two types of simulations. In the first, referred to as ‘random’, the connectivity matrix is chosen randomly at each year. In the second, referred to as ‘cycle’, we cycle through 2004-2009 connectivity matrices, generating a regular sequence of connectivity with a period of six years.

Results

Yearly variations in connectivity

Betweenness Centrality (BC) was generally highest in the central zones (zone 20 and surrounding; Figure 2) with most larvae passing through these zones during dispersal. However, BC of these zones changed significantly from very high values in 2005 to much lower values in 2008. Inter-annual variability was also high between consecutive years (e.g. compare 2004 to 2005). In addition, while the north-east end of the study area shows consistently lower values, some variability in BC at the south-west end of the study area is noticeable. This pattern is significant because we expect the BC at both ends of the study area to be low due to border effects.

A quantitative assessment of the year to year variability was obtained by simulation runs in which the connectivity matrix is chosen randomly among the yearly connectivity matrices 2004-2009, at each time-step (Figure

5). Thirty-four of the forty-seven zones in the model have highly significant p-values (<0.01), suggesting that local coral cover resulting from random yearly variations in connectivity are significantly different from the ones resulting from the mean connectivity. We further tested this following current recommendations about overreliance on p-value significance ([Halsey et al. 2015](#), [Altman and Krzywinski 2017](#)) by bootstrapping p-values and comparing the above distribution against 200 different distributions, obtained by comparing 200 sets of 500 simulation runs that use the mean connectivity matrix and different random seeds for the error term. No comparison had a single p-value >0.01 , showing that patterns of connectivity in any given year and for the mean connectivity lead to simulation results that are statistically different. Overall, this suggests that even over a 50-year simulation, using the mean connectivity matrix is not a good approximation of the yearly variability in connectivity.

Yearly variability in connectivity was investigated further by examining the annual patterns for larval inflows (acting as a “sink”) and outflows (acting as a “source”). Similar to BC, reefs acting as sinks were often located in the centre of the study region (Appendix S2: Fig. S1) but there was strong inter-annual variability in larval supply to surrounding regions in both the north-east and south-west. Sources of larval outflow were also dominated by reefs in the centre of the section region (Appendix S2: Fig. S2).

Impact analysis

Impact analysis highlights three areas as having prominent effects on coral cover in the entire region (Figure 3). These zones are located the mid-south-west (14 and 15), followed by the offshore spatially central region (21 and 22) and then the south (6 and 11). Thus, in contrast to indices related to connectivity, the zones that impact the coral cover of surrounding regions do not necessarily radiate from the centre of the study region. Yet, similar to the connectivity measures, there is considerable temporal

variability in the impact a zone has on the overall state of the system – with the connectivity matrix from year 2004 having the highest impact– as well as among regions within a given year (Appendix S3: Fig. S1).

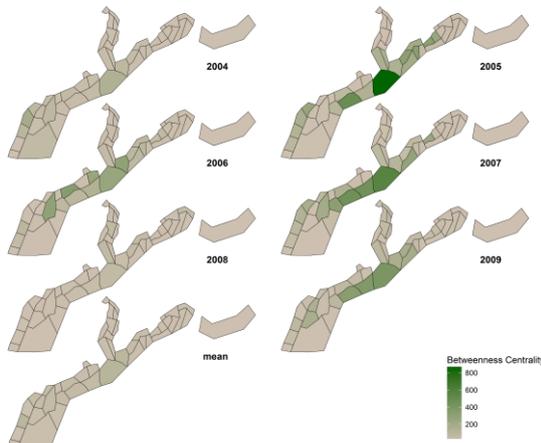


Figure 2. Betweenness Centrality (BC) for the six yearly connectivity matrices and the mean connectivity matrix.

The ranking of the zones in terms of overall regional impact differs from both the ranking of their coral cover and maximum sustainable coral cover (Appendix S1: Fig. S1). The potential for zone_i to have an impact according to Eq 2 depends on its biomass at each time-step and its connectivity. The potential of any other zone_j to be impacted depends on its connectivity to zone_i but also on how far the biomass of zone_j is from maximum sustainable coral cover at each time step. Impact is thus non-linear, because it depends on maximum sustainable coral cover, as well as path-dependent, because it depends on values of coral cover and maximum sustainable coral cover at the previous simulation step. The extent of non-linearity and path-dependence is evident wherein not only the magnitude but also the spatial pattern of the zones' impact change with varying levels of perturbation imposed on each zone (Appendix S4: Fig. S4.). Consequently a priority list of zones for conservation initiatives would change depending on the magnitude of the stressors the region is likely to experience.

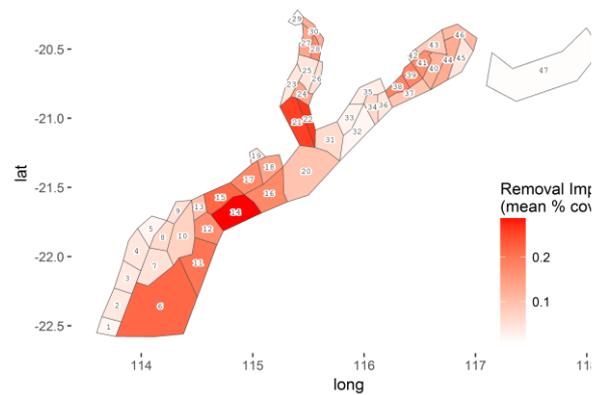


Figure 3. Impact analysis showing the change in coral cover in all remaining zones, as a result of a perturbation which destroys the coral supporting habitat in a given zone. Zones in red have higher regional impact. Zones of highest impact= 14, 22, 21, 15, 6, 11, 38, 39, 17, 16.

Recovery analysis

Similar to the impact analysis, recovery time did not show any spatial aggregation towards the centre of the study region (Figure 4). In addition, the zones that provide for fast recovery were not included in the top 10 rankings for coral cover, maximum sustainable coral cover or impact. Temporal variability was also high and followed a similar pattern to the impact analysis, with 2004 having the highest influence on recovery time (Appendix S3: Fig. S2.).

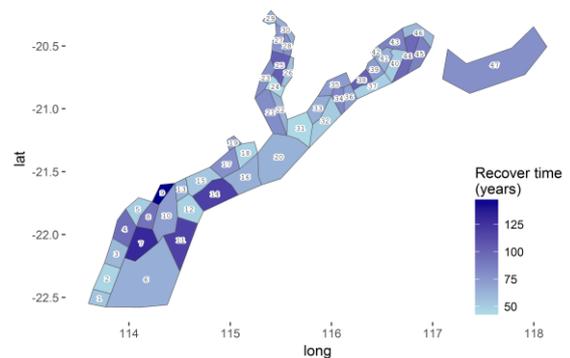


Figure 4. Recovery analysis showing the number of years needed for overall regional coral cover to recover when a single zone is unaffected and re-seeds neighbouring reefs. Blue and white colours map short to long recovery times, respectively. Listed are the 10 zones leading to faster regional recovery in decreasing order (shorter to longer)

recovery time). Zones of quickest recovery= 24, 31, 42, 2, 12, 18, 37, 5, 32, 40

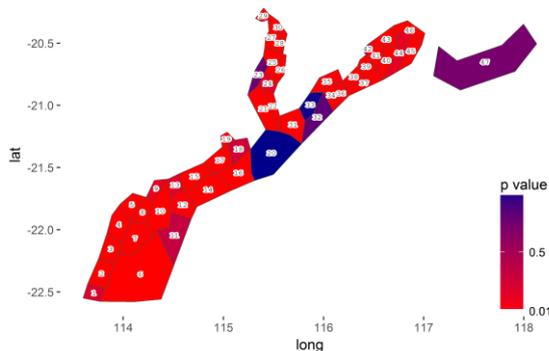


Figure 5. Comparison of model results between 500 simulation using the mean connectivity matrix vs using random yearly connectivity matrices. Colours map the p-values of the Kolmogorov-Smirnov test of the two distributions for each zone.

Sensitivity analysis

From both a scientific and management perspective, a question of considerable relevance is the relative impact of scenarios with varying local population dynamics vs self-recruitment vs external recruitment in the sustainability of a meta-population. The patterns of departure from the baseline vary considerably in the three scenarios, showing how zones can react very differently to changes in maximum sustainable coral cover, self-recruitment and external recruitment. This result held for both removal impact and recovery time (Figure 6, Figure 7). The main result from this analysis is that changes in self-recruitment have the least effect on the impact analysis while changes in maximum sustainable coral cover have the least effect on the recovery analysis. In the Pilbara network, variability in self-recruitment has a smaller overall impact on the analysis than variability in external connectivity and maximum sustainable coral cover (Figure 6, Figure 7). Interestingly, a uniform maximum sustainable coral cover (top row) seemed to have an overall negative impact on recovery time in most of the region, while the effects of fixed self-recruitment and external recruitment are more evenly distributed (Figure 7).

Joint assessment of impact and recovery under variable connectivity patterns

Yearly changes in connectivity strength result in profound differences to population impact and recovery that are lost when assessing mean connectivity trends. This result is obtained by accounting for variability in yearly connectivity patterns by using two types of simulations: ‘random’ (the connectivity matrix is chosen randomly at each year) and ‘cycle’ (we cycle through 2004-2009 connectivity matrices). To simplify comparison, we also include the set of simulations carried out with the mean connectivity matrix.

One pattern that clearly emerges is that connectivity patterns affect recovery time more often than impact values, as shown by the clear horizontal layering of the three types of simulations (Figure 8). Clearly, recovery time is much quicker when yearly connectivity changes randomly. This variability results in an irregular spreading of larvae through the region and thus enables recruitment from the source zone to a larger number of zones in the first years of the simulation, kick-starting the process of recolonization to the entire region. Conversely, under static connectivity, few zones are likely to be reached in the first years of the simulation and further recolonization needs to proceed indirectly via these newly seeded zones, delaying the recovery process. Simulation with the periodic changes in connectivity displays an intermediate behaviour.

Discussion

We have described an approach useful for prioritising areas suitable for resilience-based management in a network relevant to marine spatial planning. The results of prioritisations made in this study have immediate relevance to contemporary management decisions (Doropoulos and Babcock 2018). For example, zones marked in red in Figure 8b appear to contribute most to both high impact and quick recovery, both key components of resilience. Some of these zones are located in the Dampier Archipelago region, currently under consideration for declaration as a multiple-use marine park area. Zones in the central part of

the region also appear frequently as both high impact and quick recovery. Given recent coral bleaching in the Pilbara (Ridgway et al. 2016, Lafratta et al. 2017) the importance of these zones for the recovery and resilience of the overall region assumes broader importance and potentially greater urgency. In contrast, zones marked in blue in Figure 8b showed low contributions to impact and recovery and appear to make relatively small contributions to system resilience so might receive lower priority for conservation measures, or higher priority as potential development sites, all other things being equal. That said, care is needed when assessing the contribution of zones 1-3 because they are located close to the domain border.

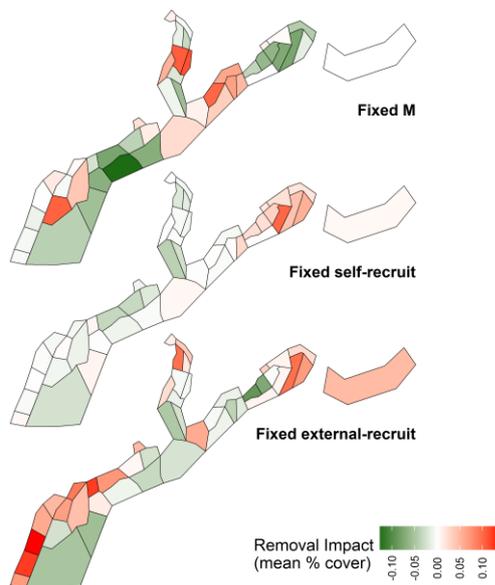


Figure 6. Relative effect of variability in maximum sustainable coral cover (top), self-recruitment (middle) and external recruitment (bottom) on the outcome of the impact analysis. Results are shown as difference against the baseline impact analysis in Figure 3, with values ranging from green (negative) to red (positive). Variability in self-recruitment has a smaller overall impact on the analysis compared to external connectivity and maximum sustainable coral cover. The patterns of departure from the baseline vary considerably in the three plots showing how zones react very differently to changes in maximum sustainable coral cover, self-recruitment and external recruitment.

Somewhat surprisingly, our study has highlighted how a single reef can have differing contributions to habitat maintenance and recovery, both of which are key attributes of resilience (Mumby and Steneck 2008). We find zones that provide large contributions to system maintenance may not necessarily do so for system recovery. Some zones show high contributions for either maintenance or recovery, but not both. Moreover, the ranking of a zones' impact can change as a function of the magnitude of the perturbation and its sign (Appendix S4: Fig. S4.).

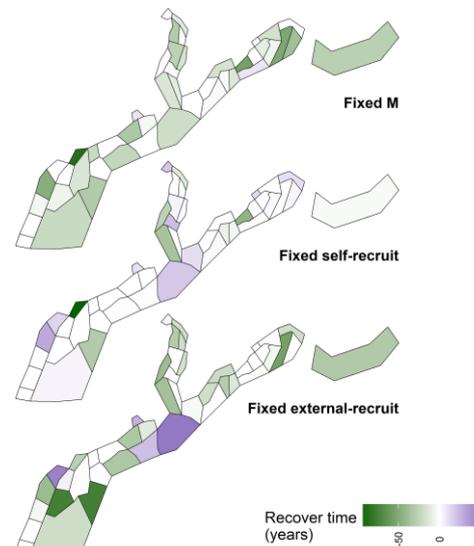


Figure 7. Relative effect of variability in maximum sustainable coral cover (top), self-recruitment (middle) and external recruitment (bottom) on the outcome of the recovery analysis. Results are shown as difference against the baseline impact analysis in Figure 4, with values ranging from green (negative) to blue (positive). Variability in external connectivity has the largest impact on the result.

Our modelling approach differs from other approaches in the meta-population literature (Hanski 2001, Ovaskainen and Hanski 2001, 2003, Figueira 2009, Jacobi and Jonsson 2011a) in a number of ways. Among these, two are particularly significant. First, we model the dynamics of population abundance (rather than presence/absence as in traditional meta-population studies) within each zone by using a variable maximum sustainable coral cover, rather than a constant carrying capacity as in (Jacobi and Jonsson 2011a). The maximum

sustainable coral cover is estimated empirically and can vary during the simulation to mimic changes in the quality of the supporting habitat. Second, rather than calculating the *contribution* a zone provides to other zones in terms of exported larvae (as in (Figueira 2009)) we calculate its *impact*, that is the fraction of exported larvae which can actually recruit to other zones, as a function of the local biomass abundance and maximum sustainable coral cover at that time step in the simulation. For a more in depth discussion of the difference between contribution and impact within an ecological modelling framework we refer the reader to (Boschetti 2007). A similar idea is used in (Ovaskainen and Hanski 2003) who provide a closed form solution in the case in which the model dynamics is governed by colonisation and extinction processes only, and no population dynamics within each zone is included.

The non-linearity and density dependence in our model prevent us from obtaining closed form solutions to the computation of impact and recovery analyses, which we carried out numerically as described in Sections Impact analysis and Recovery analysis. Our study has highlighted the importance of incorporating yearly variability when investigating dynamic systems, rather than simply investigating averages, as also noticed in other regions around the world ([Rice et al. 1999](#), [Werner et al. 2007b](#)). When considering source-sink dynamics and spatial planning, stochastic events can be important drivers of rare connectivity events rather than simply outliers (e.g. Golbuu et al. 2012). In our study system, variability in oceanic transport and its interactions with the annual lunar progression in the timing of coral mass spawning (Gilmour et al. 2016) also drives dynamic patterns of ecological connectivity. Connectivity patterns changed considerably among the years 2004-2009, significantly affecting coral connectivity in different parts of the region, subsequently affecting the role they play in overall regional coral cover. Thus, average connectivity values can overlook key components of dynamic systems.

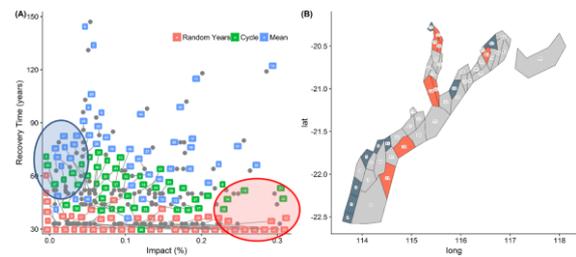


Figure 8. (left) Impact and recovery time for each zone for a connectivity matrix changing randomly every year (red), periodically cycling through the 2004-2009 connectivity matrices (green) and static mean connectivity (blue). X-axis represents the impact values as % coral cover and the y-axis shows the recovery time. (right) Zones with high impact value and fast recovery time (red) and zones with low impact value and slower recovery time (dark blue).

Differing hydrodynamic conditions emerge as a strong driver of the properties of the overall system if it were to experience long-term change into conditions represented by the regime of a particular year (Appendix S3: Fig. S1). For example, persistent conditions typical of year 2005 would produce the quickest recovery times, with such results being possible with recovery sourced from multiple reefs (Appendix S3: Fig. S2). Conditions in 2005 were characterised by north to south flow yet relatively low connectivity between areas around Dampier in the north and the rest of the system (Feng et al. 2016). In contrast, recovery times appeared to be almost twice as long under conditions representative of 2004, when currents flowed mainly south to north.

Broad scale changes to coastal and oceanic circulation and seasonality in the eastern Indian Ocean may be experienced under changing climate and are likely to influence hydrodynamic regimes and therefore overall network dynamics. Random variation in hydrodynamic connectivity appears to promote the most rapid recovery of the system (Fig. 6), with longer recovery times when hydrodynamic regimes cycle – such a phenomenon may be experienced under increased frequency of ENSO conditions in the south-east Indian Ocean (Cai et al. 2015, Zinke et al. 2015). These changes may also impact

rates of coral bleaching and other disturbances. Therefore, changing climate will have multiple paths to impact the resilience of Pilbara coral reefs.

The role of coral population dynamics in each zone was also evident, wherein contributions to system resilience were influenced not only by levels of connectivity but also by differing carrying capacities. For the same system, assessments of system resilience based on connectivity alone (i.e., rank contribution of a zone as a source and/or sink) produced a list of zones potentially important to resilience that was quite different (Feng et al. 2016) to those developed in the current analysis. Broad scale data on maximum sustainable coral cover and dynamic aspects of populations is highly valuable in this context and given apparent sensitivity of the system to properties such as growth and mortality continued efforts to obtain relevant demographic data across appropriate spatial scales should be a high priority for management.

Conclusions

The presented approach can provide valuable input to management decision-making in ranking the relative values of discrete areas based on agreed sets of prioritised attributes. Importantly, conclusions based on this approach can differ from those based on connectivity alone (Feng et al. 2016). By showing that even a single species logistic equation can lead to extremely complex behaviour when embedded in a network of 47 interacting nodes as described in this work, we also highlight that different purposes of conservation initiatives (system maintenance and system recovery) can result in very different management recommendations. This brings attention to how a careful specification of management questions can lead to more informative analyses, modelling and field work. In addition, we show that yearly variability in connectivity is poorly captured by time-averaged mean connectivity, even for a simulation spanning five decades. In this case, developing conservation initiative at the regional level can be extremely challenging especially under large ecological uncertainty. In these situations, field work spanning long

time series as well as more realistic modelling could be carried out with foresight aimed at identifying possible regional scenarios and conservation priorities that can in turn inform further field work and modelling in an iterative and adaptive manner.

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Author contributions

FB developed and ran the ecological model. RB, CD, DT and MV collected and analysed coral cover data. MF and DS ran the hydrological model. MF, DS and OB analysed connectivity data. FB, RB and CD led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

Data accessibility

Metadata associated with this project can be viewed at <http://www.marlin.csiro.au/geonetwork/srv/en/g/search#!e52c12f0-1d4d-43cb-aa19-32e08bb28603>. Particle tracking model simulation data are available at https://data.pawsey.org.au/public/?path=/PMCP/Connectivity/model_data.

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