Advancing methods in marine conservation planning with ecological connectivity and environmental DNA

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Submitted in accordance with the requirements for the degree of
Doctor of Philosophy

The University of Leeds
Faculty of Biological Sciences
School of Biology

September 2022

The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

1. The work presented in Chapter 2 of this thesis is part of a jointly authored manuscript published as a primary research article as follows: *Integrating larval connectivity into the marine conservation decision-making process across spatial scales*. **Muenzel**, **D.**, Critchell, K., Cox, C., Campbell, S. J., Jakub, R., Suherfian, W., La Sara, Chollett, I., Treml, E. A., Beger, M. 2022. *Conservation Biology*. 10.1111/cobi.14038

   In this work I was responsible for developing the research ideas, conducting the analyses related to spatial prioritisation and metapopulation assessment, and leading the writing of the manuscript.

   Co-authors helped develop the initial research concept and provided the dispersal models and habitat data. They also provided critical feedback on successive drafts of the manuscript and helped address reviewer comments during the publication process.
2. The work presented in Chapter 3 of this thesis is part of a jointly authored manuscript published as a primary research article as follows: *Comparing spatial conservation prioritization methods with site- versus spatial dependency-based connectivity*. **Muenzel**, **D.**, Critchell, K., Cox, C., Campbell, S. J., Jakub, R., Chollett, I., Krueck, N., Holstein, D., Treml, E. A., Beger, M. 2022. *Conservation Biology*. 10.1111/cobi.14008

   In this work I was responsible for generating and developing the research ideas, conducting all analyses, and leading the writing of the manuscript.

   Co-authors helped to refine the research methodology, provided the dispersal models and habitat data, and provided feedback on successive manuscript drafts.
3. The work presented in Chapter 4 of this thesis is part of a jointly authored manuscript being developed for publication as follows: *Designing marine reserve networks to mitigate larval dispersal volatility with the connectivity portfolio effect*. **Muenzel**, **D.**, Critchell, K., Treml, E. A., Beger, M.

In this work I was responsible for developing the research ideas, conducting all analyses, and leading the writing of the manuscript.
Co-authors contributed to initial conception of the research ideas, provided the dispersal models, and provided feedback on successive manuscript drafts.

4. The work presented in Chapter 5 of this thesis is part of a jointly authored manuscript being developed for publication as a primary research article as follows: *Conservation planning for coral reefs using underwater visual census and environmental DNA*. **Muenzel, D.**, Bani, A., Dixon, A., Stewart, E., De Brauwer, M., Djakiman, C., Jompa, J., Limmon, G., Masdar, H., Purnama, R., Yusuf, S., Struebig, M., Dumbrell, A., Beger, M. In preparation.
   In this work I was responsible for generating and developing the research ideas, surveying algae by underwater visual census, assisting with environmental DNA sampling, conducting the species distribution modelling and spatial prioritisation analyses, and leading the writing of the manuscript.
   Co-authors helped to refine the research methodology, assisted in the field surveying, conducted the DNA analysis and bioinformatics, and provided feedback on successive manuscript drafts.

Acknowledgements

The work presented in this thesis would not have been possible without the fantastic support from various supervisors, collaborators, and colleagues.

I would like to thank my supervisors for their role in developing this thesis. First, a huge thank you to Maria Beger for her constant support and guidance, as well as the numerous opportunities you have provided throughout my PhD. Thanks also to Chris Hassall for your helpful insights and guidance. I would also like to thank the University of Leeds School of Biology for funding this PhD through the Doctoral Training Studentship.

I would like to thank the team at Rare and all of the collaborators I worked with on Southeast Sulawesi planning. Courtney, Stuart, Raymond, Nils, Dan, Iliana, it was a privilege to be involved in the project and the workshop in DC. A special thank you to Eric and Kay for the extensive feedback and help you have provided with the research chapters.

I would also like to thank the Wallacea team, Maarten, Alessia, Cilun, Ray, Gino, Ipul, Masdar, Saad, Bahari, Njompa, Sarra and Bilqis. You made the trips an amazing experience that I will always remember fondly.

Thank you to the lab group at Leeds, Adele, Katie, Louise, James, Mark, Maarten, Betty, Fiona, Victoria, and all others. I am grateful for the extensive feedback you have all provided over the years and learned much from our weekly meetings.

A big thank you to my family for supporting me and guiding me throughout my life. Finally, a big thank you to Bob for always being at my side.

Abstract

Conservation planning identifies important areas for protection to stem the global loss of marine biodiversity. How protected areas are designed changes as new technologies improve our understanding of population dynamics and ecological processes. The interconnectedness of fragmented marine habitats is now widely documented, with the implication that dispersing species can benefit from networks of well-connected protected areas. At the same time, the ability to detect species occurrence and the taxonomic scope of biodiversity assessment has been revolutionised by environmental DNA. Here, I investigate how current practices in designing marine protected areas can be improved based on these novel understandings. In the first three chapters, I illustrate how larval dispersal can inform the management of coral reefs and reef-associated species. First, I show how dispersal connectivity can be used at multiple spatial scales of spatial planning, with a case study of marine reserve establishment in Southeast Sulawesi, Indonesia. I describe how to combine regional identification of protected area networks with local delineation of marine reserves using detailed habitat data. Second, I compare the performance of two conceptually different approaches to integrating connectivity in spatial prioritisation tools, using Marxan. Conservation priorities can either be identified based on site-specific features of connectivity, or through a spatial dependency-based approach of selecting clusters of strongly connected habitat patches. I demonstrate that features and spatial dependency can all perform best in different contexts, depending on the conservation objectives, habitat degradation, and species dispersal capabilities. Third, I explore how temporal variability of larval dispersal impacts expected reserve benefits. I show how in certain cases, using a mean of dispersal connectivity is suboptimal before suggesting how more temporally stable reserve networks can be designed. In the final chapter, I evaluate how biodiversity assessments with environmental DNA analyses can inform spatial planning and how the resulting conservation priorities compare to those based on traditional visual census surveys. I show that both survey techniques identify unique taxonomic groups and have relatively low co-detection of shared groups, suggesting that these techniques should be used in combination to set conservation priorities. Overall, this research aims to promote the wider uptake of larval dispersal and environmental DNA in conservation planning for marine ecosystems.

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Chapter 1. Introduction

Conservation biology developed in the 1980s as a ‘crisis discipline’ to address contemporary biodiversity loss (Soulé 1985), yet four decades on global biodiversity and ecosystems are declining at a faster rate than at any time in human history with few signs of slowing down (Butchart et al. 2010; IPBES 2019). The traditional framing of conservation as preservation of natural habitats in protected areas typically excludes humans and imposes a Eurocentric dichotomy between people and nature (West et al. 2006). This has been criticised for ignoring the dynamic interdependence of nature and human well-being and imposing often impossible standards (Igoe 2005). Although this ideology still predominates today, other conservation frameworks have also emerged alongside which instead take integrated, ecosystem-based approaches that aim to deliver both nature preservation and sustainable benefits to people (Mace 2014). Under this framing, protected areas should be designed together with local people and be informed by ecological principles based on best available science to deliver maximal societal and environmental benefits.

In order to ensure healthy oceans for future generations, conservation planning and the establishment of Marine Protected Areas (MPAs) is widely proposed as a solution to mitigate local threats and improve survival and recovery of marine ecosystems (Margules & Pressey 2000; Ceccarelli et al. 2021). Marine ecosystems are heavily impacted by a combination of local stressors and climate change effects of ocean warming, acidification, and extreme weather intensification (Gissi et al. 2021). At the same time, dependence on the oceans’ natural capital is increasing to meet the demands of a growing, over-consumptive human population (Costello et al. 2020). Conservation outcomes can be enhanced by using information on ecological connectivity to design well-connected MPA networks that deliver both conservation and fishery benefits (Olds et al. 2016) and by applying comprehensive data on biodiversity to set conservation priorities (Edgar et al. 2016).

Among the world’s marine ecosystems, tropical coral reefs are among the most diverse, containing at least one quarter of all marine species, despite covering less than 0.1% of the ocean floor (Hoegh-Guldberg et al. 2017). Symbioses with *Symbiodinium* algae permit scleractinian corals to thrive in oligotrophic waters, and the complex reef structures they build provide micro- and macro-habitats for a plethora of other taxa (Putnam et al. 2017). Persistence of corals and many reef species depends critically on the process of larval dispersal, as metapopulations are established across non-contiguous, often distant, reef patches (Jones et al. 2009). Besides being biodiversity hotspots, millions of people’s identities and livelihoods are dependent on healthy reefs (Burke et al. 2011; Woodhead et al. 2019), particularly in low-lying climate vulnerable island communities (Perry et al. 2011). Communities benefit from a range of important ecosystem services from direct food provision from reef fisheries (Newton et al. 2007) to coastal protection (Harris et al. 2018), sand generation (Perry et al. 2015), nutrient and water cycling (Wild et al. 2004), and tourism (Spalding et al. 2017).

Despite their socio-ecological importance, up to half of live coral cover and associated ecosystem service provision has been lost since the 1950s (Eddy et al. 2021). As the oceans have absorbed more than 90% of excess heat over the past 40 years (Zanna et al. 2019) and many marine species including corals live close to their upper thermal limits, coral reef ecosystems are particularly vulnerable to rising sea temperatures (Lough et al. 2018; Pinsky et al. 2019). Once geochemical tipping points are exceeded due to rising carbon dioxide levels, calcium carbonate reefs will undergo net erosion (Andersson & Gledhill 2013). Coral reefs also face many local threats, including land-based runoff, coastal development, reef mining for building materials, direct ship and human damage, overfishing, destructive fishing, and fishing down marine food webs (Halpern et al. 2007; Riegl et al. 2009; Burke et al. 2011).

Whilst the most effective action to reduce global coral reef decline remains rapid greenhouse gas mitigation (Hoegh-Guldberg et al. 2019), reducing local anthropogenic stressors through conservation interventions such as MPA designation can also improve the chance of coral reef survival (Kleypas et al. 2021). Removal of pressures can result in greater biomass and species richness within MPA boundaries (Russ et al. 2004; Lester et al. 2009). Benefits can also extend outside boundaries if MPAs are connected to other areas through dispersal, as they provide a demographic boost to disturbed populations (Weese et al. 2011). In addition to these conservation benefits, larval dispersal from MPAs to fished areas can improve fisheries yields through recruitment subsidies (Grüss et al. 2011). For these reasons, larval dispersal information should be explicitly incorporated into the design of well-connected MPA networks (Almany et al. 2009; Magris et al. 2014; Green et al. 2015). Additionally, MPA design can benefit from emerging technologies such as environmental DNA (eDNA) surveying, which use free-floating DNA in the environment to identify species presences. eDNA has the potential to be a game changer by providing much greater information content (i.e., taxonomic breadth) at lower cost to document and monitor biodiversity and inform conservation priorities (Bohmann et al. 2014; Lawson Handley 2015).

1.1. Marine conservation planning for coral reefs

Systematic conservation planning describes a 'best-practice' framework to protect regional biodiversity in a transparent, objective-driven, and repeatable manner at least-cost (Margules & Pressey 2000). The original six steps in the operational model (Margules & Pressey 2000) have since been expanded for fuller comprehensiveness (Figure 1.1.), but are based on the same guiding principles of connectivity, adequacy, representativeness, and efficiency (Possingham et al. 2006). Broadly, conservation planning involves setting quantitative conservation objectives, collecting spatially explicit data on biodiversity and human activities, and spatially allocating and implementing conservation interventions. Interventions include protecting sensitive areas in strict no-take marine reserves (Sala & Giakoumi 2018), regulating activities and gear-use within multi-use protected areas (Rife et al. 2013), restoring degraded reefs (Bayraktarov et al. 2019), prohibiting fishing seasonally (Game et al. 2009), and managing invasive species (Malpica-Cruz et al. 2016). Spatial management actions in MPAs are particularly suited for coral reefs as many reef-inhabiting taxa display high site fidelity and short home ranges (Christie & White 2007). These principles are broadly mirrored in other planning frameworks, such as the Convention on Biological Diversity's criteria for Ecologically or Biologically Significant Marine Areas and Networks of Protected Areas (CBD, 2008).

Figure 1.1. Summary of the eleven stages of systematic conservation planning to achieve conservation goals effectively and efficiently (Pressey & Bottrill 2009). Certain steps may be taken simultaneously instead of sequentially, and feedbacks can occur from later to earlier steps.

As conservation planning often involves the balancing of numerous objectives across vast spatial extents, decision support algorithms are frequently used to propose a set of solutions using a process of spatial prioritisation. Algorithms frame the allocation of conservation interventions as a mathematical optimisation problem with an objective function and constraints (Sarkar et al. 2006). Large-scale examples, where spatial prioritisation was used in coral reef management, include the re-zoning of the Great Barrier Reef (Fernandes et al. 2005) and the expansion of marine protected areas (MPAs) managed by the Coral Triangle Initiative (Beger et al. 2015). In both of these cases, the tool Marxan (Ball et al. 2009) was used to support decision-making by proposing solutions which satisfied different ecological, socio-economic, and political needs.

When generating a conservation plan, certain simplifying steps are necessary to reduce real-world complexity. First, conservation objectives are often framed as representation targets for features (e.g., protect 20% of fringing reefs), as these are easy to implement and evaluate. In this context, conservation features refer to what is being protected, for example a species, habitat type, or ecosystem service. Targets refer to the amount of the feature to be captured within the MPA system. However, targets are commonly criticised for failing to reflect biological principles (Svancara et al. 2005). Conservation plans should ideally go beyond representation to ensure the persistence of biodiversity (Sarkar et al. 2006; White et al. 2009; Burgess et al. 2014). As the persistence of coral reef ecosystems depends critically on larval dispersal between patchy subpopulations, dispersal must be explicitly addressed in conservation planning (Section 1.2.). Second, as it is impossible to measure a completely representative sample of biodiversity across all taxonomic and functional levels, a biodiversity surrogate or set of target species is often selected for conservation planning (Sarkar et al. 2006). This limitation is addressed by the emergent technology of eDNA biodiversity surveying, which is capable of identifying and detecting presence of a wider taxonomic diversity compared to traditional survey techniques (Section 1.3.).

1.2. Larval dispersal in conservation planning

Numerous marine faunae undergo distinct developmental stages involving egg, larval, juvenile, and adult phases that are associated with different habitat and diet requirements as well as locomotory capabilities (Pittman & McAlpine 2003). For many species, dispersal primarily occurs as larvae when they are suspended in the pelagic water column and carried away from their natal source to a settlement destination (Cowen & Sponaugle 2009). Pelagic larval dispersal is a key process in coral reefs, underpinning demographic patterns and population distributions of many reef species (Cowen et al. 2007; Mumby & Hastings 2008). Reef-building corals disperse as larvae, as do many reef-fish and invertebrate species having relatively sedentary adult stages (Cowen & Sponaugle 2009). Ocean currents carry larvae anywhere from tens of metres to hundreds of kilometres away, depending on local oceanographic patterns and species-specific larval traits (Treml et al. 2012; Green et al. 2015). This dispersal facilitates population recovery following localized mortality events (Jones et al. 2009) and helps reduce genetic drift and inbreeding through genetic exchange (Almany et al.

2009). Larval dispersal also provides some buffer against climate change impacts, as dispersal processes permit populations to track ecological niches and promote the spread of resistance traits across a genetic pool (Heller & Zavaleta 2009; Mumby et al. 2011).

Protecting dispersal in well-connected networks of MPAs is key for the survival and recovery of coral reef ecosystems (Figure 1.2.; McCook et al. 2009; Magris et al. 2014; Álvarez-Romero et al. 2018a). As biomass and reproductive output builds up within MPAs from the removal of local fishing pressures (Marshall et al. 2019), larval subsidies are generated to outside areas. These subsidies reduce the chance of local extinctions and promote metapopulation resilience (Botsford et al. 2009). By ensuring that MPAs are connected in a network, the risk of population collapse across the entire network is reduced as a diversity of protected sources are providing larvae to replace the next generation and thereby support long-term persistence (Botsford et al 2009). Depending on whether management objectives are more conservation or fishery focussed, MPA networks can be designed to provide benefits to different areas (Gaines et al. 2010). Both site-level criteria such as uniqueness, productivity, and diversity, and network-level criteria such as representativity, connectivity, and adequacy need to considered concurrently to ensure effective protection (CBD, 2008).

A wide range of tools and approaches have been developed to incorporate connectivity into conservation planning, each with different requirements for data, expertise, and computational power (McCook et al. 2009; Beger et al. 2010; White et al. 2014; Bode et al. 2016; D’Aloia et al. 2017; Krueck et al. 2017; Smith & Metaxas 2018). These tools include using measures of species-specific mean larval dispersal distance for optimal MPA spacing and sizing to meet conservation and fishery objectives by ensuring that larvae reach appropriate areas (Green et al. 2014; D’Aloia et al. 2015). More targeted approaches can be taken if measures of larval dispersal between specific subpopulations are available from modelling, tagging, genetics, or simple observation (Bryan-Brown et al. 2017). Important subpopulations can be identified using principles of graph theory to protect, for example, sites that have high self-persistence (Burgess et al. 2014; White et al. 2014) or sites acting as stepping-stones in the wider network (Magris et al. 2016). Dispersal data can also be used to identify clusters of strongly connected subpopulations for protection (Beger et al. 2010, 2015). Alternatively, metapopulation theory can help to explicitly incorporate population persistence into spatial prioritisation approaches using dynamic mechanistic models (Bode et al. 2016; Chollett et al. 2017).

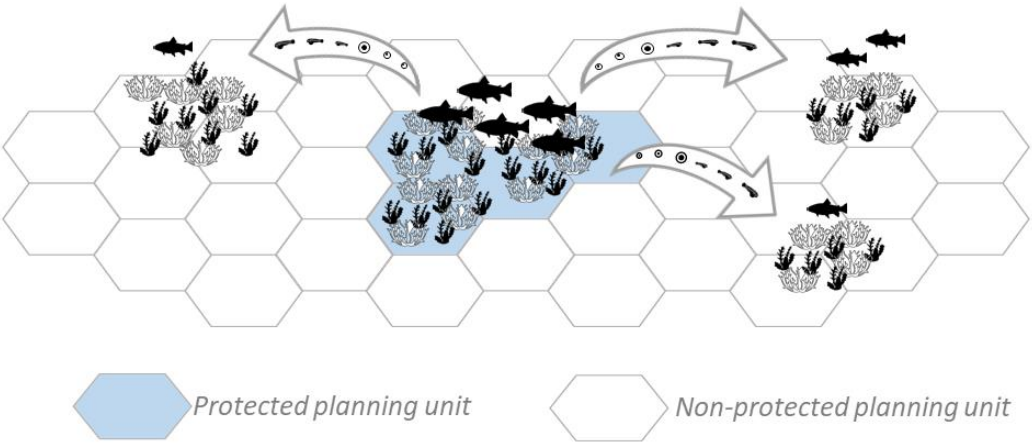

Figure 1.2. Schematic diagram of reef fish larval dispersal across a patchy coral reef system. The conservation intervention of reef protection is implemented by dividing the region into planning units and identifying priority areas using spatial prioritisation. Protected reefs can host bigger populations with increased reproductive potential which contribute larvae to both protected and non-protected areas (Harrison et al. 2012).

Despite this wide availability of approaches, only a minority of existing MPAs have adopted connectivity criteria in their design (Álvarez-Romero et al. 2018b; Balbar & Metaxas 2019). One barrier to wider uptake is the challenge of planning at the various spatial scales where larval dispersal and governance systems operate (Sarkar et al. 2006). The often large spatial scale of larval dispersal and smaller scale at which MPAs are implemented can lead to a scale mismatch whereby implemented actions cannot address the conservation problem (Guerrero et al. 2013). Systematic assessments such as regional spatial prioritisation are best suited for designing connected MPA networks (Mills et al. 2010), but many such assessments fail to result in concrete implementations (Cheok et al. 2018). Demonstrations on how to integrate regional and local planning steps would therefore help bridge this gap (Chapter 2) and can be used alongside other guidelines for protected area network design (CBD, 2008).

Another barrier is the lack of clear guidelines concerning which tools and approaches are more appropriate for a given context. Spatial prioritisation tools such as Marxan (Ball et al.

2009) necessarily treat connectivity as a static feature that is not directly related to persistence, requiring *post hoc* evaluations to assess ecological outcomes (Bode et al. 2016). Methods which treat connectivity differently in the objective function may generate different solutions, but how this relates to conservation objectives and expected benefits is unclear. By describing which factors affect the performance of different methods, conservation practitioners can be assisted in the selection between different methods for their respective planning systems (Chapter 3).

A dimension of larval dispersal not yet considered in conservation planning is its variability through time. Both direction and strength of larval flow can vary substantially across seasons and years as different oceanographic conditions operate, with the magnitude of temporal fluctuations being comparable to differences between species (Catalano et al. 2021). As a result, the larval subsidies which MPAs provide can also vary, resulting in uneven conservation benefits over time (Berumen et al. 2012). From a conservation planning perspective, consistency in MPA contributions is desirable to reduce the risk of adverse demographic changes and to provide stable fishery recruitment and fishery yields (Gaines et al. 2010). Networks of complementary MPAs can buffer temporal volatility via a portfolio effect, where a reduction in larval subsidies from some constituent components is offset by an increase from others in any given spawning period (Harrison et al. 2020). As empirical data on temporal larval dispersal patterns become more widely available, methods describing how to explicitly incorporate such a portfolio effect into MPA network design will become necessary (Chapter 4).

1.3. Biodiversity representation in conservation planning

Conservation planning requires comprehensive, detailed, and up-to-date data on biodiversity and environmental health so that interventions for threat-reduction are effectively allocated (Edgar et al. 2016). Obtaining such data for the large spatial scales at which conservation planning is generally undertaken poses some challenges (Dalleau et al. 2010). Generally, data from *in situ* field monitoring is highly accurate, but very localised. Underwater Visual Census (UVC), for example, can classify and quantify the number and biomass of numerous coral reef species. However, UVC is relatively resource-intensive and requires specialised taxonomic expertise, thereby limiting its spatial scope (Thomsen & Willerslev 2015). Thus, instead of considering all taxonomic levels, many conservation plans use biodiversity surrogates, such as coral habitat types (Mumby et al. 2008) or keystone species (Olds et al. 2014). This approach simplifies data collection and permits the use of extensive but taxonomically coarse datasets, such as remote-sensing coral reef maps, to set representation targets (Hedley et al. 2016). The use of surrogates has been questioned, however, given mixed evidence for their ability to represent a wide range of taxa (Beger et al. 2007; Mellin et al. 2011).

eDNA is a promising tool that can provide alternative or complementary biodiversity assessments over large spatial scales (Bani et al. 2020), including for coral reefs (DiBattista et al. 2017; Oka et al. 2021). The DNA which organisms shed via their skin, mucous, saliva, etc. into the surrounding environment is detectable at very low quantities and does not require the taxonomic expertise needed for UVC (Bohmann et al. 2014). Recent cost reductions in next-generation sequencing and the ability to process samples in the field have made it feasible and scalable to employ eDNA to survey and monitor remote tropical habitats (Huerlimann et al. 2020). eDNA has contributed to various conservation applications including monitoring invasive species (Ardura et al. 2015), detecting rare or cryptic species (Huhn et al. 2020), establishing trophic interactions (Uthicke et al. 2018), and assessing community level biodiversity (Bakker et al. 2019). By using a metabarcoding approach, universal primers can amplify eDNA fragments belonging to many different species, giving a taxonomic list of biodiversity for each sampled site (Miya 2022).

Although eDNA has been used for decades in microbial research, its application in marine biodiversity monitoring is more recent. eDNA-based species occurrence information is yet to be integrated into marine conservation planning (Ruppert et al. 2019; Bani et al. 2020). Comparisons between UVC and eDNA based surveys of tropical reef fish and invertebrates show both overlaps and differences in the species detected, but a much greater taxonomic breadth captured by the latter, particularly of small and difficult to detect species (Nguyen et al. 2020; Polanco Fernández et al. 2021). Marine eDNA retains a spatial signal of local community composition despite water mixing, but how far this extends depends largely on local biological and oceanographic factors influencing rates of eDNA degradation (Rees et al. 2014). It is unclear whether conservation priorities would differ if assessments were based on eDNA or traditional survey techniques, and how the two can best inform the spatial prioritisation process of protected areas (Chapter 5). As eDNA methods and workflows are refined, they will play an important role in providing large-scale and real-time data to monitor the rapid change of coral reefs under anthropogenic threats.

1.4. Thesis aims and objectives

The overarching objective of this thesis is to advance current practices and methods in conservation planning for coral reefs using information on larval dispersal and eDNA. MPA networks are a crucial conservation tool in the fight against ongoing coral reef degradation (Almany et al. 2009), and methods in their design must be continually updated based on latest ecological understanding. The first three research chapters address three knowledge gaps, respectively, related to the use of larval dispersal information in coral reef MPA network design to promote its wider uptake and improve management outcomes. The fourth research chapter addresses the use of novel eDNA surveying methods for coral reef biodiversity assessments. Together, the four chapters address the twin goals of achieving the persistence and representation of coral reef biodiversity in conservation planning (Figure 1.3.).

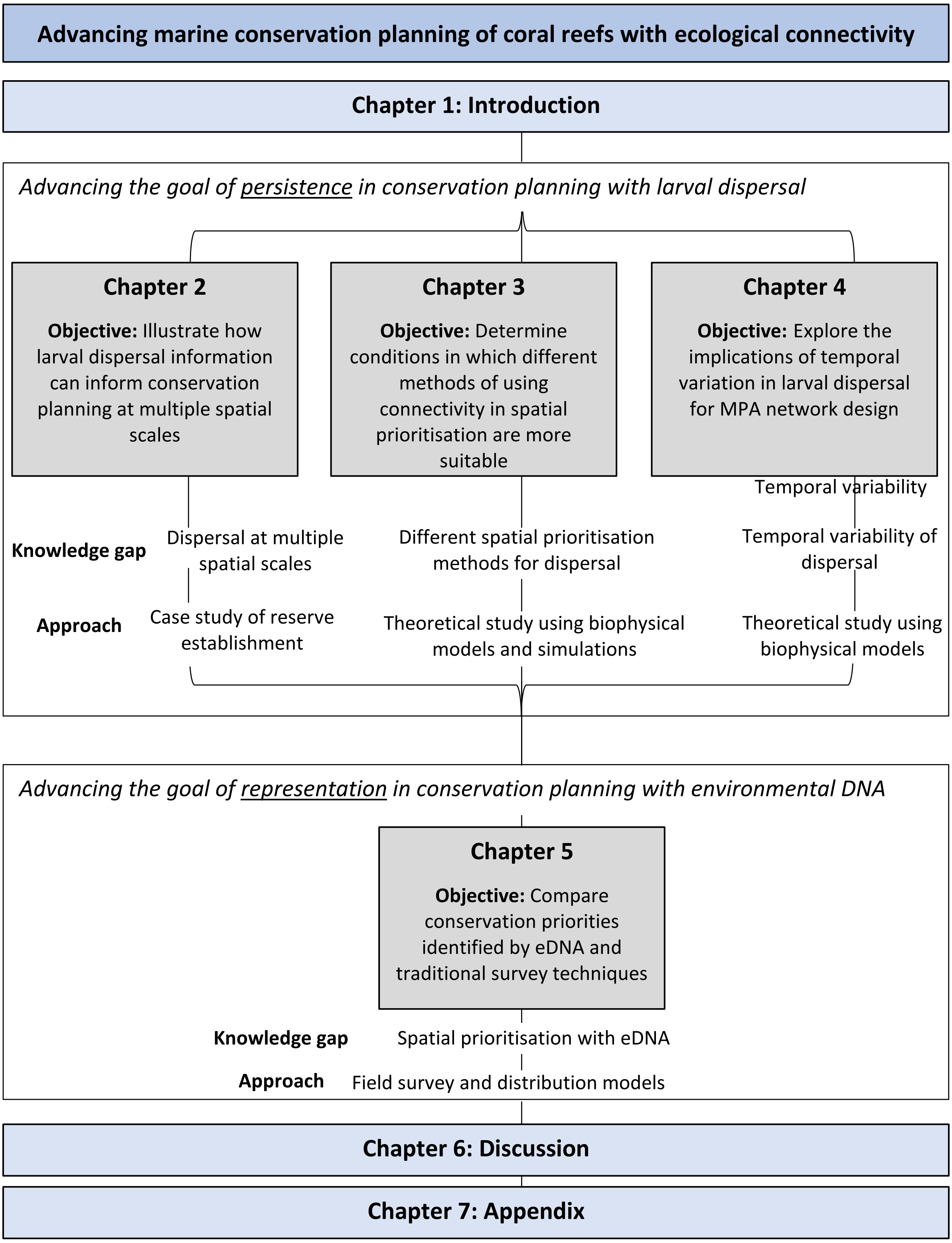

Figure 1.3. Schematic diagram showing how chapters in this thesis are structured. The first three research chapters address different knowledge gaps to promote wider usage of larval dispersal in marine conservation planning of coral reefs. The fourth research chapter addresses the use of eDNA surveying to identify conservation priorities.

Chapter 2 addresses the challenge of using larval dispersal information at different spatial scales of planning. Regional planning and local actions often do not inform each other, resulting in a mismatch of scales (Mills et al. 2010). This chapter presents a case study of reserve design in the province of Southeast Sulawesi, Indonesia, where biophysical models of larval dispersal were used to inform both local and regional planning. It illustrates how planning steps at both spatial scales can be integrated to capitalise on the advantages of working at either scale. This chapter also demonstrates how local communities can be involved in local decision-making to foster effective local governance. Due to travel difficulties with the COVID-19 pandemic, specific data on stakeholder responses could not be collected.

Chapter 3 compares the performance of two common approaches to use connectivity information in spatial prioritisation under different contexts. There is a wide range of available tools and approaches to use connectivity in MPA network design, without clear guidance on how to select between them. Using a combination of simulated seascapes and case studies of biophysical dispersal models, this chapter investigates the conditions under which certain approaches are more suitable over others.

Chapter 4 explores the implications of temporal variability of larval dispersal for MPA network performance. The magnitude and direction of larval dispersal can vary substantially over time (Catalano et al. 2021), and MPA networks containing complementary MPA components can buffer against this variability (Harrison et al. 2020). This chapter examines how the common practice of using time-averaged means of dispersal estimates in spatial prioritisation performs when dispersal is temporally variable and proposes methods to achieve more temporally consistent conservation benefits.

Chapter 5 presents the use of eDNA metabarcoding surveys to assess coral reef biodiversity for conservation planning. eDNA sampling is emerging as a promising tool for marine biodiversity monitoring and provides much greater information content compared to traditional methods. This chapter investigates how eDNA based assessments of coral reefs in the Wallacea region compare with traditional UVC methods and describes their use in identifying priority areas for management.

As we enter the post-2020 Global Biodiversity Framework and area-based conservation targets are raised to cover 30% of land and sea by 2030 (Ceccarelli et al. 2021), there is an opportunity to apply ecological principles and latest scientific understanding to maximise conservation and societal outcomes. To this end, the current thesis presents research and guidance around the use of information on larval dispersal in various steps of conservation planning and spatial prioritisation of MPA networks for the protection of tropical coral reef ecosystems.

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Chapter 2. Integrating larval connectivity into the marine conservation decision-making process across spatial scales

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Published in Conservation Biology

2.1. Abstract

Larval dispersal connectivity is typically integrated into spatial conservation decisions at regional or national scales, but implementing agencies struggle with translating these methods to local scales. Here, we demonstrate approaches to incorporate dispersal connectivity at both regional (hundreds of kms) and local (tens of kms) scales to design networks of no-take reserves in Southeast Sulawesi, Indonesia. We used Marxan with Connectivity to design marine reserve networks for four commercially important reef species across the region, and decision trees combining network-based connectivity metrics and habitat quality to design reserve boundaries locally. Priority areas for protection and expected benefits differed among species. As reef quality varied considerably across reefs, we highlight that reef degradation must inform the interpretation of larval dispersal patterns and the conservation benefits achievable from protecting reefs. Methods described here can be readily applied by conservation practitioners, in this region and elsewhere, to integrate connectivity data across multiple spatial scales.

2.2. Introduction

The exchange of larvae between subpopulations is a fundamental ecological process in many marine ecosystems (Almany et al. 2009). Recent technological advancements have popularised the adoption of larval connectivity into the design of no-take marine reserves (Magris et al. 2014), aiming to make metapopulations more resilient to localised disturbances (Almany et al. 2009) and to provide adjacent non-protected areas biodiversity and fishery benefits via spillover (Harrison et al. 2012). Methods to incorporate larval connectivity into reserve design range from complex mechanistic metapopulation models (Bode et al. 2016; Chollett et al. 2017) to simpler static optimisations using software such as Marxan (White et al. 2014; Beger et al. 2015; Daigle et al. 2020) to basic rule-of-thumb type guidelines (McCook et al. 2009) and decision trees (Smith & Metaxas, 2018). Despite this diversity, barriers remain for wider uptake by conservation practitioners working on less studied areas and species. Data availability, level of expertise, computational power, and specific stakeholder needs limit the suitability of certain approaches (Bode et al. 2016). Additionally, approaches tend to be limited to a single spatial scale (Cheok et al. 2020), with spatial prioritisation incorporating connectivity often used at regional scales (Beger et al. 2015) and rules-of-thumb such as reserve sizing used at smaller scales (Krueck et al. 2017). These barriers highlight the need for further guidance around integrating connectivity into conservation planning.

An ongoing challenge is how effects of spatial scale should be explicitly considered in reserve design (Cheok et al. 2020). Planning outcomes are affected by the different scales at which both human governance systems and larval dispersal processes operate (Huber et al. 2010). This issue is particularly relevant in tropical coral reef ecosystems, characterised by fragmented habitat patches hosting fish species with relatively sedentary adult stages (Almany et al. 2009) and larvae that can disperse tens of metres to tens or hundreds of kilometres (Green et al. 2015). Whilst conservation actions such as reserve establishment are often undertaken locally, reserve networks are most effective when designed regionally to account for dispersal (Mills et al. 2010). Consequently, multi-scale planning where governance and actions at different scales inform one another is required to improve conservation outcomes and minimise scale mismatches (Cheok et al. 2020).

A further challenge is that reefs vary from semi-pristine to highly deteriorated states depending on exposure to anthropogenic stressors (Norström et al. 2016). Larval dispersal models often make the simplifying assumption that larval production relates to habitat quantity, but not habitat quality, even though both influence reproductive output (Magris et al. 2016). Regional analyses using coarse data may fail to reflect the heterogeneity of the area, but considerable resources may otherwise be required to collect fine-resolution habitat quality data for a larger region (Mills et al. 2010). In many situations, designating sites based on habitat extent and quality can be more important than decisions based on measures of connectivity (Cabral et al. 2016). Tropical reefs generally require a high coral cover to support large fish populations that yield a large larval output (Wilson et al. 2010) regardless of protection status (Jones et al. 2004). To be effective, reserve network design must therefore concurrently consider connectivity and habitat quality at multiple spatial scales of significance.

Here, we integrate connectivity into marine spatial planning at regional and local scales to demonstrate a connectivity-based planning and consultation process of no-take reserve networks which took place in the province of Southeast Sulawesi, Indonesia. The conservation organization Rare's Fish Forever programme is establishing networks of marine reserves coupled with Managed Access Areas (MAAs) where local fishers are granted the exclusive right to fish. These are being designed for biodiversity protection and fishery benefits over 30 years with a focus on four commercially important fish species. Following an initial, assessment-based selection of a system of MAAs across the province, we used simple decision trees combining habitat quality data and measures of larval dispersal to help delineate reserve boundaries at the local, district scale (tens of kms). In the subsequent expansion of the reserve network at the regional, provincial scale (hundreds of kms), we used Marxan, a spatial prioritisation tool, to identify connected priority areas for protection. Methods were specifically chosen to be easily communicable in non-specialist, community consultations. We highlight the importance of integrating scale and habitat quality when using larval dispersal patterns in spatial prioritisations.

2.3. Methods

2.3.1. Planning region

The province of Southeast Sulawesi in central Indonesia is located in the heart of the Coral Triangle biodiversity hotspot (Figure 2.1.A). Following the Indonesian government's 2018 announcement to protect 30 million ha of marine area by 2030, there has been a provincial drive to designate additional marine areas as Managed Access Areas (MAA), inside of which smaller no-take marine reserves are established. Joint village management bodies are formed from joint-village fishing community groups and allocated co-management rights to manage MAA resources, developing a management plan with assistance from district governments.

Our objective was to develop proposals for expansion of a network of marine reserves across the province to place 20% of coral reefs under strict protection. Data on coral reef habitat occurrence was obtained from local habitat surveys (Suherfian 2020) and the publicly available, global coral reef datasets (UNEP-WCMC 2018). We did not consider other habitat types as our dispersal models described dispersal between reef patches, although other habitats such as mangroves and seagrasses in adjacent areas are important for ontogenetic development of reef species. Due to time and resource constraints, the entirety of 20% of reefs is not being protected at once, but instead through sequential expansion of reserves coupled with MAAs. The iterative workflow of local delineation of reserves followed by regional identification for reserve network expansion is repeated as long as the 20% target is not met (Figure 2.2.).

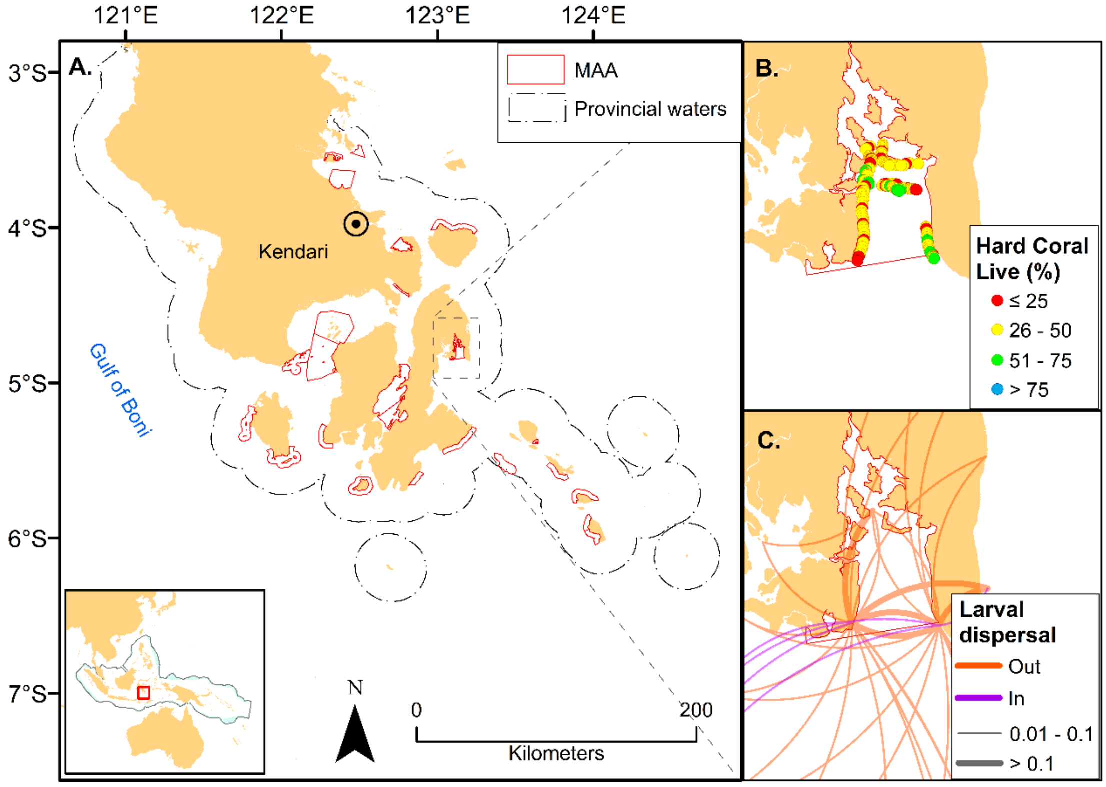
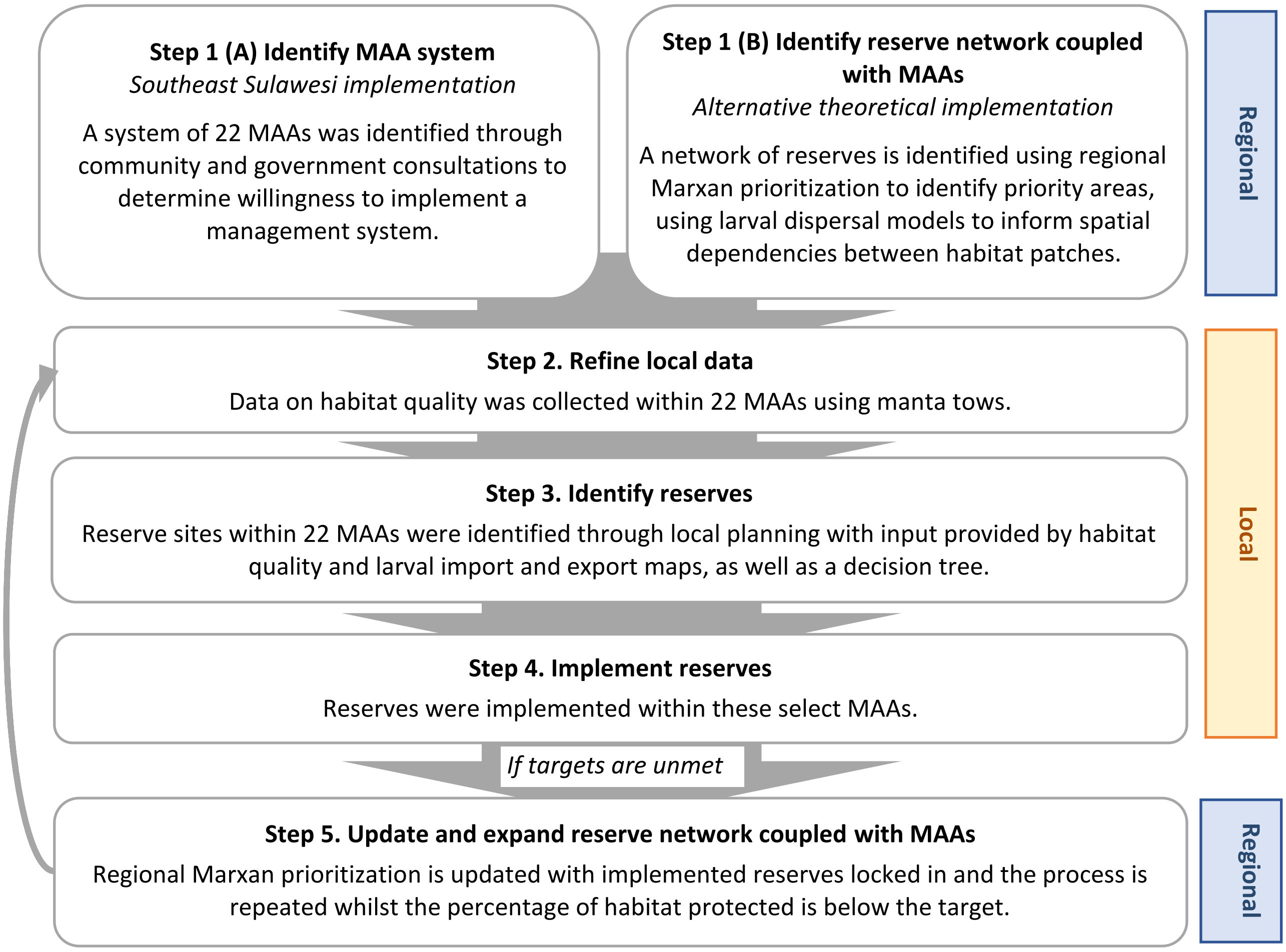


Figure 2.1. A. Map of the planning area of Southeast Sulawesi, Indonesia, showing provincial waters and the 22 Managed Access Areas (MAA) identified through government consultations. The inset shows the location of the province within the wider Coral Triangle region. B. An example of one of the MAAs, Kulisusu, with benthic data of habitat quality and C. incoming and outgoing coral trout larval connectivity as proportion of larvae arriving at a reef originating from a donor reef. Connections <0.01 have been omitted for ease of visualisation.

An initial system of 22 MAAs was established in 2019 through assessments with government partners and community inputs (Figure 2.2. Step 1A). Assessments involved broad baseline profiling of fisheries, local governance, and willingness of district government and communities to implement a management system, accompanied by behaviour campaigns to build stakeholder support and policy development. This was followed by no-take reserve delineation undertaken at the local scale, combining additional habitat quality data available only locally with measures of larval import and export (Figure 2.3.). Following reserve establishment within the 22 MAAs, we used Marxan with Connectivity to identify potential priority areas for expanding the reserve networks across the province.

The socio-political constraints in Southeast Sulawesi meant that initial MAA selection was carried out by first, identifying willing government and community partners. However, in other implementations of this two-scale process the initial selection of reserves may be carried out through regional conservation prioritisation (Figure 2.2. Step 1 B, Appendix 7.1.1.).



Step 1 (A) Identify MAA system
Southeast Sulawesi implementation
A system of 22 MAAs was identified through community and government consultations to determine willingness to implement a management system.

Step 1 (B) Identify reserve network coupled with MAAs
Alternative theoretical implementation
A network of reserves is identified using regional Marxan prioritization to identify priority areas, using larval dispersal models to inform spatial dependencies between habitat patches.

Step 2. Refine local data
Data on habitat quality was collected within 22 MAAs using manta tows.

Step 3. Identify reserves
Reserve sites within 22 MAAs were identified through local planning with input provided by habitat quality and larval import and export maps, as well as a decision tree.

Step 4. Implement reserves
Reserves were implemented within these select MAAs.

If targets are unmet

Step 5. Update and expand reserve network coupled with MAAs
Regional Marxan prioritization is updated with implemented reserves locked in and the process is repeated whilst the percentage of habitat protected is below the target.

Figure 2.2. Steps describing the iterative workflow to establish a network of marine reserves coupled with Managed Access Areas through combined regional and local planning processes.

2.3.2. Larval dispersal modelling

We modelled larval dispersal for the commercially important fishery species of coral trout (*Plectropomus leopardus*), emperor (*Lethrinus lentjan*), snapper (*Lutjanus malabaricus*), and rabbitfish (*Siganus canaliculatus*), using coupled biological-oceanographic models with a 500 m horizontal resolution, the highest resolution currently available for the region (Treml et al. 2012).

Species life history parameters were taken from literature using closest species and closest location where specific data was unavailable. Reef habitat was divided into 487 discrete patches ranging in size from 0.25 to 122.75 km^2 using natural clustering of habitat and geomorphological attributes of the coastlines. A nearest-neighbour and overwater distance algorithm was used for initial clustering of reef habitat within the model. In locations where these algorithms failed to identify unique reef patches, we used the underlying fine scale habitat maps to identify ecologically meaningful and geomorphologically appropriate patch boundaries. Patches were contiguous with a low outer boundary to area ratio. Patches were subsequently used as conservation planning units, the fundamental spatial management unit. Larval dispersal simulations were initiated from each reef patch in months when spawning occurs for each species to generate a matrix of inter-patch dispersal probability. Dispersal probability was scaled by the relative habitat amount in each patch to generate a larval flow matrix. The larval flow matrix was then converted to a migration matrix by dividing by column sums (Caswell 2014; Daigle et al. 2020) for use in local and regional planning steps (additional details in Appendix 7.1.2.).

2.3.3. Local reserve placement

The small number of planning units in each of the 22 MAAs precluded the use of software-driven spatial prioritisation for local decision support. Whilst smaller planning units could be used by downscaling the connectivity matrix (Beger et al. 2015), this would overstate data quality (Mills et al. 2010). Additionally, there are advantages to using planning units which follow habitat patch delineations (Nhancale & Smith, 2011). Instead, priority areas for reserve designation were identified through consensus-based workshops with stakeholders using maps of habitat quality and larval flow, as well as simple decision trees to qualitatively assess site desirability (Figure 2.3.).

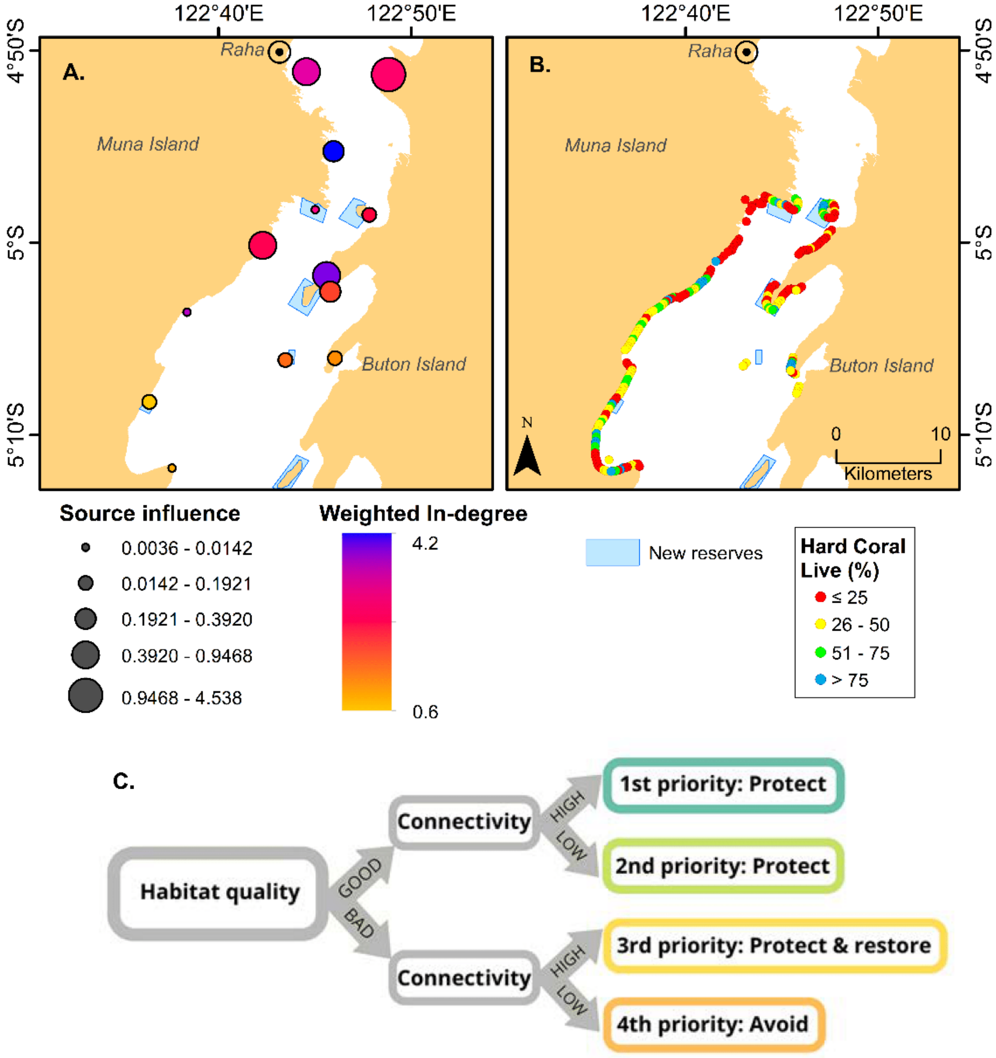


Figure 2.3. Inputs used in local decision-making. Map of Pasi Kolaga, one of the 22 managed access areas, showing A. coral trout larval import metric of weighted in-degree and export metric of source influence and B. percentage live hard coral cover from benthic surveys. Newly designated reserves following community consultations are shown in blue. C. Simple decision tree to rank the desirability of planning units within managed access areas for reserve designation. The first priority for reserve placement is areas of high quality reef and high import and/or export. High quality reefs with low connectivity are prioritised over areas of high connectivity and low quality. Reefs with low quality but high larval import and export may be options for protection if additional restorative management actions can be taken.

Habitat quality within MAAs was assessed using manta tow surveys (Figure 2.1.B, Figure 2.3.B). Trained snorkel divers were towed behind a boat and recorded benthic cover for 250-300 meter stretches, after which the boat stopped to give time for divers to record their quantitative assessment of substrate cover. Habitat quality was recorded in percentage as either live hard coral, dead hard coral, soft coral, macroalgae, rubble, rock, or sand over the towed distance. Surface personnel recorded the starting and ending coordinates of each tow. We incorporated additional habitat quality data for local decision-making, accounting for widespread reef degradation resulting from pervasive destructive fishing practices in the region (Burke et al. 2012).

Larval import was calculated as weighted in-degree (Opsahl et al. 2010) where

$$k_i^{in} = \sum_{j}^{N} x_{ji} \; for \; j \neq i \qquad \text{(Eqn. 2.1)}$$

$$s_i^{in} = \sum_{j}^{N} M_{ji} \; for \; j \neq i \qquad \text{(Eqn. 2.2)}$$

the in-degree k_i^{in} is the column sum of an adjacency matrix x and the sum of incoming weights s_i^{in} is the column sum of the migration matrix M. These were combined into weighted in-degree with an $\alpha = 0.5$ to balance the number of incoming connections with their weight, ensuring a diversity of larval sources for offsetting risks, using

$$C_{D-in}^{w\alpha}(i) = k_i^{in} \times \left(\frac{s_i^{in}}{k_i^{in}}\right)^{\alpha} \qquad \text{(Eqn. 2.3)}$$

Larval export was calculated as source influence (Roberts et al. 2020), a measure of export contribution of a patch to downstream patches, as the row sum of a migration matrix M where

$$SrcInf_i = \sum_{j}^{N} M_{ij} \; for \; j \neq i \qquad \text{(Eqn. 2.4)}$$

2.3.4. Integrated regional spatial prioritisation

We used Marxan with Connectivity as spatial dependencies (Beger et al. 2010) to identify reserve network expansion which included the reserves established in the 22 MAAs. The objective was to cover 20% of coral reef habitat and maximise larval flow between reserves. Marxan solves a minimum set problem of identifying efficient spatial reserve configurations which meet a target for habitat representation whilst minimising overall socioeconomic cost using the following objective function:

$$\overbrace{\sum_{PUs} Cost}^{a} + \overbrace{\sum_{ConValue} SPF \times \text{Penalty}}^{b} + \overbrace{\text{CSM} \sum_{PUs} Connectivity}^{c} = \begin{matrix}\text{Marxan}\\ \text{Score}\end{matrix} \qquad \text{(Eqn. 2.5)}$$

Each of the 487 planning units (*PUs*) contained a certain amount of coral reef conservation feature calculated from the regional data (UNEP-WCMC et al. 2018; Suherfian 2020) and was assigned planning unit size as a proxy for cost (Ardron et al. 2010). PUs are the potential sites or spatial management units which are either selected or not selected for protection in prioritisation solutions. As larger planning units contained more habitat area, the use of size as a proxy for cost ensured that solutions did not exclusively pick the biggest planning units. We did not incorporate fishery displacement as a cost layer given the unavailability of fishery data at the scale of the province. However, impacts on fishery were considered during local planning when stakeholders agreed on local reserve delineations. The objective function minimised the cumulative cost (Eqn. 2.5a) and the penalty associated with failing to protect conservation features (Eqn. 2.5b) weighed by a species penalty factor (*SPF*).

Dispersal connectivity was incorporated as an additional penalty to be minimised (Eqn. 2.5c), where a high penalty was incurred if only one of a pair of strongly connected planning units was selected (Beger et al. 2010). This Connectivity penalty replaced the traditional 'boundary.dat' file used in Marxan to describe physical boundary lengths between planning units to create spatially compact solutions. The connectivity weighting factor (*CSM*) weighed the penalty of missing connectivity against the other elements in the objective function and was calibrated such that cost of solutions was similar to baseline runs without connectivity. To create the Connectivity file we converted the larval migration matrix into a weighted edge list readable by Marxan. Reserves which were established in the 22 MAAs were locked in to solutions, and the spatial dependency component ensured that subsequently selected planning units were connected to established reserves, forming a functionally connected network (Beger et al. 2015; Daigle et al. 2020).

We assessed the potential benefits of reserve network configurations using discrete time, age-structured, single species metapopulation models to assess biomass change of the fish species over 30 years after reserve implementation assuming total compliance with no fishing inside reserves (Appendix 7.1.3. ; Garavelli et al. 2018). At each one year time step, settlers undergo density-dependent survival, and adults are exposed to natural and fishing mortality and produce eggs which are distributed across planning units following the larval dispersal probabilities. We did not adjust fishing mortality to account for displaced fishing adjacent to implemented reserves, assuming instead that fishing is constant across space. We compared the performance of reserve networks to a random selection of reserves to gauge the potential biomass increase achieved by incorporating connectivity in conservation planning. Reserves were implemented for 30 years after running models to equilibrium for 250 years, and biomass change was normalised so a baseline of 1 represented biomass before any reserve designation.

2.4. Results

2.4.1. Local reserve placement

The 22 MAAs ranged in size from 17 to 511 km^2, with individual areas containing between 2 and 14 larval dispersal planning units. Live coral cover varied between planning units, with roughly 50% of planning units containing <30% live hard coral, whilst 10% of planning units contained >50% live hard coral cover (Appendix 7.1.4.).

Consensus-based workshops with stakeholders were carried out by trained facilitators from the district government and supported by the Rare Indonesia team. Each meeting was attended by 20-30 participants representing the villages situated within the MAA, women from villages, and workers in various fishery-related roles in the community (e.g., fishers, buyers). Facilitators used the larval export and import map, manta tow map, and the decision tree tool to discuss where the community could agree to place the no-take reserves (Figure 2.3.). These scientific inputs were negotiated and traded off to achieve the best ecological result whilst accommodating community fishing practices. In general, the connectivity data was well-received by communities and used in the reserve design with socioeconomic factors complementing this decision-making, with habitat quality data used in combination with local understanding.

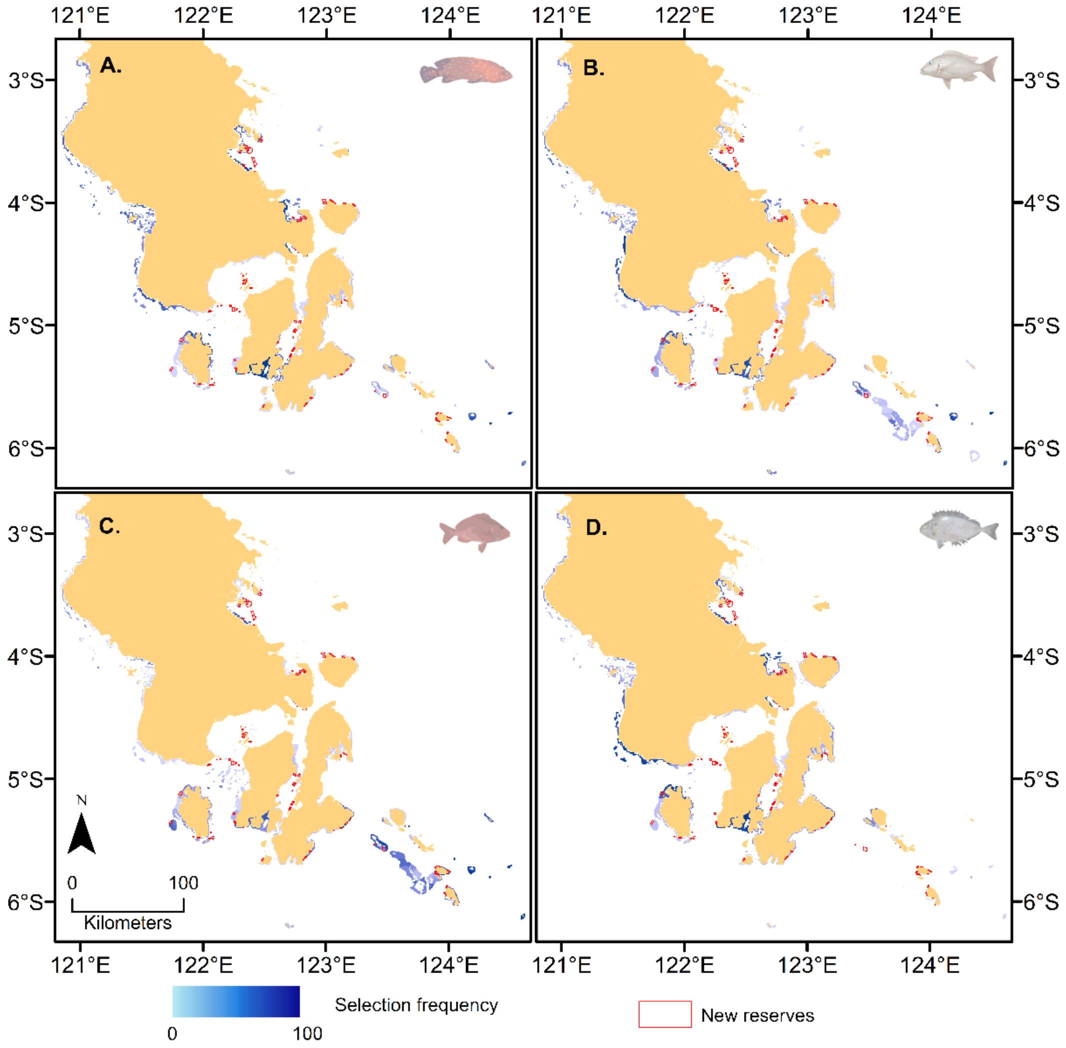


Figure 2.4. Maps showing the selection frequency of planning units when Marxan prioritization is run with the 89 new reserves established in November 2020 locked in for A. coral trout, B. emperor, C. snapper, and D. rabbitfish. Following stakeholder-driven selection of the 89 reserves with local inputs, Marxan regional prioritization identifies priority planning units for subsequent network expansion.

2.4.2. Integrated regional prioritisation

Following the community consultations for reserve delineation, 89 reserves were designated locally within the 22 MAAs by November 2020 protecting 59 km^2 of coral reef and reaching 15% of the regional habitat protection target (Figure 2.4.). A Marxan regional prioritisation was run with these reserves locked in (i.e., they are contained in all solutions), identifying potential areas for subsequent reserve network expansion to protect 20% of reef across the province (Figure 2.4.). These reserve networks generated greater expected benefits in biomass gain compared to a random selection of reserves for protection, with variation across species (Figure 2.5.). Removal of fishing pressure from designated planning units resulted in an immediate biomass increase within reserves and a delayed increase outside reserves during which the adult population in reserves built up, which increased larval export to non-reserves. Coral trout and emperor had greatest expected biomass increase, followed by snapper and rabbitfish. Certain runs of random selection achieved nearly similar benefits in

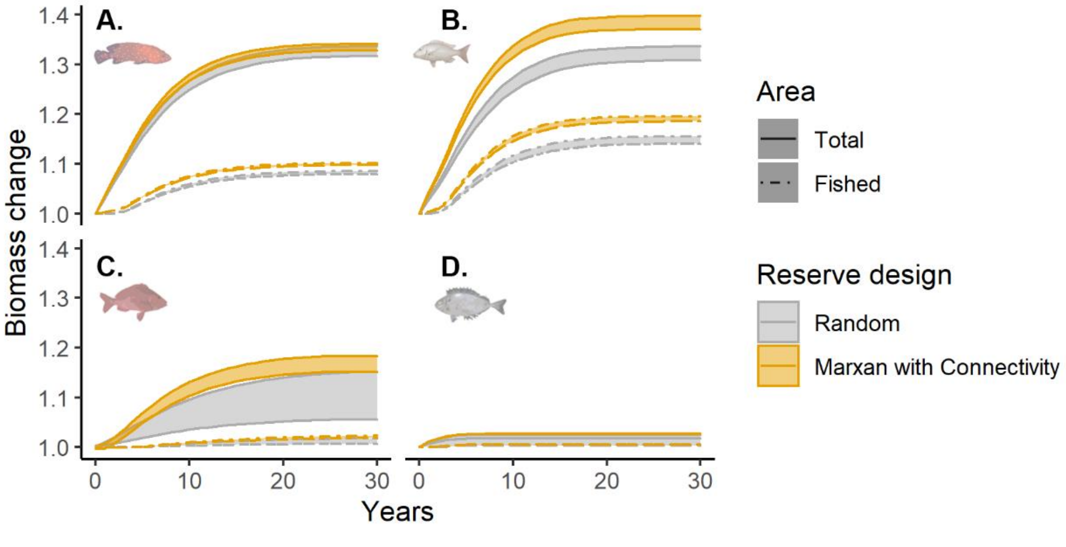


Figure 2.5. Biomass change across all planning units and in fished areas for the top five Marxan solutions of A. coral trout, B. emperor, C. snapper, and D. rabbitfish. Yellow lines show the performance of reserve networks designed from the stakeholder-driven selection of 89 reserves in the 22 MAAs and expanded to cover 20% of habitat using Marxan with Connectivity. Grey lines show results of randomly generated reserve systems having similar levels of protection.

three of the species. There was little overlap in the priority areas identified across different species, although certain locations around the south of Muna Island and north of the provincial capital Kendari were consistently selected with high selection frequencies (Appendix 7.1.5.).

2.5. Discussion

This study illustrates a two-pronged approach using larval dispersal patterns to inform both regional and local scale spatial planning during the sequential establishment of a reserve network. Where local planning may benefit from using high resolution data but result in a possible collection of disconnected reserves, regional planning is better able to create a functionally connected network based on lower resolution connectivity data (Mills et al. 2010). We integrated steps at these two spatial scales to combine the advantages of both. Local data and knowledge, including habitat quality, marine use conflicts, and traditional ecological knowledge (Drew, 2005) became available through local engagement. Engaging stakeholders in workshops allowed discussions on the relative importance of different areas for different marine uses. By directly involving stakeholders in reserve planning, better understanding and compliance with management interventions could be fostered, increasing the likelihood of management success (Sterling et al. 2017).

At the same time, local actions need to be viewed in a wider ecological context to recognise the interdependence of habitat patches through dispersal and the multiscale nature of conservation problems (Guerrero et al. 2013). By combining these local approaches with a regional network prioritisation, locally selected reserves were connected to a wider reserve network to maximise larval exchange. Metapopulation models verified that explicitly designed, connected networks generated greater potential benefits than randomly placed reserves (Figure 2.5.). By following an iterative workflow as presented here, reserve network configurations can be regularly updated as resources and willing implementing partners become available for expansion of protection. Regularly updating regional priorities as local actions are taken provides greater potential to capitalize on previously investigated areas, even if objectives are not necessarily achieved more rapidly (Cheok et al. 2018).

In contrast to many conservation projects using only data on habitat occurrence (Nolan et al. 2021), we additionally considered habitat condition. Larval dispersal is influenced by both (Magris et al. 2016), as highly degraded sites hosting smaller fish populations would not realise estimated dispersal strengths (Hock et al. 2017), unless restored. A high proportion of reefs in Southeast Sulawesi had low live hard coral cover, suggesting that connectivity may well be overestimated for these reefs. Given the importance of habitat quality data for connectivity over other data types (Berglund et al. 2012), we decided to collect data of where degraded reefs occurred. Manta tows provided an easy to perform method with large spatial coverage. Refining other data types, such as improving the cost information by collecting socioeconomic data across the province was cost prohibitive. Refining dispersal modelling to a finer resolution was also not feasible, as even finer resolution would require higher resolution data (bathymetry, life history parameters, currents, tidal forcing) and specific expertise—few or no conservation projects would have access to these resources.

As it was logistically unfeasible to collect data on reef quality for the entire province, habitat quality could not be used to adjust potential contributions of habitat patches to regional connectivity as in other studies (Magris et al. 2016). Ideally, use of fine-scale biodiversity data is preferable at all scales of conservation planning due to its higher information content and precision (Hermoso & Kennard 2012), especially in heterogenous or disturbed environments (Rouget 2003). Regional analyses using coarse data risk underestimating site irreplaceability (Rouget 2003) and increase uncertainty regarding species occurrences and the success of conservation actions (Hermoso & Kennard 2012). Additionally, the importance of conservation features can be apparent at one scale but missed at another (Huber et al. 2010). However, given the trade-off between resource-intensive data collection and other steps in conservation planning, the two-scale approach we describe here provides one possible solution to this issue by limiting data collection to a subset of selected areas.

Using connectivity in Marxan requires certain simplifying assumptions, for example that connectivity is static and unchanging. However, temporal variability and state of the reef system can dramatically change the importance of individual reefs in network-wide connectivity (Boschetti et al. 2020). Temporal variability of larval flow may also be substantial, and consistency in larval supply among and from reserves is likely to be desirable (Harrison et al. 2020). Our Marxan prioritisation used the mean larval connectivity over a 20-year period, but whether using such a mean achieves temporal stability will need to be explored in future research. We chose not to communicate this additional complexity in community consultations as we did not quantify the variability in expected reserve benefits. Whilst Marxan only accepts static connectivity information, more complex implementations may become possible in the future.

A core assumption behind the decision tree used in local planning is that reefs with higher live coral cover are more desirable for reserve designation than deteriorated sites. A counterargument promulgates that in certain contexts, greater net conservation benefits are achieved by protecting higher risk sites if reserves accelerate post-disturbance habitat recovery (Game et al. 2008). However, this presupposes that the region is generally non-degraded to begin with and that lower risk sites will not deteriorate substantially in the short-term. In Southeast Sulawesi where large tracts of reefs are rubble fields and the remaining area of high coral cover reefs is low, this does not hold true. Moreover, whilst moderately impacted sites may be candidates for restorative conservation actions, such actions have high implementation costs making widespread adoption difficult (Vercammen et al. 2019).

The methods described here can be applied to other countries with some caveats. Public data repositories (UNEP-WCMC 2018) may contain errors and require ground-truthing. Additionally, parameters may be unavailable for the species of interest, and variability in life history parameters has a strong influence on dispersal outcomes (Treml et al. 2015). Although we accounted for this by using best available data for the relevant species, it is likely that unquantified variability remains and therefore, uncertainty in our modelling output. For these reasons decision-making should be realistic about uncertainty (Milner-Gulland & Shea 2017), using outputs within a larger decision-making process informed by many data sources. Where larval dispersal modelling is not available, local scale habitat quality should nonetheless be used to inform decisions.

Preliminary discussions with stakeholders in Southeast Sulawesi highlighted the need for methods that could be easily communicated and understood in community consultations. Considering this, we chose the openly accessible and transparent decision support tool

Marxan and simple import and export metrics, instead of more conceptually abstract metrics (Daigle et al. 2020). Stakeholder buy-in and community adherence may diminish if practitioners are unable to understand and effectively communicate methods used (Arias 2015), requiring a balance between complexity and practicality.

A growing body of evidence demonstrates how connectivity can inform reserve network design (Beger et al. 2010; Bode et al. 2016; Chollett et al. 2017; D'Aloia et al. 2017; Magris et al. 2014; Smith & Metaxas, 2018; White et al. 2014) and the importance of connectivity to support biodiversity persistence and sustainable fisheries (Fontoura et al. 2022). To promote wider uptake, this study demonstrates that effective conservation approaches can be centred on local stakeholder needs. The approach described was designed to inform community-based decision-making processes combining methods at two spatial scales using straightforward concepts. Our implementation was successful in fostering community buy-in and stakeholder participation and is predicted to generate positive conservation and fisheries benefits.

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Chapter 3. Comparing spatial conservation prioritisation methods using site-versus linkage-based connectivity

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Published in Conservation Biology

3.1. Abstract

Larval dispersal is an important component of marine reserve networks. Two conceptually different approaches to incorporate dispersal connectivity into spatial planning of these networks exist, with an open question as to when either would be most appropriate. Candidate reserve sites can be selected individually based on local properties of connectivity, or with a spatial dependency-based approach of selecting clusters of strongly connected habitat patches. The first acts upon individual sites, whilst the second acts upon linked pairs of sites. We used a combination of larval dispersal simulations representing different seascapes and case studies of biophysical larval dispersal models in the Coral Triangle region and the province of Southeast Sulawesi, Indonesia, to compare the performance of these two methods in the spatial planning software Marxan. We explored the reserve design performance implications of different dispersal distances and patterns, based on the equilibrium settlement of larvae in protected and unprotected areas. We further assessed different assumptions about metapopulation contributions of unprotected areas, including a worst-case scorched earth of 100% depletion and more moderate scenarios. Our results suggest that the spatial dependency method is suitable when dispersal is limited, a high proportion of the area of interest is substantially degraded, or the target amount of habitat protected is low. Conversely, if subpopulations are well-connected, the scorched earth assumption is relaxed, or more habitat is protected, protecting individual sites scoring highly in metrics of connectivity is a better strategy. Spatial dependency methods generally produced more spatially clustered solutions with more benefits inside than outside reserves compared to site-based methods. Therefore, spatial dependency methods potentially provide better results for ecological persistence objectives over enhancing fisheries objectives, and vice versa. Different spatial prioritisation methods of using connectivity are appropriate for different contexts, depending on dispersal characteristics, unprotected area contributions, habitat protection targets, and specific management objectives.

3.2. Introduction

Ecological connectivity refers to the movement of energy and matter across realms, consisting of both biological and physical processes (Beger et al. 2010a). Here, we focus on the component of larval dispersal connectivity, defined as the movement of larvae between spatially fragmented habitats, a key element in designing successful marine reserve systems (Magris et al. 2014; Álvarez-Romero et al. 2018; Balbar & Metaxas 2019). As many marine life histories involve a mobile pelagic larval and relatively sedentary adult stage (Cowen & Sponaugle 2009), ecologically relevant larval dispersal needs to be sustained between protected marine habitats for long-term population persistence (Andrello et al. 2015; Schill et al. 2015; Engelhard et al. 2017). Metapopulations have greater stability when connective pathways permit rescue effects of new colonists following local disturbances (Schnell et al. 2013), whilst more broadly, gene flow can reduce the chance of patch extinctions resulting from genetic drift or inbreeding (Almany et al. 2009). Unlike structural connectivity, which is determined only by habitat distributions, larval dispersal is a form of functional connectivity which relates species-specific responses to these structures.

Networks of well-connected marine reserves are routinely designed using spatial conservation prioritisation techniques, a biogeographic-economic analysis in which conservation actions are allocated to important areas for biodiversity (Kukkala & Moilanen 2013). Spatial data is collected across a planning region of important conservation features, such as species, habitats, or ecosystem services, and of socioeconomic variables, such as opportunity cost or acquisition cost (Ban & Klein 2009). Algorithms are then used to identify efficient reserve systems that minimise cost whilst maximising the amount of biodiversity features allocated for protection (Margules & Pressey 2000). In early implementations, connectivity was incorporated via generic guidelines (McCook et al. 2009), such as setting minimum reserve sizes (Green et al. 2009) or determining optimal reserve spacing (Moffitt et al. 2011). Various reserve design software also provided functionalities to create spatially compact reserves by minimising the ratio of outer boundary edge length to area (Game et al. 2008; Lehtomäki & Moilanen 2013), which may help protect movements between physically adjacent habitat patches, e.g., through ontogenetic migration (Edwards et al. 2010). However, as advances were made in genetic, hydrodynamic, and ecological methods, allowing quantitative measurements and simulations of connectivity between subpopulations (White et al. 2019), more sophisticated approaches were developed to incorporate this new data.

There are three broad ways by which larval connectivity can be incorporated in spatial conservation prioritisation tools for biodiversity protection (Daigle et al. 2020). In the first method (hereafter called the spatial dependency method), a measure of connectivity between all pairwise adjacent and non-adjacent habitat patches creates a penalty for protecting only one of a pair of strongly connected patches (Beger et al. 2010b). In the second (hereafter called the connectivity-based features method), metrics describing properties of connectivity are calculated for each habitat patch and given targets (White et al. 2014b; Magris et al. 2016). Both these approaches are applied to represent larval connectivity alongside conventional features such as species abundance and cost, whilst giving the user a degree of control over the relative weighting of different components (White et al. 2014b; Beger et al. 2015; Magris et al. 2016). In the third approach, the cost layer to be minimised is replaced by an inverse measure of connectivity (Krueck et al. 2017; Weeks 2017). As this final method precludes the use of real socioeconomic costs and limits the applicability for real-world planning, we consider it as a distinct application and focus on the former two from hereon (Figure 3.1.).

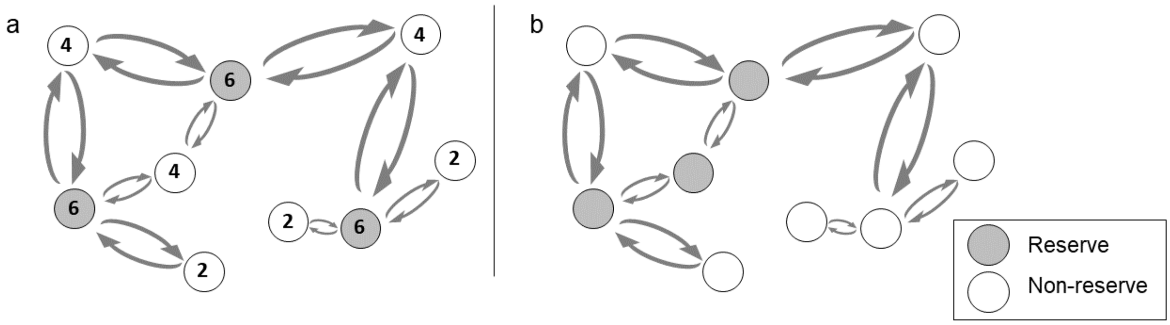

Figure 3.1. Conceptual representation of a network of reefs (circles) connected by incoming and outgoing larval dispersal (arrows). (a) Example of the connectivity-based features method where reefs having the highest degree (values inside circles), defined as the cumulative number of incoming and outgoing connections, are selected in solutions. (b) Example of the spatial dependency method selecting a cluster of strongly connected reefs.

The spatial dependency and connectivity-based features methods take two conceptually different approaches to connectivity, with implications for their applicability in certain contexts. The former selects clusters of multiple, highly connected sites at a time, using strength of connection between pairwise sites to identify important linkages to protect (Beger et al. 2010b). This is a potentially better strategy in a worst-case ‘scorched earth’ scenario where unprotected areas are highly degraded with no larval output (Edwards et al. 2010). If persistence of individual subpopulations depends on larval supply from outside sources, then protecting upstream sources and downstream destinations together can help ensure sufficient larval exchange to avoid localised collapses. In contrast, the latter takes a ‘site-based’ approach where individual high-ranking sites are selected for reserve designation based on local properties of connectivity. As this does not guarantee protection of upstream larval sources supplying these sites, the supply of incoming larvae may be severely reduced under a scorched earth scenario (Figure 3.1.; White et al. 2014b). A cursory comparison of the two in the northern Californian coast revealed that the connectivity-based features method generally achieved greater total population biomass, except for species with relatively widespread larval dispersal where performance was similar (White et al. 2014b). The Californian boundary current system has linear, relatively simple oceanographic patterns that result in directional flow of larvae along the coastline. However, optimal strategies for reserve site configurations may differ under more complex dispersal patterns (Kininmonth et al. 2011). Additionally, assumptions about contributions of non-reserves to the wider metapopulation matter. Most unprotected patches contribute to overall larval supply, but worst-case assumptions are often made (Hastings & Botsford 2003; Edwards et al. 2010; Mumby et al. 2011; Cabral et al. 2016).

Here, we compared the spatial dependency and connectivity-based features methods to incorporate larval connectivity in the conservation planning software Marxan (Ball et al. 2009). We compared the performance of these two approaches under alternative assumptions about larval dispersal patterns and metapopulation contributions of unprotected sites. Reserve networks were designed for a number of representative simulated seascapes and two case studies in the Coral Triangle region and the province of Southeast Sulawesi, Indonesia. Different spatial reserve configurations were assessed by calculating equilibrium settlement inside and outside reserves as an approximate proxy for conservation and fishery benefits, respectively. To help inform the feasibility of implementing different methods, we also evaluated the degree of spatial clustering of reserve networks. Our findings are intended to help researchers incorporate connectivity data into reserve network design. Whilst our assessment is based on marine systems, our findings are relevant to terrestrial landscapes and reserve design as well.

3.3. Methods

3.3.1. Simulated seascapes

To test the spatial dependency and connectivity-based features methods on a range of different larval dispersal conditions, we created a graph-theoretic seascape representation where nodes represent habitat patches and weighted edges connecting nodes give the probability of dispersal between patches. Graph theory is increasingly used in marine spatial planning and connectivity research due to its minimal data requirements and efficient algorithms (Minor & Urban 2007; Moilanen 2011; Ospina-Alvarez et al. 2020). Similarly, graph theory has informed planning for connectivity in coral reef ecosystems (Treml et al. 2008; Kininmonth et al. 2011; Magris et al. 2016).

Patches of equal size (N = 100) were randomly placed in two-dimensional cartesian space (dimensions 5000 x 5000). An Euclidean distance matrix D_{ij} giving interpatch distance was passed through the function $P_{ij} = e^{-1/\theta \times D_{ij}}$ to obtain the probability of dispersal from patch i to j assuming a negative exponential larval dispersal kernel (Urban & Keitt 2001). We tested a range of values for the exponential decay rate parameter (θ) which gives the mean dispersal distance, from 50 to 250 by intervals of 50 chosen from a preliminary set of runs. Connections smaller than 1e-6 were removed, such that networks were not fully connected. Local retention, the probability of larvae originating from a patch retained in that same patch, was assigned values similar to dispersal to close neighbouring patches.

In this basic near neighbour seascape pattern, connections were strongest between close neighbours and weakened with increasing distance. However, in some marine environments, strong currents may carry larvae over long distances and increase the probability of dispersal to distant habitat patches (Bode et al. 2006). These long-distance connections can form a ‘small world’ network whereby any two distant habitat patches are connected by relatively few steps (Watts & Strogatz 1998), a pattern which has been observed in the Great Barrier Reef (Kininmonth et al. 2010). To examine the effects of these patterns, we simulated a second seascape with small-world links where a certain proportion of edges were randomly rewired to create new dispersal pathways which had high probabilities over long distances.

As each iteration of seascape generation involved random patch placement, 100 replications were generated for each of the ten different configurations (five mean dispersal distances and two patterns of near neighbour and small-world links), to avoid potential artifacts and analyse average reserve design method performance for all different seascape scenarios. All seascapes were generated using the *igraph* package (Csárdi & Nepusz 2006) in R (R Core Team 2021).

3.3.2. Case studies: Coral Triangle region and Southeast Sulawesi, Indonesia

In addition to the simulated seascapes, we compared the two methods of incorporating connectivity using two case studies for which we had coupled biophysical models describing larval dispersal of different marine species over different spatial scales (Figure 3.2.; Figure S7.2.1.). In contrast to the simulated seascapes, these dispersal models quantified asymmetric flow between patches based on realistic currents and larval traits, mortality in the pelagic stage, and complex spatial distribution of habitat patches.

Model outputs were available for larval dispersal of coral trout (*Plectropomus leopardus*) and a sea cucumber (*Holothuria whitmaei*) for the Coral Triangle region (Beger et al. 2015). The dispersal models simulated larval transport from 425 reef patches by advection and diffusion in surface ocean currents with larval biological traits and larval behaviour obtained from literature. Maximum pelagic larval duration of these two species were 35 days and 15 days, respectively. Models were also available for the commercially important fishery species of mud crab (*Scylla serrata*) and rabbitfish (*Siganus canaliculatus*) for the province of Southeast Sulawesi, Indonesia. Larval dispersal was modelled for 487 reef patches for rabbitfish and 216 mangrove patches for mud crab with life history parameters taken from literature (Table S7.2.1.). Maximum pelagic larval duration of these two species were 38 days and 19 days, respectively.

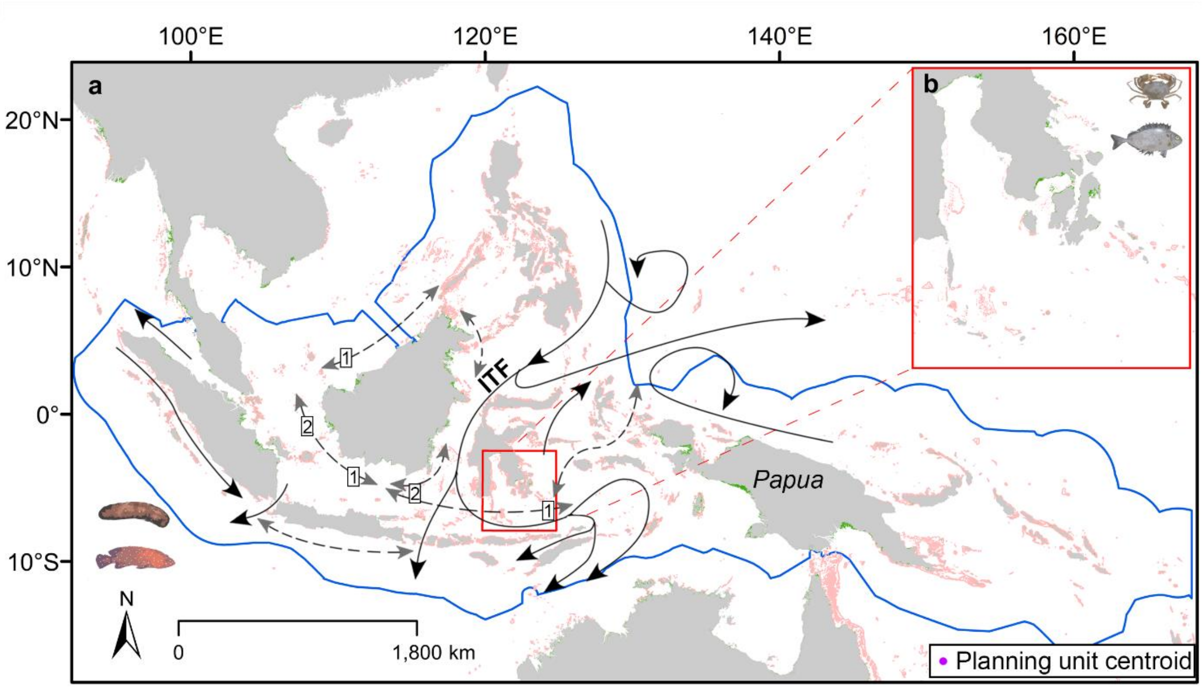

Figure 3.2. Map of the two case studies with (a) the Coral Triangle region (blue) with larval dispersal models for coral trout and sea cucumber and (b) the province of Southeast Sulawesi, Indonesia (red) with larval dispersal models for rabbitfish and mud crab. Solid arrows indicate permanent, major ocean currents including the Indonesian Throughflow (ITF). Dashed arrows indicate dominant current direction during the southwest monsoon (1; November-February) and northeast-monsoon (2; May-August; currents adapted from van der Ven et al. 2021). Reef habitat is shown in pink and mangroves in green.

3.3.3. Marxan prioritisation

Habitat patches were used as spatial planning units and assigned the same, uniform habitat area and cost to eliminate the effects of these components on solutions, ensuring that any differences could be solely attributed to the method by which Marxan used connectivity. We ran a range of protection targets from 5-30% of the habitat feature by 5% increments. Marxan runs were first performed without any connectivity to establish a baseline of effectiveness which may incidentally be capturing some amount of connectivity, followed by runs using the spatial dependency method (Beger et al. 2010b) and the connectivity-based features method (White et al. 2014). Following standard practice (Game et al. 2008), we used 100 Marxan repeat runs for each uniquely generated seascape or species to account for flexibility in solutions generated by the simulated annealing algorithm. We then chose the top ten solutions given by the lowest Marxan score to assess performance of methods.

The spatial dependency method was implemented following Beger et al. (2010b) by replacing the physical boundary file in Marxan with an edge list of interpatch larval dispersal probabilities. The value of the connectivity strength modifier, a parameter which weighs the connectivity component against the cost and biodiversity targets in the objective function, was set as the maximum possible value whilst keeping total costs similar to baseline runs without connectivity.

The connectivity-based features method was implemented following White et al. (2014) by calculating a number of patch-specific metrics of connectivity used in previous studies (Table 3.1.; Jacobi & Jonsson 2011; Magris et al. 2015, 2016; Schill et al. 2015; Roberts et al. 2020). Metrics were converted into quartiles to create discrete conservation features (Daigle et al. 2020), and targets were set at the highest possible value whilst keeping costs similar to baseline runs. As the simulated seascapes had symmetric dispersal, the metrics for incoming and outgoing degree and flow were identical and combined into 'Flow' and 'Degree'.

3.3.4. Assessment of protected area networks

We compared the effectiveness of different spatial reserve solutions by applying the dispersal-per-recruit-model implemented in the R package *ConnMatTools* (Kaplan et al. 2017) to calculate equilibrium settlement inside and outside reserves as well as cumulatively across the total system. This model is a simplified discrete-time metapopulation model assuming sedentary adults, dispersive larvae, and a density-dependent settler-recruit relationship, relevant for many benthic invertebrates and reef fishes (Kaplan et al. 2006). All habitat patches were initially saturated at the maximum recruitment carrying capacity, and the consequent equilibrium settlement at each patch was calculated by dispersing larvae according to interpatch dispersal probability (Kaplan et al. 2006). We used a hockey-stick settler-recruit relationship which increases linearly until a maximum is reached (Barrowman & Myers 2000) with the slope at low egg production chosen to correspond to 35% of natural egg production (White, 2010), a threshold for persistence commonly assumed in fishery management (Kaplan et al. 2006).

Table 3.1. Summary of graph-theoretic metrics used in the site-based connectivity-based features method in Marxan.

Name	Description
Betweenness centrality	A measure of the number of shortest paths across the network that pass through a patch (Minor & Urban 2007). This metric can highlight important stepping-stones in a network.
Eigenvector centrality	A measure of the contribution of a patch to the growth rate of a linear metapopulation, calculated using both number and strength of connections (D'Aloia et al. 2017).
Google PageRank	Similar to eigenvector centrality, measures the importance of a patch in the wider network using both the number and local density of connections (Kininmonth et al. 2019). Originally derived from internet web pages ranking, it has also been used to assess species extinction risk (Allesina & Pascual 2009).
Local retention	A measure of how self-sustaining a patch is, calculated as the proportion of individuals originating from a patch that are retained within that patch (Burgess et al. 2014).
In- Out-degree	The number of connections whilst ignoring connection strengths, measuring the involvement of the node in the network (Opsahl et al. 2010). This can be divided further into in-degree and out-degree for incoming and outgoing connections, describing properties of 'sink-ness' and 'source-ness', respectively, .
In- Out-flow	The cumulative weight of incoming and outgoing connections from a habitat patch to neighbouring patches (Urban & Keitt 2001). This can be divided further into in-flow and out-flow for incoming and outgoing connections, describing properties of 'sink-ness' and 'source-ness', respectively.

The parameter of lifetime egg production (LEP) in the dispersal-per-recruit model, which gives the relative reproductive output of habitat patches, was set as 1 for reserves and either 0, 0.25, 0.5, or 0.75 for non-reserves. This represents a range of assumptions regarding non-reserve contribution: a worst-case scorched earth condition of 100% reduction (LEP = 0) where non-reserves were highly degraded or overexploited and made no contribution, to more benign scenarios of 75%, 50%, and 25% reduction.

We used Bayesian linear models implemented in the R package *rstanarm* (Goodrich et al. 2020) to quantify the fixed effects of the Marxan connectivity method on reserve system performance. Bayesian tests are considered more appropriate for analysing simulation model results, given that p-values in frequentist statistical hypothesis tests can be artificially decreased as greater computational power permits a larger sample size of simulations (White et al. 2014a). We chose the median of the posterior distribution to represent a point-estimate of effects and calculated 89% credible intervals based on highest density interval using the R package *bayestestR* (Makowski et al. 2019).

3.4. Results

3.4.1. Simulated seascapes

Mean dispersal distance, pattern of dispersal, and conditions outside reserves were found to influence the performance of reserve networks designed using different Marxan methods (Figure 3.3.). In the near neighbour pattern where dispersal probability declined exponentially with increasing distance, more methods performed similarly well if non-reserves were less degraded (LEP = 0.75). Spatial dependency tended to perform better under worse assumptions (LEP = 0 and 0.25) or at lower mean dispersal distances, whilst the converse was true for connectivity-based features methods. Of all metrics, protecting patches which scored highly in Google PageRank performed well most often, although eigenvector centrality also performed well for seascapes with high mean dispersal distances. In the small-world links pattern where strong dispersal events were emulated between distant patches, spatial dependency performed comparatively worse, only performing well when either very little habitat was protected (5%) or for seascapes having lower mean dispersal distances. Protecting patches with high Google PageRank performed well for all combinations of habitat protection and non-reserve contributions, whilst eigenvector centrality and flow also performed well for seascapes having higher and lower dispersal distances, respectively.

In general, the gain in conservation benefits from incorporating connectivity compared to baseline scenarios were higher when non-reserves were more degraded (Figure S7.2.2. & Figure S7.2.3.). Under scorched earth assumptions (LEP = 0), the best connectivity method produced up to a 30-fold higher total equilibrium settlement compared to baseline runs using no connectivity, whereas this difference was only 1.3-fold in the most benign assumption (LEP

= 0.75). There were also differences in the relative proportion of equilibrium settlement inside versus outside reserves depending on which method was used (Figure S7.2.2. & Figure S7.2.3.). If non-reserves made little or no larval contributions (LEP = 0 and 0.25), spatial dependency methods generally produced reserve networks with a greater proportion of settlement inside than outside reserves compared to connectivity-based features methods, even when cumulative settlement was similar between the two. However, under more benign assumptions (LEP = 0.5 and 0.75) the relative proportion inside and outside reserves was similar across methods.

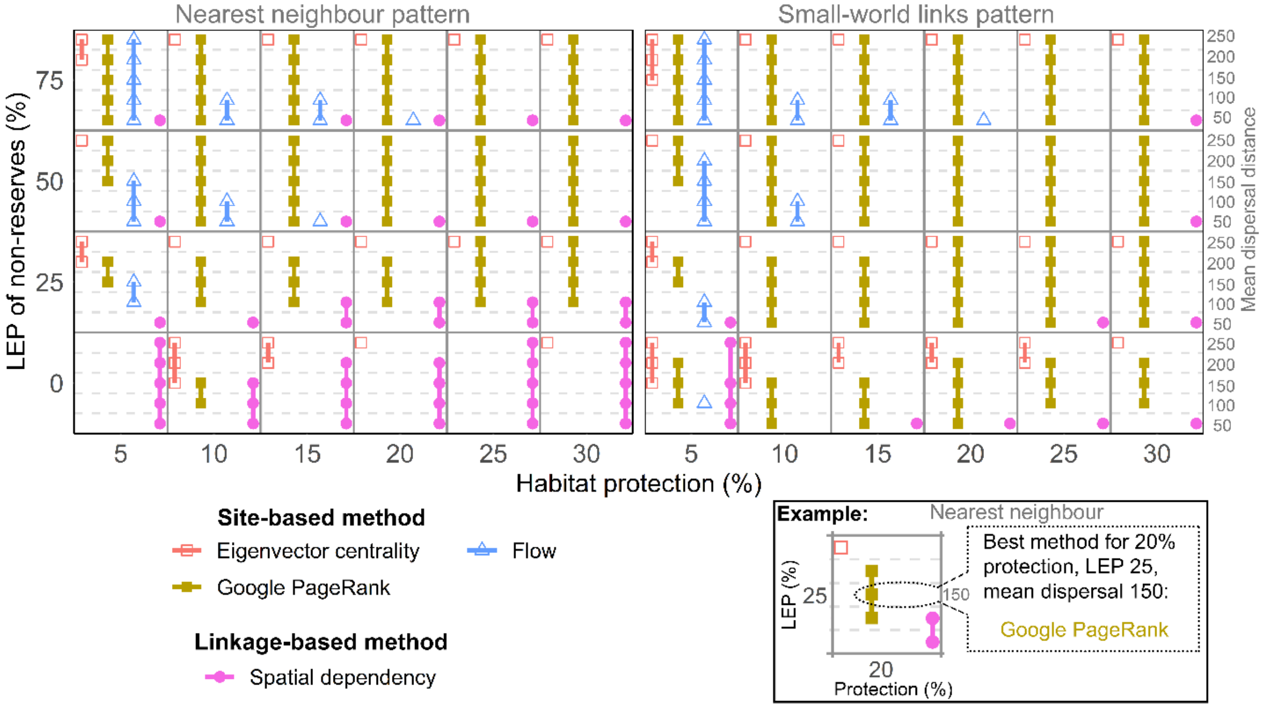

Figure 3.3. Marxan methods achieving highest total equilibrium settlement in simulated seascapes. Each cell is a different combination of habitat target and lifetime egg production (LEP) assumption. In each cell, the position of the point indicates for which of the five dispersal distances (50, 100, 150, 200, 250) the method performed best, with lowest dispersal at the bottom and greatest dispersal at the top. Where multiple symbols occur in a row these methods performed equally well. A worst-case, scorched earth assumption outside reserves is given by LEP = 0.

3.4.2. Case studies: Coral Triangle and Southeast Sulawesi, Indonesia

The two case studies corroborated the observation from simulated seascapes that the spatial dependency method performed comparatively better when non-reserves made little or no larval contributions or the total amount of habitat protected was low (Figure 3.4.). For coral trout and sea cucumber in the Coral Triangle region under a scorched earth scenario, reserve networks designed with the spatial dependency method achieved highest equilibrium settlement. As the amount of habitat protected increased or assumptions were relaxed (LEP = 0.25, 0.5, and 0.75), connectivity-based features methods performed equally well or better. Protecting patches scoring highly in Google PageRank consistently achieved good outcomes, whilst in-flow, local retention, and eigenvector centrality occasionally performed equally well. Outcomes for the Southeast Sulawesi case study were markedly different. Here, the connectivity-based features method with targets set for local retention achieved greatest equilibrium settlement compared to all other methods, with in-flow, Google PageRank, and spatial dependency occasionally performing equally well for certain habitat targets and non-reserve assumptions.

As in the simulated seascapes, the performance gain from incorporating connectivity was lower when non-reserves were less degraded and made higher contributions. The relative proportion of settlement inside and outside reserves in the case studies also showed similar trends to the simulated seascapes (Figure S7.2.4.). Spatial dependency produced higher proportions inside reserves compared to connectivity-based features methods, particularly when non-reserves made little or no contributions. However, this trend was more evident in the Coral Triangle species than the Southeast Sulawesi species.

The degree to which reserve solutions were spatially clustered differed depending on which method was used (Figure S7.2.5. – Figure S7.2.8.). As expected, the spatial dependency method tended to create clusters of reserves concentrated in certain parts of the region, although more than one distinct cluster could be selected if habitat targets were sufficiently high. For example, two spatially distinct clusters of reserves were identified for coral trout if 20% of habitat was protected (Figure S7.2.5.), explained by the presence of two succinct subnetworks within the eastern and western parts of the Coral Triangle region, with little larval flow past the island of Papua. Use of certain metrics including eigenvector centrality, in-degree, and out-degree also created more spatially clustered solutions. In contrast, use of other metrics resulted in individual reserves being more evenly distributed across the region.

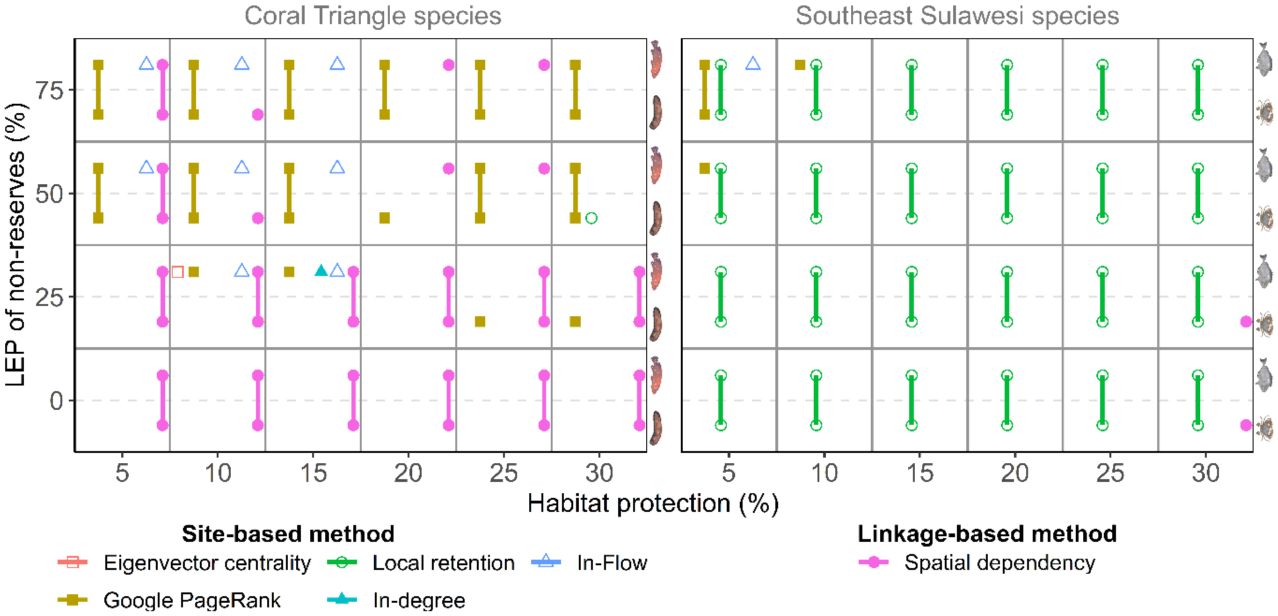

Figure 3.4. Marxan methods achieving highest total equilibrium settlement in the two case studies. Each cell is a different combination of habitat target and lifetime egg production (LEP) assumption. In each cell, the position of the point indicates for which of the two species the method performed best, with coral trout and rabbitfish at the top and sea cucumber and mud crab at the bottom. Where multiple symbols occur in a row these methods performed equally well. A worst-case, scorched earth assumption outside reserves is given by lifetime egg production LEP = 0.

To understand why setting targets for local retention performed substantially better in the Southeast Sulawesi species compared to the Coral Triangle species (Figure 3.4.), we investigated the distribution of local retention of habitat patches and the effect on within patch equilibrium settlement (Figure S7.2.9.). The Coral Triangle species showed a left-skewed distribution of local retention with many patches retaining a high proportion of larvae, whilst the inverse was observed in the Southeast Sulawesi species where most patches retained few larvae and only a small number of patches had high retention (Figure S7.2.9.a, c, e, g). The consequence of this relationship was that Marxan selected all the best patches for retention with highest pre-reserve settlement in both regions. Remaining sites had very low retention and significantly lower pre-reserve settlement in Southeast Sulawesi (Figure S7.2.9.f, h), but had higher retention and similar or greater pre-reserve settlement in the Coral Triangle (Figure S7.2.9.b, d).

3.5. Discussion

Using a combination of simulated seascapes and case studies, we explored how spatial dependency and site-based methods of incorporating connectivity in the spatial conservation prioritisation tool Marxan compared under a range of alternative seascape patterns and assumptions. Our results showed that there was no single method which consistently performed best. Assumptions about metapopulation contributions of unprotected areas, larval dispersal ability, and the proportion of habitat protected determined how well either method performed. In general, spatial dependency performed better when dispersal distance was limited, a high proportion of the area of interest was substantially degraded, or the target amount of habitat protected was low. Instead, the connectivity-based features method achieved higher equilibrium settlement when dispersal was greater, areas were less degraded, or more habitat was protected. However, choice of method will also depend on whether management objectives are focussed more on prioritising settlement within reserves to rebuild populations that are severely depleted or on prioritising settlement outside reserves to support fisheries, and whether spatial clustering of reserves is a desirable characteristic. The spatial dependency-based methods created more spatially clustered solutions and generally produced more benefits inside reserves, with a trade-off of benefits outside reserves, as compared to the site-based methods.

As expected, a key determinant in performance of methods was the assumption regarding the contribution of non-reserves. In classical reserve theory and conservation planning, a conservative scorched earth assumption is often taken where larvae from non-reserves make no contribution (Hastings & Botsford 2003; Edwards et al. 2010; Mumby et al. 2011; Cabral et al. 2016). This often applies to terrestrial systems where unprotected areas are converted for other land use to unsuitable habitats (Almany et al. 2009). However, this strict premise may not always be true in marine ecosystems where spillover and adult movements can sustain biodiversity outside reserves (Sale et al. 2005; Russ & Alcala 2011). However, for naturally patchy and increasingly degraded reef systems this assumption may be justified to explore worst-case scenarios under ongoing habitat loss given the ongoing deterioration of reefs worldwide (Burke et al. 2011). Overfishing and removal of key functional groups such as grazing herbivores is common in many tropical coastal fisheries which, combined with declining water quality and other stressors, have caused widespread phase shifts to algal dominated reefs supporting fewer fish (Hughes et al. 2007; Roth et al. 2018). The precautionary assumption of a scorched earth may therefore be permitted unless unprotected habitat areas can confidently be expected to host relatively healthy populations, if for example, pressures such as fishing and coastal run-off are well regulated and policies are enforced (MacNeil et al. 2015; Richmond et al. 2019).

Larval dispersal characteristics were also key determinants in the relative performance of the two connectivity methods. At lower dispersal distances in the simulated seascapes where habitat patches were only connected to a few near neighbours, the spatial dependency method achieved greater equilibrium settlement. Instead, when the network conditions became more well-connected, through either small-world links, a greater dispersal distance, or unprotected patches acting as stepping-stones by relaxing assumptions of degradation, the connectivity-based features methods performed as well or better. More specifically, metrics describing properties of network centrality, defined as the importance of a node in a wider network, such as Google PageRank and eigenvector centrality performed well in this context. This result is supported by previous findings suggesting that species with shorter dispersal distances tend to benefit from denser networks of marine protected areas, whilst those with longer dispersal distances can benefit from more distributed networks (Shanks et al. 2003; Treml et al. 2012).

The case studies showed that performance of connectivity methods also depended on how dispersal strength was distributed across patches. Highest equilibrium settlement was achieved in Southeast Sulawesi by designating habitat patches with high local retention as reserves. White et al. (2014b) also found that protecting reefs with high local retention achieved greater biomass in reserve systems for four out of five reef species in the northern California coast compared to protecting reefs with high network centrality. Similarly, Burgess et al. (2014) make the recommendation that protecting local retention, and thereby self-persistence, is generally an advantageous strategy. However, this strategy did not perform better than the spatial dependency method for the Coral Triangle species, where many habitat patches had similarly high levels of local retention, indicating different performances when local retention had either left- or right-skewed distributions. The larger size of planning units in the Coral Triangle, where mean size was roughly 350 times bigger compared to Southeast Sulawesi planning units, is likely why local retention was overall much higher as most short-dispersing larvae were retained within planning units. As the size of planning units relative to the scale of dispersal processes influences the value of connectivity metrics, this in turn affects the performance of different connectivity-based features methods.

The results presented here require some important caveats to be considered. First, the performance metric of equilibrium settlement relates to an objective of designing reserves with high maximum spawning potential across both protected and unprotected areas. However, other performance indicators may be more appropriate for different management objectives. Second, the oceanographic models in each of the case studies are resolved at different spatial scales, and dispersal simulations are known to have difficulty in accurately quantifying local retention. Currents close to the shoreline are more accurately predicted in the 500 m resolution Southeast Sulawesi models compared to the coarser ten km resolution Coral Triangle models. Correctly accounting for these coastal boundary layers, where current velocities are reduced, can substantially change the prediction of larval local retention (Nickols et al. 2015). This highlights the ongoing need for validation of dispersal models (Bode et al. 2019) and the use of cross-validating studies employing different methods (McCook et al. 2009) as the use of dispersal estimates in conservation planning become more widespread.

Apart from the conditions outside reserves and characteristics of larval dispersal, choice of method will also be informed by some of the practical benefits and drawbacks associated with either method. The connectivity-based features method has no theoretical limit on how many different metrics of connectivity can be added as conservation features in the same prioritisation problem, meaning that connectivity can be incorporated for multiple species having contrasting dispersal abilities (Magris et al. 2016, 2018). In contrast, the spatial dependency method can only use one connectivity dataset per prioritisation problem. Connectivity of multiple species could be aggregated into a single matrix to allow use with this method, but there is no guarantee that this will be an appropriate surrogate for each species (Magris et al. 2018). Regardless of which method is selected, *post hoc* population viability analyses or real-world evidence of conservation impacts are required as neither method explicitly links connectivity to demographic processes (Bode et al. 2016). This will be especially important when multiple species are used to evaluate whether contrasts are correctly captured for each species or lost if effects are averaged out.

Whilst we used Marxan in our analyses, our results are likely to apply to other similarly functioning tools. The R package *prioritizr* has a nearly identical framing of an objective function containing objectives, constraints, and penalties, but us an integer linear programming algorithm to identify exact optimal solutions (Hanson et al. 2021). As with Marxan, asymmetric connectivity can be incorporated as a boundary penalty between planning units or as a conservation feature. Zonation is another commonly used tool in which a priority ranking of the entire landscape is performed where sites most valuable for biodiversity have highest ranks (Lehtomäki & Moilanen 2013). Ways to incorporate connectivity include boundary length penalties and conservation features, with additional options also available such as including interactions between different environment types and data layers (Lehtomäki & Moilanen 2013). Although different tools will undoubtedly generate different solutions, these approaches broadly fall into either spatial dependency-based or site-based categories as connectivity is used either between sites or for a single site, and similar considerations as we have discussed here will apply.

Our comparative analyses show that different methods of using connectivity in spatial conservation prioritisation are appropriate under different contexts. When a high proportion of habitat in the area of interest is heavily degraded or the metapopulation is not widely connected, the spatial dependency method of protecting clusters of highly connected habitat patches could be a desirable prioritisation approach to rebuild and sustain populations. In other instances, protecting sites which have high Google PageRank scores, measuring patch importance in the wider network based on weight and number of connections, or local retention scores, measuring the proportion of larvae retained in each patch, could be more advantageous. As the use of connectivity in marine spatial planning becomes more widely adopted, these results highlight the importance of *post hoc* evaluations and the need to understand assumptions and possible limitations associated with dispersal estimates.

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Chapter 4. Designing marine reserve networks to mitigate larval dispersal volatility with the connectivity portfolio effect

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4.1. Abstract

Marine reserve networks designed to enhance larval dispersal provide important biodiversity benefits. Such designs are commonly based on time-averaged means of dispersal estimates. Therefore, it is unclear whether they capture the connectivity portfolio effect, the process by which variation in individual reserve performance is buffered by the reserve network when dispersal is temporally variable. Here, we evaluate the implications of dispersal variability for network performance and derive general rules for their design. We modelled larval dispersal of four commercially important reef species for 20 years in Southeast Sulawesi, Indonesia, using a biophysical model incorporating life histories and biological ocean currents. We then built reserve network scenarios informed by dispersal as either an interannual mean or for individual years, and assessed reserve networks using two performance metrics: protection of a high amount of larval flow from reserves and the connectivity portfolio effect. We discover that using mean dispersal can create subpar reserve networks in highly variable systems compared to using dispersal in specific years. Moreover, we were able to improve network performance in certain cases by identifying reefs with the highest flow contribution across years and including these as conservation features to be protected. Species whose spawning windows span variable seasonal or climate patterns (e.g., El Niño Southern Oscillation) are likely to benefit more when temporal variability is explicitly considered. The steps outlined here illustrate how information from multiple temporal connectivity datasets can help inform a spatial prioritisation framework to accommodate larval dispersal volatility.

4.2. Introduction

Many marine fauna disperse predominantly during larval stages, creating demographic and genetic connectivity between subpopulations (Cowen & Sponaugle 2009) and strengthening the long-term persistence of metapopulations (Hanski 1999). Spatial patterns of larval distribution are largely driven by physical oceanographic forces including currents, fronts, and eddies (White et al. 2010; Catalano et al. 2021), although pelagic larvae of some taxa can exert a degree of navigational control as swimming and sensory capabilities are developed (Sundelöf & Jonsson 2012). As large-scale climate oscillations and interannual circulation patterns such as El Niño Southern Oscillation periodically change the strength and direction of ocean currents, fish and invertebrate larval supply and recruitment can display substantial temporal fluctuation (Wilson et al. 2018). These changes in recruitment enhance or diminish growth rates of metapopulations, depending on the covariance between subpopulations (Williams & Hastings 2013). Although the magnitude of larval dispersal fluctuations can be substantial (Catalano et al. 2021), this variation is currently not considered when designing no-take marine reserve networks for biodiversity conservation and fisheries management.

As new marine reserves are established globally, conservation planners hope to better protect the ecological processes sustaining population persistence and recovery, including larval dispersal connectivity (Magris et al. 2014; Balbar & Metaxas 2019). Well-managed marine reserves host more and larger individuals given enough time for recovery from human disturbance (Edgar et al. 2014) and can provide high larval contributions as increasing numbers of older females spawn disproportionately more offspring (Hixon et al. 2014). However, if the design is based on a static snapshot of dispersal patterns in an otherwise highly dynamic system, expected benefits of larval supply enhancement may differ over time (Berumen et al. 2012; Thompson et al. 2018). Ideally, a reserve network should contain complementary reserve components to buffer the impact of varying larval flows, and thus create a portfolio effect which maximises the overall conservation benefit (Harrison et al. 2020). Even if contributions of individual reserves vary over time, asynchrony between connected reserves can generate stability at a network level. Despite the known performance benefit of reserve networks which capture such connectivity portfolio effects (Harrison et al. 2020), there are no methods to explicitly design marine reserve networks which buffer temporal variability of larval dispersal.

Spatial prioritisation is routinely used to integrate larval connectivity information into reserve network design, providing a framework for efficiently allocating conservation actions to achieve quantitative targets (White et al. 2014; Schill et al. 2015; Magris et al. 2016). There are several options to this end, including setting spatial dependencies between habitat patches to create functionally compact networks (Beger et al. 2010), setting targets for metrics describing properties of connectivity at each habitat patch (White et al. 2014; Magris et al. 2015), and using connectivity to inform a spatial cost layer (Weeks 2017). Dispersal here is typically parameterised with a single, time-averaged, mean connectivity dataset which describes the mean probability or strengths of dispersal between habitat patches over a given time period (White et al. 2014; Beger et al. 2015; Magris et al. 2016). Where dispersal is estimated from biophysical models, simulations may be run for multiple years and seasons to capture decadal-scale or seasonal variability, but ultimately these are combined to produce time-averaged mean dispersal (Treml et al. 2012; Schill et al. 2015). This simplifying step is often necessary due to the type of data accepted by spatial prioritisation tools, for example where only a single connectivity matrix can be used in a tool (Beger et al. 2010). Whether the practice of using mean dispersal captures connectivity portfolio effects is unknown.

Here, we explored the implications of using mean larval dispersal estimates for reserve network design with the following three research questions: i) how do reserve networks differ when they are designed using either an interannual mean of larval dispersal or dispersal in individual years, ii) do observed differences correlate with any major climatic drivers, and iii) can we improve these networks to provide more consistent protection of high larval export across variable dispersal events. We used biophysical larval dispersal models of three fish and one invertebrate species over 20 years in the province of Southeast Sulawesi, Indonesia (Figure 4.1.), to test a range of scenarios. Reserve networks were designed in the decision support tool Marxan (Ball et al. 2009), using either an interannual mean of larval dispersal or dispersal in individual years to consider larval dispersal dependencies between reefs (Beger et al. 2010). To compare the performance of different networks we calculated the cumulative larval flow from reserves and a connectivity portfolio effect following Harrison et al. (2020) which quantifies the degree to which a network dampens dispersal volatility.

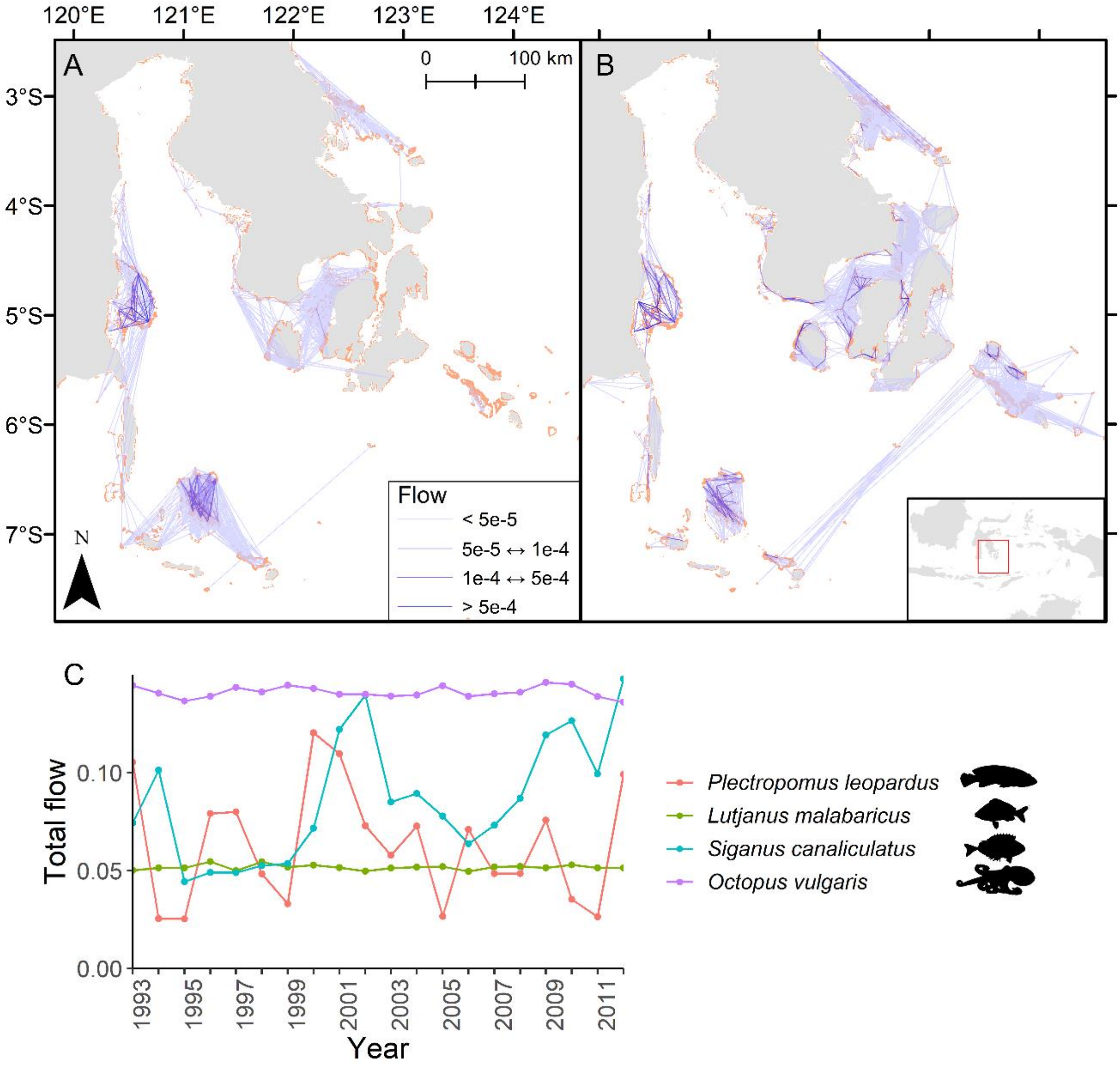

Figure 4.1. Overview of larval dispersal in Southeast Sulawesi, Indonesia, for three fish and one invertebrate species. (a, b) Map of the province with reef-shaped planning units shown by orange polygons and an example of *Plectropomus leopardus* larval flow in (a) 1999 and (b) 2000, estimated by coupled biological oceanographic dispersal models. Connections <1e-6 are not shown. (c) Cumulative annual larval flow strength across all planning units from 1993 to 2012 for each of the four species.

4.3. Results

4.3.1. Comparison of planning scenarios

Based on coupled biological ocean circulation models simulating larval dispersal from coral reef patches between 1993 and 2012, the magnitude of temporal variability differed between species. In *Plectropomus leopardus* and *Siganus canaliculatus*, larval flow fluctuated by 79% and 70% between highest and lowest flow years, whereas in *Lutjanus malabaricus* and *Octopus vulgaris* flow decreased by 9% and 7%, respectively (Figure 4.1.). Consequently, the priority areas identified for protection, termed the spatial prioritisation solutions, were more distinct in the former two species compared to the latter when different dispersal years were used to design reserve networks (Figure 4.2.). Distinct clusters of solutions were formed when using years of lower flow in *P. leopardus* (1994, 1995, 1999, 2005, 2010, and 2011) and in *S. canaliculatus* (1995, 1996, 1997, and 1998). Solutions for *O. vulgaris* were the least differentiated by scenario, meaning similar reef patches were being selected regardless of which dispersal dataset was used to parameterise the spatial prioritisation (Figure 4.2.).

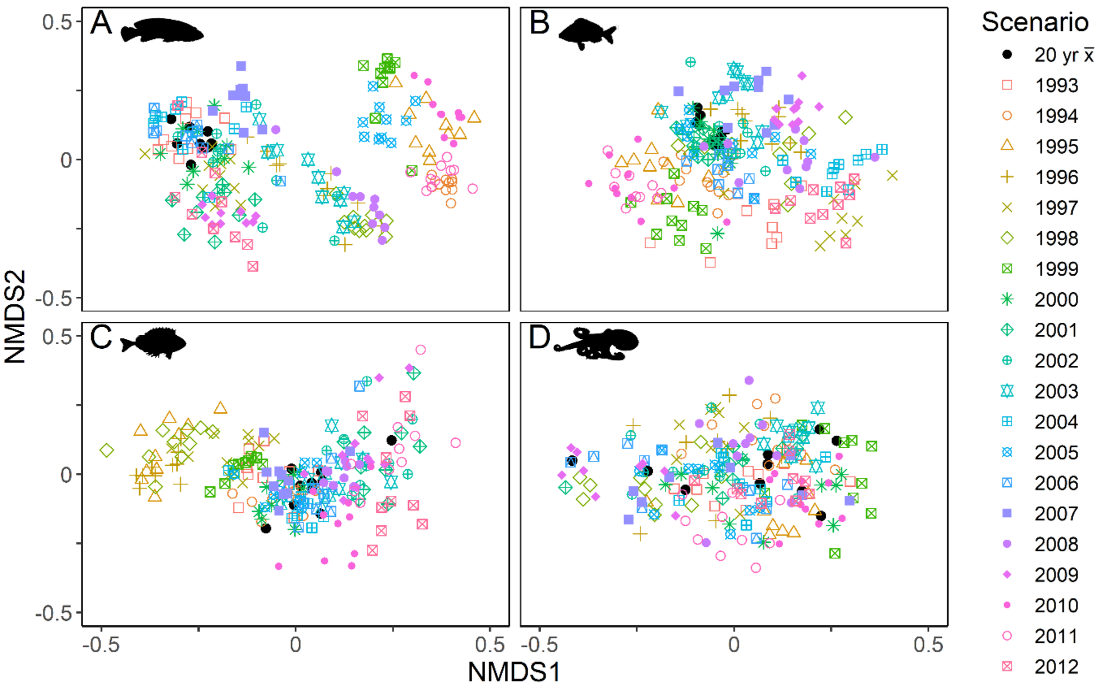

Figure 4.2. Non-metric multi-dimensional scaling (nMDS) plot of the top ten Marxan solutions coloured by scenario based on a Jaccard resemblance matrix. Each scenario involves a reserve network designed using the larval dispersal of either a 20-year mean or individual years for A) *P. leopardus*, B) *L. malabaricus*, C) *S. canaliculatus*, and D) *O. vulgaris*.

Similarities in the spatial prioritisation solutions correlated with different climatic indices, depending on the species (Figure 4.3.). The indices achieving the highest correlations with the nMDS ordination structure according to an envfit analysis were Oceanic Niño 3.4 Index for *P. leopardus* ($r^2 = 0.31$, P = 0.001), *L. malabaricus* ($r^2 = 0.16$, P = 0.001), and *O. vulgaris* ($r^2 = 0.1$, P = 0.001), and Pacific Decadal Oscillation index for *S. canaliculatus* ($r^2 = 0.16$, P = 0.001). These results corresponded with an overlap between when these climate drivers were at their most influential and the spawning windows of each species (Figure S7.3.1.), from September to November for *P. leopardus*, October to February for *L. malabaricus*, and March to September for *S. canaliculatus* (Table S7.3.1.). In contrast, *O. vulgaris* with year-round spawning had fewer significantly correlated indices with lower r-square values overall compared to three fish species.

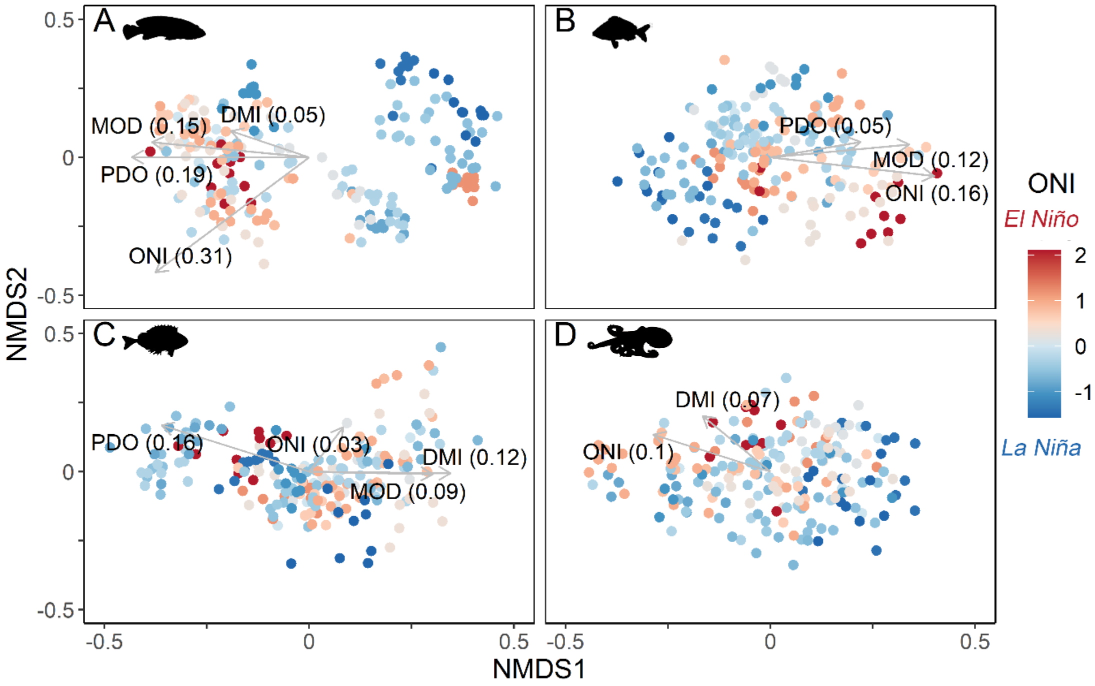

Figure 4.3. Non-metric multi-dimensional scaling (nMDS) plot of the top ten Marxan solutions of the individual year and 20-year mean scenarios (Figure 4.2.) with colours indicating strength of the Oceanic Niño 3.4 Index for A) *P. leopardus*, B) *L. malabaricus*, C) *S. canaliculatus*, and D) *O. vulgaris*. Climatic indices that are significantly correlated ($\alpha < 0.05$) with the nMDS surface are plotted as vectors with parenthetical values showing r-square values. Indices are the Oceanic Niño 3.4 index (ONI), Dipole Mode index (DMI), Pacific Decadal Oscillation index (PDO) and El Niño Modoki index (MOD).

4.3.2. Assessment of reserve performance and portfolio effect

There was a considerable difference in the performance of reserve networks designed using either individual years or the 20-year mean of larval dispersal (Figure 4.4.). Designing networks with mean dispersal achieved mixed performance across species. Using mean dispersal achieved relatively high flow in *P. leopardus* and *O. vulgaris*, moderate flow in *S. canaliculatus*, and the lowest of all in *L. malabaricus*. Portfolio effects of networks designed with mean dispersal were lower than networks designed using individual years in all species except *L. malabaricus*, where the mean scenario achieved the highest values. No single scenario obtained both highest portfolio effects and highest flow in any species, and the performance of specific years was not consistent across species. Notably, the top ten best Marxan solutions for each scenario also displayed large variability (Figure 4.4., error bars on the x- and y-axes).

To improve on the mean scenario network designs and provide a more consistent protection of larval supply over time, we identified planning units contributing a high amount of larval flow in each of the 20 years and set representation targets for these in the spatial prioritisation. For each individual year, we identified the top 15 planning units with the highest portfolio effect and added these as conservation features. In these modified ’20 year mean + target’ scenarios, either one or both performance metrics could be improved beyond the 20 annual or 20-year mean scenarios (Figure 4.4., black triangle). In *P. leopardus* and *S. canaliculatus*, modified scenarios scored highest portfolio effects and flow, whilst in *L. malabaricus* and *O. vulgaris*, higher flow was achieved whilst portfolio effects remained comparable to the original mean scenarios without additional conservation features. The optimal target for these highly contributing conservation features differed between species at 10% for *P. leopardus*, 30% for *L. malabaricus* and *S. canaliculatus*, and 40% for *O. vulgaris*, with other targets achieving lower performance.

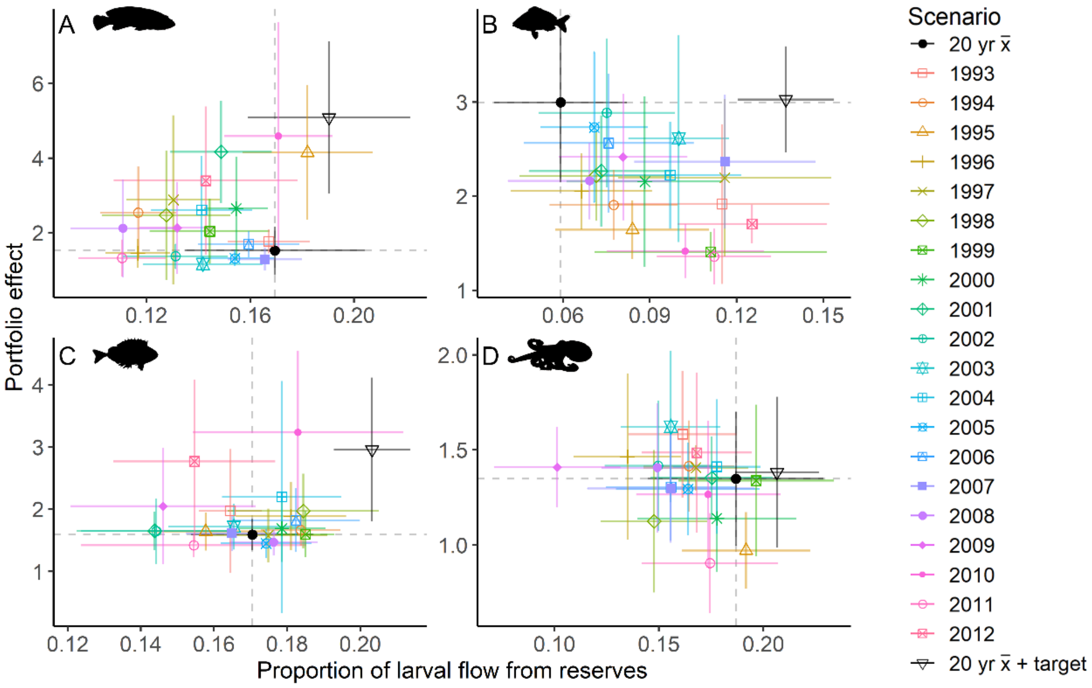

Figure 4.4. Performance of reserve networks designed using either larval dispersal of individual years, a 20-year mean, or a 20-year mean with additional targets for highly contributing planning units. Performance is measured as the proportion of total flow originating from protected sites (x-axis) and the mean-variance portfolio effect (y-axis). Horizontal and vertical error bars show the standard deviation of top ten Marxan runs for respective axes. Dashed grey lines divide the plots into four quadrants with the mean run as the centroid. High portfolio effects and high flow provide the greatest consistent benefits over time. Panels are for A) *P. leopardus*, B) *L. malabaricus*, C) *S. canaliculatus*, and D) *O. vulgaris*.

4.4. Discussion

Larval dispersal can display substantial temporal variation across years (Thompson et al. 2018; Wilson et al. 2018; Catalano et al. 2021), but what this variation means for performance of marine reserve networks is less understood. Our results highlight that using a single time-averaged mean dispersal estimate to design reserve networks can underachieve the possible benefits of generating a temporally consistent export of larval flow. Using connectivity of specific years can result in greater cumulative larval flow from reserves and greater portfolio effects in certain cases. Additionally, network designs can be improved further to explicitly consider dispersal volatility by identifying highly contributing habitat patches across different dispersal events and including these as conservation features. There are differences between species however, in that using mean dispersal may be adequate for species or seascapes with low annual variability, as in *O. vulgaris*, but not when high variability exists.

Differences between species in our study system likely result from species-specific life history strategies, such as in their spawning time. Changing oceanographic patterns and the effect of large-scale climatic oscillations at different times of the year produce drastically different dispersal patterns (Thompson et al. 2018; Wilson et al. 2018; Bashevkin et al. 2020); our results confirm that these patterns influence marine reserve benefits substantially. East-southeast directional winds during the rainy monsoon season from November to March in Sulawesi are generally stronger compared to the north-northwest winds in the dry season from June to October (Janßen et al. 2017). Spawning windows overlapping with only one of these seasons and coinciding with when climate drivers are at their most influential (Figure S7.3.1.), as in the case of *P. leopardus*, could result in greater variability of larval success. In contrast, year-round spawners such as *O. vulgaris* may experience lower variability in annual recruitment as they spawn under more variable oceanographic conditions, although additional species would need to be investigated to confirm the generality of this observation. Other life history parameters such as pelagic larval duration and larval mortality are also critical in shaping dispersal patterns and compounding to the oceanographic variability (Treml et al. 2012), and identifying common drivers of temporal variability across species may facilitate the design of multi-species reserve networks (Magris et al. 2016).

Using a single, average estimate of dispersal to understand ecological dynamics and make conservation decisions is problematic, especially where dispersal variability within a species is comparable in magnitude to variability between species (Catalano et al. 2021). Single estimates may fail to reflect rare long-distance dispersal events in anomalous years that can nonetheless have an important role in demographic patterns and post-disturbance recovery (Treml et al. 2008; Thompson et al. 2018). Although such rare events could be detected by combining multiple empirical approaches, such as genetic parentage analysis with population assignment tests (D’Aloia et al. 2022), approaches should ideally be repeated across multiple years or dispersal events to quantify temporal variability. Where cyclical climatic drivers such as El Niño Southern Oscillation operate, dispersal should be quantified across the full range of possible conditions (e.g., covering the range from strong La Niña to strong El Niño years).

The method by which larval dispersal connectivity between subpopulations is measured, whether through modelling, tagging, genetics, or simple observation (Bryan-Brown et al. 2017), determines whether temporal variability information can be used in conservation planning. Biophysical and individual-based modelling can identify variability if run over different spawning seasons (Rochette et al. 2012; Treml et al. 2012), with the only limitations being availability of underlying forcing data and computational time. Tagging and certain genetic approaches such as genetic parentage analysis can also distinguish between separate settlement periods or recruitment cohorts and thereby quantify variability at some level (Fodrie et al. 2011; Harrison et al. 2020; Riginos & Beger 2022). Methods that measure genetic differentiation between subpopulations would be unsuitable in many cases, as these provide only a single measure of realised dispersal aggregated across historical, evolutionary time frames (Riginos et al. 2011). Similarly, seascape connectivity as measured from the spatial arrangement of different habitats and its influence on species movement will also only provide a single proxy of connectivity (Engelhard et al. 2017). Choice of method must be considered early on in a conservation planning process if a system is known to be highly dynamic and consistency of conservation benefits across time is a desirable outcome.

Spatial prioritisation tools like Marxan are widely used amongst conservation practitioners given their many advantages including the ability to explore trade-offs, balance multiple objectives, handle many data layers, and incorporate zoning (Ball et al. 2009). However, there is a drawback in that only simple, static forms of connectivity can be integrated (Bode et al. 2016; Daigle et al. 2020). Complementarity or asynchrony of planning unit contributions cannot be addressed by the objective function whose elements consist of conservation features, cost, and a single connectivity or physical boundary dataset (Ball et al. 2009), as the identity of complementary planning units changes dynamically depending on the underlying configuration of reserve solutions. This difficulty was evidenced in the large range of portfolio effect values across different solutions, including in the improved network scenarios (Figure 4.4.). However, the modification presented here of setting targets for conservation features fits neatly within the prioritisation framework and can augment conservation benefits in certain cases.

Whilst the analysis presented here cautions against time-averaged means of annual dispersal estimates to design reserve networks, some important caveats need to be addressed. First, biophysical dispersal models are only models of real, complex systems. In a perfect world, model estimates for each year would be cross-validated through other genetic, tagging, or modelling approaches (Balbar & Metaxas 2019). Second, we implicitly assumed that larval flow scaled linearly with recruitment, since conservation benefits are only generated if larvae successfully recruit into the adult population. However, many marine fish and invertebrate species exhibit density-dependent recruitment, resulting in a levelling off of recruitment at high settler density (Caley et al. 1996). On the other hand, highly exploited species with low population abundance can be assumed to have a linear settler-recruit relationship. Third, we assumed that historic patterns of larval flow are representative of future variability. Changes in position and intensity of global ocean currents due to climate change have already been observed and are projected to continue (van Gennip et al. 2017), which will require the integration of projection models into assessments of reserve network performance.

Connectivity is increasingly used to inform reserve system implementation (Balbar & Metaxas 2019), but the impacts of variability in connectivity are less understood. We show that considering this variability is important if we want to be as safe from unintended inefficiencies as possible. We develop a method that can be applied everywhere if multiple years of dispersal data are available. Although we only test four species, we find support for the notion that generalist life histories with lower dispersal variability (e.g. frequent dispersal, *O. vulgaris*) can be adequately represented with the mean, whereas more specialised ones with higher variability cannot (e.g. specific dispersal time, aggregations, *P. leopardus*). This concept may be similarly applied to particular seascapes characterised by high or low oceanographic variability. We show that reserve network design can be improved to dampen volatility, and the next steps will be to work out how many years of data are required, and how these are best selected where biophysical model are used to inform conservation planning. Overall, our method can likely help capture volatility in connectivity, and perhaps enhance the performance of marine reserve networks even across future environmental and ecological changes.

4.5. Methods

4.5.1. Larval dispersal models

We modelled the larval dispersal of four commercially important reef species: coral trout (*Plectropomus leopardus*), snapper (*Lutjanus malabaricus*), rabbitfish (*Siganus canaliculatus*), and octopus (*Octopus vulgaris*), in the Indonesian province of Southeast Sulawesi using a coupled hydrodynamic and biological model (Figure 4.1.). Fine scale hydrodynamics were produced in the Delft3D-FLOW system using geostrophic, wind, and tidal forcing for the period of 1993 to 2012 with a 500 m average horizontal resolution. Local habitat survey data (Suherfian 2020) and a global coral reef dataset (UNEP-WCMC et al. 2018) were used to identify 487 coral reef patches. These patches were used to initiate dispersal simulations during spawning windows relevant for each species in each year, using competency and pelagic larval duration life history parameters obtained from literature (Table S7.3.1.). Two types of connectivity matrices were produced for each year with columns and rows corresponding to recipient and donor planning units, respectively. The flow matrix described the amount of movement between planning units, whilst the migration matrix derived by dividing the former by column sums gave the proportion of larvae arriving at a recipient planning unit.

4.5.2. Marxan conservation planning

Marxan identifies spatially explicit reserve configurations which meet quantitative targets for biodiversity features whilst minimising socioeconomic costs (Ball et al. 2009). The planning region is divided into planning units which are either designated or not designated as reserves in final solutions. We used the 487 reef patches of the dispersal model as planning units, with patch size as a proxy for cost and a constant 20% target of coral reef habitat protection. To incorporate larval connectivity and create coherent networks that maximise larval flow between reserves, we implemented connectivity using the migration matrix with asymmetric directionality as spatial dependencies among planning units (Beger et al. 2010). This approach creates high penalties in solutions that fail to protect a pair of strongly connected planning units.

We ran different scenarios to explore how solutions compared if reserve networks were designed using either connectivity of a single year or the multi-year mean. In the 20 individual year scenarios, the migration matrix of the relevant year from 1993 to 2012 was used to parameterise the Marxan spatial dependencies. The mean scenario used a mean connectivity matrix, calculated as the element-wise mean across the 20 annual matrices. Following standard practice (Ball et al. 2009), we performed 100 Marxan runs per scenario and used the top ten solutions, defined as having the lowest scores, for further analysis.

The similarity of Marxan solutions was compared using routine multivariate statistics in R (R Core Team 2021). Following Harris et al. (2014) we first performed a hierarchical cluster analysis using non-metric multidimensional scaling (nMDS) to visualise the overlap of the top ten solutions of each of the 21 scenarios. We compiled a data matrix where each row was a solution and each column was a planning unit, creating a Jaccard distance matrix using the metaMDS function (*vegan* package; Oksanen et al. 2020). Next, to determine whether any climate indices correlated with the nMDS ordination, we performed an envfit analysis with explanatory variables consisting of the Oceanic Niño 3.4 index (Trenberth & Stepaniak 2001), El Niño Modoki index (Ashok et al. 2007), Indian Ocean Dipole index (Saji et al. 1999), and Pacific Decadal Oscillation index (Mantua et al. 1997), all major drivers of oceanographic patterns in Indonesia affecting strength and direction of major surface currents (Thompson et al. 2018).

4.5.3. Assessment of reserve performance and portfolio effect

We used two performance metrics to compare how scenarios achieved stable protection of larval flow in a marine reserve network over time. First, we quantified how much larval flow originated from protected reefs to the total system. For each year we summed the rows of the flow matrix corresponding to planning units identified by solutions and normalised this by dividing by the total flow of that year. The final metric was calculated as the sum across all years. Second, the mean-variance portfolio effect of each solution was calculated following Harrison et al. (2020), quantifying the dampening factor by which temporal variability in individual reserve performance is buffered by the reserve network. The portfolio effect can be calculated from a power-law relationship describing an increasing performance variability with mean of individual components. The predicted performance of a single reserve consisting of the sum of individual reserves was compared to the observed performance of the portfolio of reserves. Where Harrison et al. (2020) used genetic parentage analysis to define performance as the relative contribution of a reserve to local recruitment for each recruitment cohort, we here defined performance as the larval flow contribution of a planning unit in each year, assuming a linear relationship between outgoing flow and recruitment contribution in the absence of genetic data.

4.5.4. Improving reserve network performance

After evaluating the use of mean and annual dispersal, we explored whether the performance of the reserve networks could be improved further. We created a new conservation feature consisting of highly contributing planning units across all years and added these to scenarios using mean connectivity. First, we subset to the solutions across all scenarios with a portfolio effect value in the fourth quartile. From these, the new conservation feature was defined as the top 5% of designated planning units with highest flow in each of the 20 years. To determine a suitable target for this new conservation feature which resulted in networks achieving highly in both performance metrics, we tested a range from 10% to 50% by 10% increments whilst keeping the cost of solutions similar to the original scenarios.

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Chapter 5. Conservation planning for coral reefs using underwater visual census and environmental DNA

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5.1. Abstract

Spatially and taxonomically comprehensive and current data on biodiversity and ecosystem conditions are necessary to effectively manage vulnerable coral reef ecosystems. Emerging biodiversity surveying technologies such as environmental DNA (eDNA) metabarcoding, which detects organisms from environmental samples, have the potential to revolutionise this process. As the use of eDNA analyses in coral reef ecosystems grows, the question of how eDNA can inform the design of protected area systems arises. Here we quantify whether and how conservation priority areas differ when biodiversity information from eDNA analyses is used in planning, relative to traditionally used visual census. We surveyed a total of 147 coral reefs across the hyper-diverse Wallacea region within the Coral Triangle with underwater visual census and eDNA metabarcoding. First, we evaluated the overlap in detection of taxonomic groups by the two methods. Next, we extrapolated survey data using species distribution models and identified priority areas for conservation using spatial prioritisation and explored their similarity. Our results showed that the overlap in detection was generally low at species level and increased with higher taxonomic ranks. Despite low overlap, there was a moderate agreement in the placement of protected areas. Incidental protection occurred for 39% of eDNA species when targets were set for species detected by visual survey, and 62% vice versa. This study demonstrates that eDNA metabarcoding can complement traditional survey methods to design protected area systems, although issues around incomplete taxonomic reference databases and low shared detection need to be investigated further.

5.2. Introduction

Emerging technologies for biodiversity monitoring have the potential to revolutionise conservation management (Bohmann et al. 2014; Deiner et al. 2017; Ruppert et al. 2019; Bani et al. 2020). For example, advances in efficiency and cost reduction in DNA sequencing have made environmental DNA (eDNA) a promising tool for wildlife and biodiversity monitoring (Bohmann et al. 2014). The DNA which organisms shed into their surroundings via skin cells, saliva, urine, faeces, or other pathways can be detected non-invasively in samples taken from the environment (Ficetola et al. 2008), the fragments of which are then matched to reference databases to obtain taxonomic identities (e.g., species). As extra-cellular DNA is generally quick to break down in situ (but see Bálint et al. 2018), the detection of DNA is interpreted as a spatiotemporally explicit signal of an organisms' presence. Detection is not limited to single species, as samples can provide records of entire communities using metabarcoding, whereby universal primers bind to regions of genes that are conserved across taxa (Deiner et al. 2017). eDNA metabarcoding can provide highly comprehensive data over wide geographic areas to inform conservation decisions (Ruppert et al. 2019).

eDNA analysis is particularly suited to study and manage hyper-diverse ecosystems, including coral reefs (Gaither et al. 2022). Coral reefs host between one quarter and one third of marine biodiversity, yet traditional methods of surveying reef diversity often focus on a subset of large and well-studied taxonomic groups as surrogates (Plaisance et al. 2011). For example, the popular method of underwater visual census (UVC) is conducted by a group of taxonomists whilst diving (Caldwell et al. 2016). Individual taxonomic expertise and detectability of species limit which taxa can be surveyed, with bias against certain groups such as cryptic or shy species (Edgar et al. 2004; Pais & Cabral 2018). As UVC is also time and resource-intensive, the geographic area covered tends to be limited and can result in patchy data. The remoteness of many of the world's coral reefs may also favour methods requiring fewer surveyors and equipment (West et al. 2022). Given the ongoing loss and degradation of coral reefs worldwide (Eddy et al. 2021), eDNA metabarcoding surveys can help address the urgent need for detailed, extensive, and rapid biodiversity surveys to effectively allocate conservation resources (Bohmann et al. 2014; Edgar et al. 2016; Stat et al. 2017; Marwayana et al. 2022).

Amongst the world's coral reef regions, the Wallacea region in Indonesia and Timor-Leste stands out for its unparalleled levels of endemism and biodiversity (Figure 5.1.; Struebig et al. n.d.; Mittermeier et al. 2011). Situated in the heart of the Coral Triangle, Wallacea is a transition zone between Asia and Australasia where Pacific and Indian Ocean fauna overlap (Carpenter & Springer 2005). Complex geological processes and island effects have led to widespread speciation and ecological diversification, with new species still being discovered (Michaux 2010; Rheindt et al. 2020). At the same time, economic development centred on natural resource exploitation is widespread (Yusuf & Moore 2020; Voigt et al. 2021). Given the importance of this region, eDNA can facilitate the documenting and monitoring of Wallacea's unique and threatened biodiversity to mitigate threats and aid conservation (Struebig et al. n.d.). eDNA metabarcoding has already been successfully used to characterise the distribution of fish across Indonesian coral reefs (Gelis et al. 2021; Marwayana et al. 2022), as well as other taxa such as echinoderms, molluscs, and chordates (Madduppa et al. 2021).

Several studies have compared the use of eDNA with traditional coral reef biodiversity monitoring techniques. A comparison of UVC data from the Reef Life Survey programme (Edgar & Stuart-Smith 2014) and eDNA metabarcoding data from five tropical regions revealed 47% overlap in fish families detected by both methods (Mathon et al. 2022). eDNA metabarcoding and capture-based surveys of fish species in Okinawa, Japan, had 24% overlap in shared detection (Oka et al. 2021). Meanwhile, detection of sessile benthic taxa in coral reefs in north-western Australia was also low with 42% overlap in shared genera (West et al. 2022). Non-detection by eDNA has been attributed to incomplete reference databases and lack of sampling. As a result, studies generally recommended combining traditional surveys and eDNA metabarcoding as complementary monitoring techniques, instead of using one as a replacement of the other. Notably, eDNA was often able to capture wider biogeographical patterns and diversity trends despite differences in taxonomic detection (DiBattista et al. 2017; Mathon et al. 2022; West et al. 2022).

A common use of coral reef biodiversity data is in conservation planning to design protected areas. Spatially explicit data on the distribution of species, for example from UVC, can identify areas that will return the greatest conservation benefits if protected (Dalleau et al. 2010; Olds et al. 2014). This process is often undertaken with spatial prioritisation software which use transparent, reproducible algorithms to balance ecological and socioeconomic objectives (Margules & Pressey 2000). Complementary areas which capture regional biodiversity at lowest cost are identified for conservation. Given the relative nascency of the field, there is currently no consistent framework for translating eDNA data into spatial prioritisation plans (Bani et al. 2020). As eDNA metabarcoding can provide much higher information content over a greater number of sites compared to traditional survey techniques, it is unclear whether similar priority areas would be identified if the objective was to protect regional biodiversity.

In this study, we compare the use of UVC and eDNA metabarcoding biodiversity surveys of coral reefs in the Wallacea region for the purposes of conservation planning. First, we explore similarities and differences in the detection of taxonomic groups at reefs surveyed by both methods. Next, we work out a framework of how to use eDNA data to identify priority areas for protection. We extrapolate survey data across space and design protected area systems which meet a 30% target of species protection across Wallacea, in line with latest IUCN targets for 2030 (Ceccarelli et al. 2021). We compare three separate scenarios where targets are set for species recorded by UVC, eDNA, or both, to determine whether and how different data collection methods influence the selection of conservation priorities. As eDNA analyses are increasingly carried out, there is an unrealised opportunity to use the big datasets they produce in conservation planning. We provide a first look at how eDNA can be incorporated in the process of spatial prioritisation to design protected area systems.

5.3. Methods

5.3.1. Field surveys

We surveyed a total of 147 Indonesian coral reef sites within the Wallacea region between June 2019 and April 2021 with UVC and eDNA metabarcoding. UVC was carried out at 46 sites, of which 36 were also surveyed using eDNA. An additional 101 sites were surveyed by eDNA only, but not by UVC (Figure 5.1.). UVC surveys of coral, fish, and macroalgae were carried out by a team of four taxonomists on SCUBA at 8m depth, covering four 50m belt transects at each site. For each transect, two observers identified and counted non-cryptic fish at species level across a 50m x 5m belt and laid out a 50m tape. This transect was followed by one observer counting algae to species or genus level across a 2m x 30m belt and one observer counting coral colonies to species level across a 0.5m x 20m belt.

eDNA sampling was carried out by collecting 1L of seawater on SCUBA just above the reef at 8m depth. Where sampling overlapped with UVC, three samples were collected at the beginning, middle and end of each 50 m transect. For other sites, 6 replicate samples were collected by swimming a similar approximate distance. Bottles for collection were first bleached for 30 minutes at 10% concentration with a Milton tab and rinsed with surface seawater. eDNA samples were then filtered using Merck Sterivex 0.22 µm and filled with 2 ml of Longmire for preservation. As controls, blank samples consisting of PCR water were also filtered in the same conditions during the survey period.

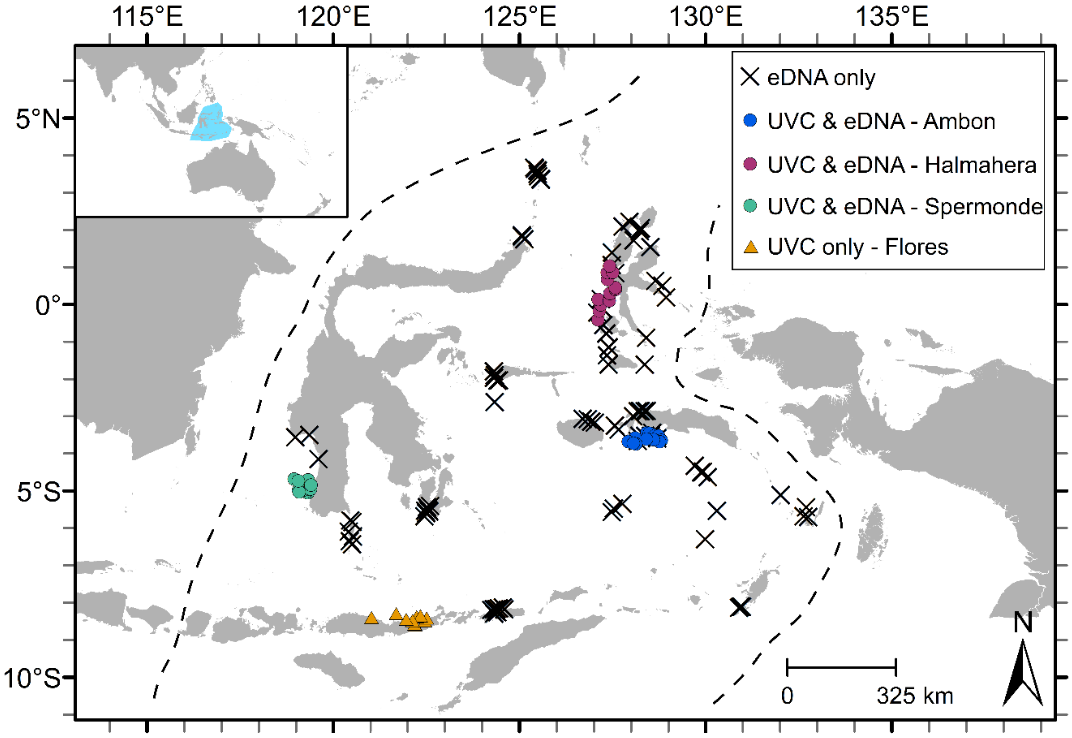

Figure 5.1. Map of the Wallacea biogeographical region bounded by Lydekker's line in the west and Wallace's line in the east. Coral reef sites surveyed using either underwater visual census (UVC), environmental DNA (eDNA) metabarcoding, or both are shown.

5.3.2. eDNA analysis

We used a metabarcoding approach to assess community compositions with the two universal primers of 18S for eukaryotes and COI for metazoans. Sterivex were extracted using the Qiagen DNeasy Power Water Sterivex kit. Longmire, removed from the Sterivex, was centrifuged for 40 minutes at 6000 g. The supernatant was discarded and the pellet was resuspended in the first solution of the DNeasy PowerWater Sterivex kit. The rest of the extraction was performed following the user manual. Extracted DNA was stored at -20°C until library preparation. Field blanks were extracted in the same way as the samples and additional extraction blanks were included in the extraction procedure.

Library preparations followed the standard Illumina protocol of two stage PCR and index using dual indexing. PCR negatives, field blanks, and extraction blanks were sequenced as well. The PCR protocol was 12.5 µl of AppletonWoods Taq , 1 µl of reverse and 1 µl of forward primers (10 µM) modified with Illumina adaptors and Golay, 2.5 µl of DNA and 8 µl of water to make a final volume of 25 µl. We used established thermal protocols for COI (Leray et al. 2013) and 18S (Albaina et al. 2016). Samples were quantified and pooled in equal molarity and sequenced on Illumina NovaSeq. Spermonde samples were sequenced on a run of their own, COI for the remaining eDNA samples were sequenced on a second run, and 18S eDNA samples were sequenced on a third. All runs were performed at the Earlham Institute in Norwich, UK.

Raw sequences were analysed following a bioinformatics pipeline (Dumbrell et al. 2016). Briefly, quality trim was performed using Sickle followed by error correction with SPAdes software (Bankevich et al. 2012). Sequences were paired-ended using the pear algorithm inside the pandaseq utility (Masella et al. 2012). For reads with a high overlap we stripped the primers after the overlap had already been computed as the algorithm was more reliable at the cost of its speed. Paired sequences were filtered using the mothur software to remove short sequences and those with homopolymers (Kozich et al. 2013). Clean sequences were then checked for chimeras and clusters of 97% similarity using the vsearch algorithm. Taxonomy was assigned using vsearch classifier inside qiime2 environments on a custom dataset created using RESCRIPt (Robeson et al. 2021). Taxonomic assignments were manually checked to remove any mismatches or taxa that are not present in coral reefs.

Samples were cleaned using negative controls in a microDecon library (McKnight et al. 2019). The decontaminated Operational Taxonomic Unit table was then cleaned of any records that were misassigned. Data were normalised using the CSS method with the function phyloseq_transform_css available in the metagMisc library (Mikryukov 2019) in R (R Core Team 2021), and each sample was the sum of six replicates along a transect.

5.3.3. Comparison of species detection

In the 36 sites surveyed using both UVC and eDNA, we explored how often species or higher taxonomic classifications were detected by both methods. This provided an estimate on the reliability of eDNA detection, based on how often species observed visually are present or absent from eDNA samples. We also matched fish species with their position in the water column based on functional trait data from FishBase (Froese & Pauly 2022) to investigate whether detection by either method was influenced by where the fish are generally found.

5.3.4. Species distribution modelling

We extrapolated the UVC and eDNA records from surveyed sites using species distribution models (SDMs) which use statistical algorithms to relate observed data to environmental covariates to predict probabilities of observation in non-surveyed areas (Elith & Leathwick 2009). Ensemble SDMs combining different algorithms can improve predictive accuracy by reducing uncertainty caused by differences amongst modelling techniques (Ramirez-Reyes et al. 2021). We created ensemble models which combined Random Forest, Generalised Linear Model, and Generalised Additive Model algorithms, weighted by the performance of each model.

Species counts from UVC and eDNA presence-absence data were modelled assuming a Poisson and binomial distribution, respectively. In the eDNA data, SDMs were only built for Operational Taxonomic Units that were matched to species, as multiple unassigned Operational Taxonomic Units could belong to the same species. Explanatory variables were selected from a range of possible environmental parameters (Table 5.1.) which have previously been used for coral and reef fish distribution modelling (Freeman et al. 2013; Cacciapaglia & van Woesik 2015; Ottimofiore et al. 2017). Variables with the greatest explanatory power were selected from a set of preliminary models with the restriction that no more than one predictor variable was used per 10 datapoints to avoid model overfitting (Peduzzi et al. 1996). Variables with a variance inflation factor >10 were removed to avoid collinearity (Salmerón et al. 2018).

We used cross-validation to evaluate the predictive accuracy of models by dividing data into 80% training and 20% testing splits a total of 1000 times. We evaluated count models using Root Mean Square Error (RMSE) and Pearson’s correlation, where only models with an average RMSE smaller than half the range of the data and an average correlation >0.25 were retained in the ensembles. We evaluated presence-absence models using the Area Under the Curve (AUC), where only models with AUC >0.7 were retained in the ensembles (Fielding & Bell 1997). The final ensembles contained data from all sites and were used to predict species distributions across 40,922 1 km^2 coral reef pixels in the Wallacea region (Dixon et al. 2022). We selected probability thresholds for classifying presences and absences to give the maximum value of Kappa, a measure which compares model predictive accuracy to accuracy expected to occur by chance (Allouche et al. 2006). All models were run in R (R Core Team 2021) using the *randomForest* (Liaw & Wiener 2002), *mgcv* (Wood 2011), and *base* packages.

Table 5.1. List of environmental covariates used to parameterise species distribution models.

Variable	**Description**
SST mean	Mean sea surface temperature at 0.01° resolution between 2005.01.01 – 2020.01.01 (Dixon et al. 2022).
SST range	Range of sea surface temperature at 0.01° resolution between 2005.01.01 – 2020.01.01 (Dixon et al. 2022).
DHW above 4	Number of days above 4°C-weeks at 0.01° resolution between 2005.01.01 – 2020.01.01 (Dixon et al. 2022). Degree heating weeks >4 is a measure of accumulated temperature anomalies that are associated with increased probability of coral bleaching (Kayanne 2017).
DHW max	Maximum degree heating weeks between 2005.01.01 – 2020.01.01 (Dixon et al. 2022).
Mean pH	Mean pH at 0.083° resolution between 2000 – 2014 from the Bio-Oracle dataset (Tyberghein et al. 2012; Assis et al. 2018).
Mean salinity	Mean salinity at 0.083° resolution between 2000 – 2014 from the Bio-Oracle dataset (Tyberghein et al. 2012; Assis et al. 2018).
Mean chlorophyll a	Mean chlorophyll a at 0.083° resolution between 2000 – 2014 from the Bio-Oracle dataset (Tyberghein et al. 2012; Assis et al. 2018).
Dissolved oxygen	Mean dissolved oxygen at 0.083° resolution between 2000 – 2014 from the Bio-Oracle dataset (Tyberghein et al. 2012; Assis et al. 2018).
Mean PAR	Mean photosynthetically available radiation at 0.083° resolution between 2000 – 2014 from the Bio-Oracle dataset (Tyberghein et al. 2012; Assis et al. 2018).
Wave exposure	Wave exposure metric modelled as a function of wind speed, wind direction, and fetch length (Chollett & Mumby 2012). Daily wind speed and direction were obtained from NOAA's Blended Sea Winds at 0.25° resolution between 2005.01.01 – 2020.01.01 (Zhang et al. 2006). Fetch length for each reef pixel was calculated using the R package *windfetch* (Seers 2021).
Human pressure	Sum of human population within 10km radius of reef cell as a proxy for human pressure. Population count in 2020 was downloaded from WorldPop at 0.0083° resolution (Gaughan et al. 2013).

5.3.5. Spatial prioritisation

We used Marxan (Ball et al. 2009) to identify priority areas for conservation based on the extrapolated UVC and eDNA data. Marxan is a spatial prioritisation tool which selects management areas (termed 'planning units') to meet user-specified conservation targets at least cost. We used 1 km^2 reef pixels (Dixon et al. 2022) as planning units and set a 30% protection target for each species using three different scenarios. First, targets were set for species recorded by UVC only. Second, targets were set for species recorded by eDNA only. Third, targets were set for species recorded by both survey techniques. Each of the three scenarios were run 100 times following standard practice (Game & Grantham 2008). Planning units that are frequently selected across 100 runs are considered important areas for conservation. To remove any confounding variables which may influence priority selection, we used no boundary penalty which would otherwise create compact solutions, set the status of all planning units as available for selection, and assigned each planning the same cost of 1 (Game & Grantham 2008).

We compared solutions from the three separate spatial prioritisation scenarios using UVC species only, eDNA species only, and species from both in two ways. First, we determined the degree of agreement in which priority areas are identified by calculating Cohen's Kappa statistic on the selection frequency of planning units (Wilson et al. 2005). Kappa ranges from -1 to 1, with 1 indicating full agreement. Second, we evaluated how well setting targets for species detected by either UVC, eDNA, or both managed to incidentally protect species for which targets were not yet set.

5.4. Results

5.4.1. Comparison of species detection

Across the 36 sites, UVC and eDNA identified 993 and 2,073 unique species, respectively, of which 191 were identified by both (Table 5.2.). Only 17% of Operational Taxonomic Units were matched to species in databases, although this increased at higher taxonomic ranks. eDNA methods generally identified a much greater taxonomic breadth including fungi, protists, and animals which were not visually surveyed (Figure 5.2.A).

Table 5.2. Comparison of taxonomic diversity at 36 surveyed coral reef sites in the Wallacea region as determined by underwater visual census (UVC) and environmental DNA (eDNA) metabarcoding using COI and 18S primers. Shared groups are taxonomic classifications that were detected by both survey methods. OTUs are Operational Taxonomic Units.

Taxonomic rank	**Survey method**			**No. shared groups**
	UVC 150,097 counts	**eDNA – COI & 18S primer** 119,301 OTUs		
	No. groups	No. groups	% OTUs assigned	
Domain	3	4	100	3
Phylum	5	75	92	5
Class	7	216	78	7
Order	45	622	62	40
Family	100	1415	51	78
Genus	287	2,201	44	155
Species	993	2,073	17	191

Co-detection by both methods was relatively low at species level and increased with higher taxonomic ranks (Figure 5.2.B, C). Species observed visually at a given site were only detected by eDNA an average of 5%, 12%, and 6% of the time for coral, fish, and macroalgae (Figure 5.2.B). In part, this is caused by species which are missing from taxonomic databases which cannot be matched to Operational Taxonomic Units. We circumvent this issue by considering instead the detection of shared taxonomic groups, for example a species which has been both visually observed and detected by eDNA across any of the 36 sites. Detection of shared taxonomic groups was also low at species level, increasing with taxonomic ranks (Figure 5.2.C). Across all sites, shared species were detected on average 79% of the time by UVC only, 11% of the time by eDNA only, and 10% of the time by both survey methods.

Detection of fish by either UVC or eDNA metabarcoding was related to its position in the water column (Figure 5.3.). Pelagic and demersal species were detected more often by eDNA than UVC, whilst cnidarian-associated species were detected more often by both methods than would be expected by chance ($\chi^2_{DF=16} = 515.39$, $p<0.001$). Detection of a species by both methods at a given site did not guarantee co-detection in other sites (Figure 5.3.A).

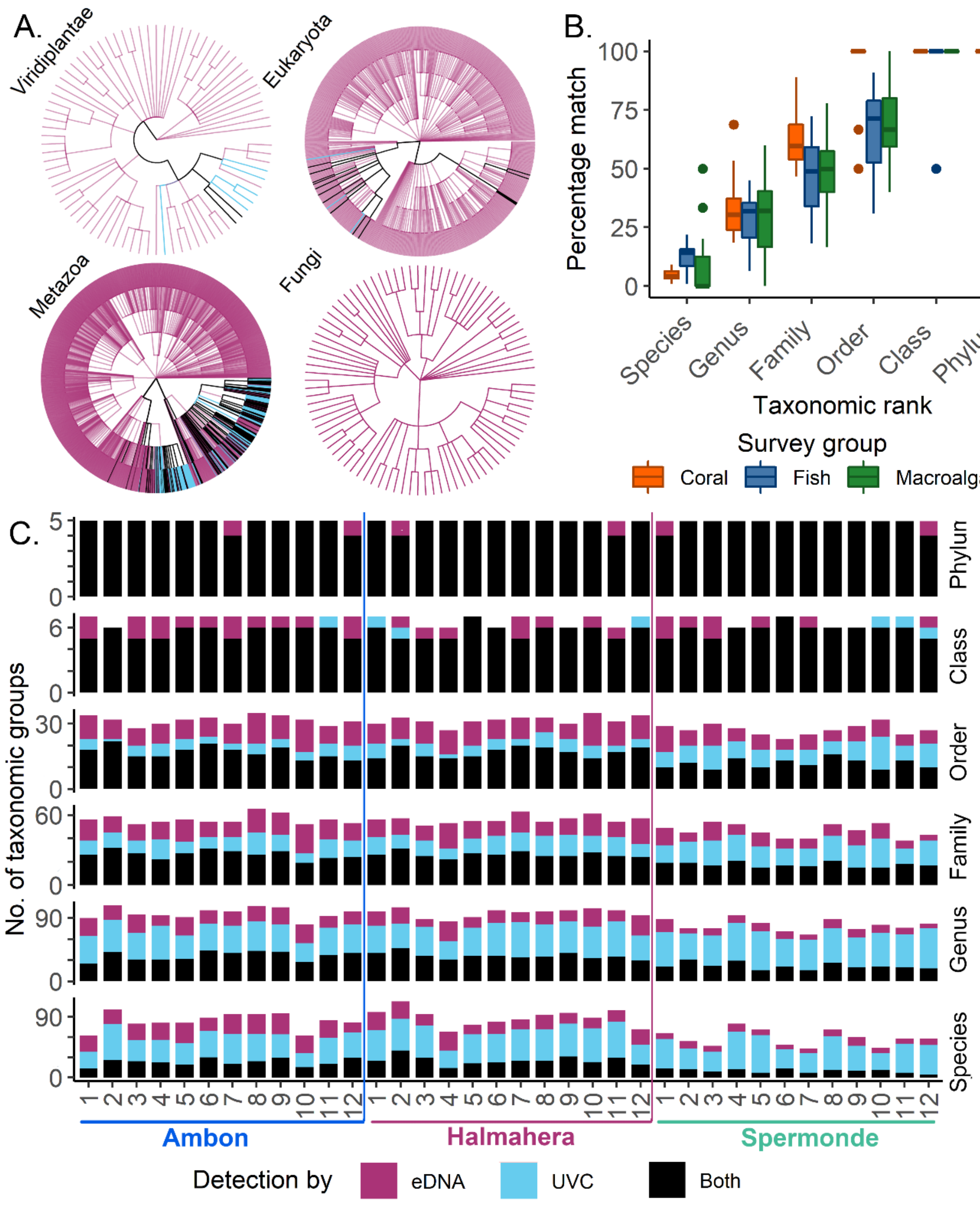

Figure 5.2. Comparison of the marine taxonomic diversity identified by UVC and eDNA metabarcoding using a COI and 18S primers across 36 surveyed sites in the Wallacea region. A) Phylogenetic tree pruned at genus level showing genera identified by either one or both methods across all sites. B) Percentage of taxonomic groups identified by UVC that were also identified by eDNA at individual sites. C) Detection of shared taxonomic groups (Table 5.2.) by either one or both methods at individual sites.

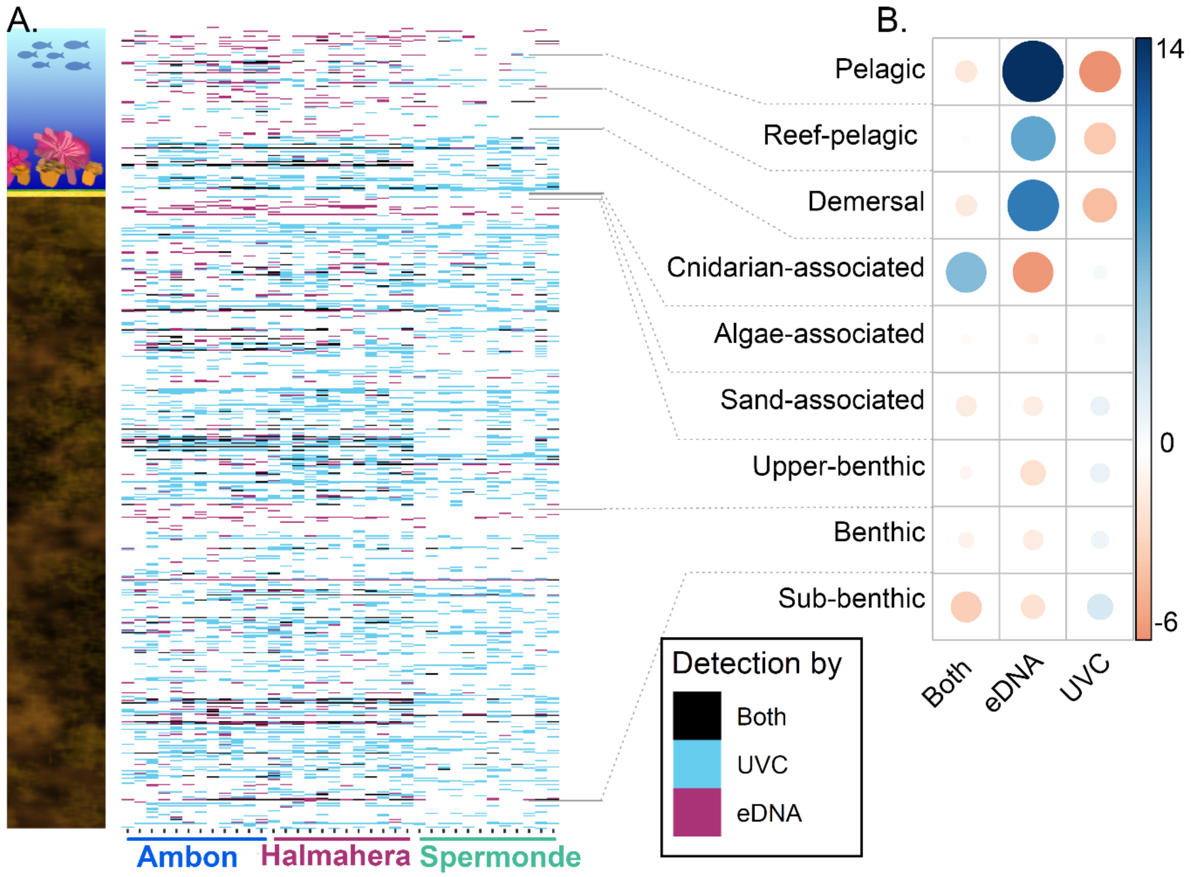

Figure 5.3. A) Detection of fish species in 36 sites by either UVC, eDNA metabarcoding, or both survey methods, according to their position in the water column. B) Plot of Chi-square Pearson residuals showing associations between the number of detections and position of the species. Size of circles is related to strength of residuals, with smallest size at values of 0. Pelagic and demersal species are detected more by eDNA than UVC, and detection by both is greater in cnidarian-associated species.

5.4.2. Species distribution modelling and spatial prioritisation

SDMs were successfully generated for 116 and 186 species for UVC and eDNA, respectively, with an overlap of nine species (Table S7.4.1.). SDMs failed for most of the recorded species due to low species prevalence across sites and weak relationships with environmental covariates, resulting in low predictive power of models.

Spatial prioritisation identified some similar areas as conservation priorities regardless of whether targets were set for UVC species only, eDNA species only, or both (Figure S7.4.1. –

Figure S7.4.3.). The agreement between solutions was considered ‘slight’ (García-Barón et al. 2021) as Kappa values ranged between 0.02 and 0.1 (**Error! Reference source not found.**B). Cost of solutions was lowest if targets were set for UVC species only and highest if set for both UVC and eDNA species, although this difference was only an increase of 8% (**Error! Reference source not found.**A). In comparison, the number of conservation features for which targets were set in the UVC only, eDNA only, and both scenarios were 116, 186, and 302, respectively. This suggests that the cost increase is not directly scaling with the number of conservation features. Although the scenario Solutions were somewhat successful in protecting species even if targets were not set for them specifically (**Error! Reference source not found.**C). If spatial prioritisation targets were set for UVC species only, 41% of eDNA species also met or exceeded the target level of protection. If spatial prioritisation targets were set for eDNA species only, 58% of UVC species also met or exceeded the target level of protection.

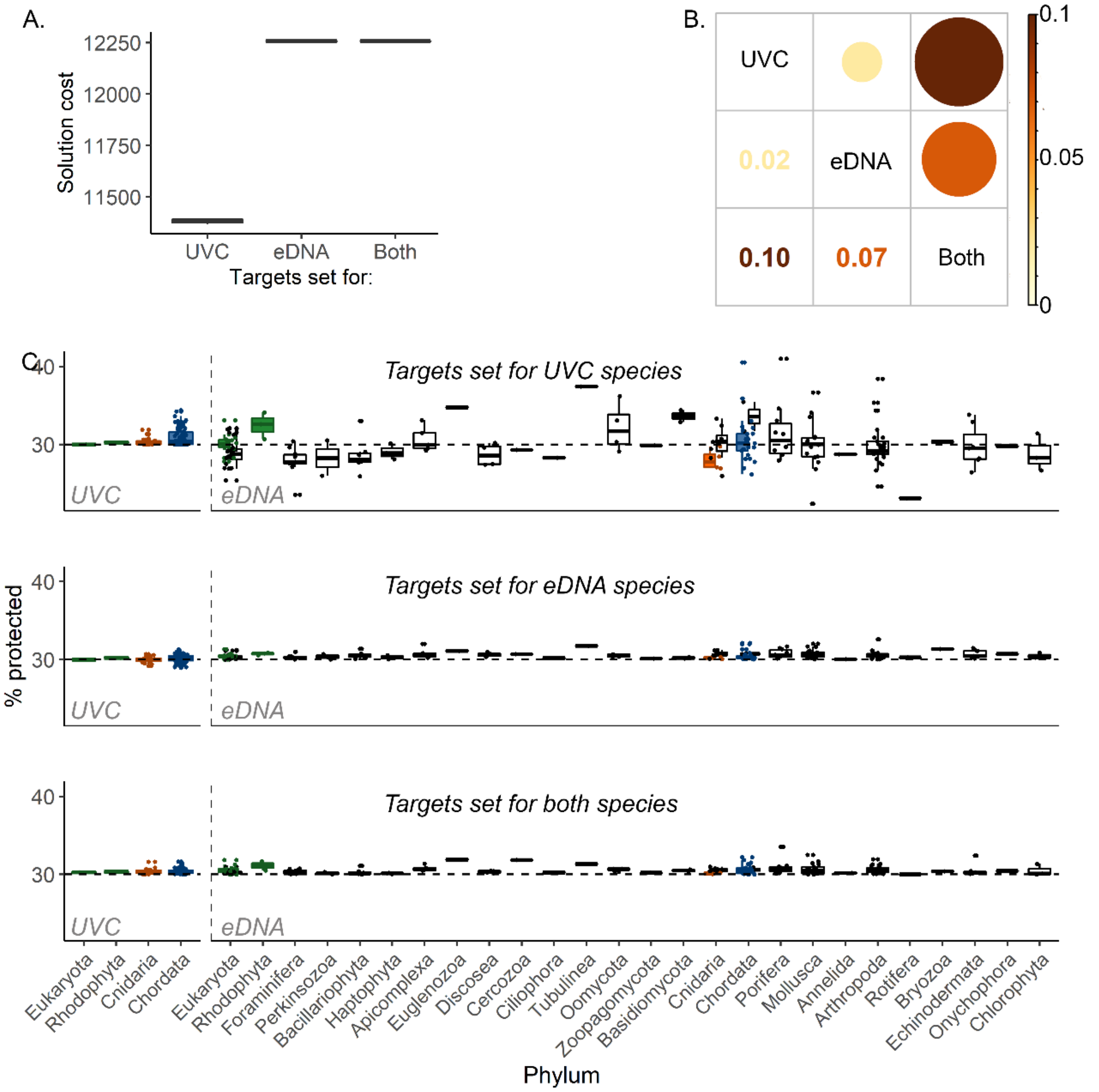

Figure 5.4. Summary of three spatial prioritisation analyses where targets were set for either species recorded by UVC, eDNA, or both. A) The cost of the top ten solutions with the lowest score for each scenario. B) Similarity of selection frequencies, the number of times planning units were selected out of 100 runs, given by the Kappa statistic (Wilson et al. 2005). C) The percentage of protection for UVC species (left column) and eDNA species (right column). The dashed horizontal line indicates the conservation target set at 30%.

5.5. Discussion

This study demonstrates how eDNA metabarcoding can complement traditional coral reef biodiversity survey techniques such as UVC to inform protected area design in hyper-diverse marine regions such as Wallacea. We identified a greater overall taxonomic diversity across coral reef sites with eDNA using COI and 18S primers compared to UVC, yet both methods identified unique taxonomic groups not detected by the other. Taxonomic groups were detected with both methods at a given site only 10% of the time. By spatially extrapolating survey data with species distribution models and identifying priority areas for conservation, we found a low overlap in areas identified depending on whether conservation targets were set for species identified by UVC or eDNA. A greater proportion of UVC species were incidentally protected when targets were set for eDNA species than vice versa, at 58% compared to 41%. Taken together, the difference in identified taxa, low probability of co-detection, and moderate incidental protection suggest that both UVC and eDNA survey data should be used in combination to inform protected area design.

Our spatial prioritisation scenarios had the objective to protect 30% of identified species, assuming that it is desirable to protect the entire breadth of biodiversity (Pollock et al. 2020). In practice, most conservation efforts focus on a subset of often charismatic or flagship species as a proxy for wider biodiversity (Davies et al. 2018). However, there is value in protecting wider biodiversity, as species interactions and 'hidden' diversity (e.g., microbial diversity) sustain ecosystem resilience, functioning, and integrity (Delgado-Baquerizo et al. 2016; Harvey et al. 2017). As UVC and eDNA detected different taxonomic groups, the greatest protection of regional biodiversity would be achieved by combining the two datasets to set conservation targets. This approach would also protect more varied ecological niches and a greater functional trait space, the phenotypic space occupied by a set of species that determines their effect on processes and responses to environmental factors (Aglieri et al. 2021), since different survey techniques may be biased towards different functional groups (e.g., fish water column position in Figure 5.3.). Setting conservation targets for species surveyed by both techniques only increased the cost of protected area solutions by 8%, suggesting that protected areas need not be substantially more expensive to protect greater levels of biodiversity.

Apart from setting broad biodiversity targets as we did, data from eDNA can inform conservation in other ways (Bohmann et al. 2014; Bani et al. 2020; Huerlimann et al. 2020). For example, eDNA analysis can help specifically detect species of conservation concern or invasive species (Rees et al. 2014). As rare taxa may be more difficult to detect due to false negative detection, use of taxon-specific primers and a large number of sampling replicates is recommended for this purpose (West et al. 2020). If survey data is used to model species occurrence across space, thresholds for presence-absence need to reflect management objectives, as the importance of minimising commission (false positive) or omission (false negative) error rates will be context-dependent (Rondinini et al. 2006). Other opportunities for using eDNA metabarcoding include protecting ecological networks (Tulloch et al. 2018) and trophic interactions (Devloo-Delva et al. 2019).

eDNA also poses new challenges that need to be resolved in conservation planning. Not all taxa identified in eDNA samples are equally important to protect. Different taxa contribute to ecosystem functioning in different ways. For example, keystone species are important as they can have a disproportionately large role with many downstream effects (Davic 2003), whereas other species may be less important if there is high functional redundancy and multiple species fulfil similar functions (Mouillot et al. 2014). Prevalence and extinction risk will also determine the importance of protecting a species. Given the wealth of information eDNA metabarcoding generates, managers must consider which groups are important and why, as well as what they indicate. Some taxa may also be indicators of areas undesirable for protection, such as certain bacteria found in sewage pollution (Wear & Thurber 2015).

One obstacle we encountered in using survey data to identify priority conservation areas was that single species distribution models failed for most of the recorded species. Rare or threatened species have low prevalence, which can result in sample sizes too small to build reliable statistical models. Apart from increasing sampling effort, one solution could be to use joint species distribution models (Ovaskainen et al. 2017). These methods model species responses to both the environment and to other species, recognising effects of interspecific interactions such as competition, predation, and facilitation (Mittelbach & Schemske 2015). Using such community models can improve predictions of rare species compared to single species models (Zhang et al. 2020), making them suitable to analyse the big community data that eDNA generates (Pichler & Hartig 2021).

Given the low co-detection of shared taxonomic groups by UVC and eDNA, some thought should be given as to why this is the case and how detection could be improved. Compared to terrestrial sampling, the marine environment poses additional challenges as water dilutes eDNA. Abiotic factors such as temperature, salinity, and ultraviolet radiation lead to eDNA breakdown (Harrison et al. 2019). Differences in the time of day or strength of wind, currents, and tides during our surveys may explain some of the variability in co-detection. eDNA dispersion in the sea can be as short as 30 m (Murakami et al. 2019), up to several kilometres (Jeunen et al. 2019), depending on local conditions. Additionally, less abundant species may be more difficult to detect at populous sites, as co-amplification of DNA from many taxa lowers the sampling depth for rare species (Nguyen et al. 2020). Additional research into eDNA dispersion and decay in tropical marine environments will be necessary to refine future study designs and sampling efforts.

As only 17% of the Operational Taxonomic Units were matched to species, our study echoes the need for more complete reference databases of marine fauna and flora (DiBattista et al. 2017; Polanco Fernández et al. 2021). Expanded barcoding efforts are particularly needed in areas such as the Coral Triangle, where comparatively little research focus is given despite high levels of biodiversity and human resource dependence (Barber et al. 2014; Limmon et al. 2017). Barcoding corals can be challenging as their mitochondrial DNA, where COI is encoded, is highly conserved (Neigel et al. 2007). Solving this challenge may require genome-wide sequencing to develop nuclear markers of variable genomic regions which can be used in eDNA metabarcoding (Adams et al. 2019). In the case of fish and corals, genomic introgression from hybridisation between species can impede species assignment (Montanari et al. 2012; Harrison et al. 2017). Developing custom genetic databases of reference species to supplement genetic repositories and using taxon-specific primers will greatly improve species assignment.

eDNA will undoubtedly play a growing role in future coral reef conservation efforts. Corroborating other research comparing eDNA and other techniques (Oka et al. 2021;

Polanco Fernández et al. 2021; Mathon et al. 2022), we show that eDNA metabarcoding can complement traditional survey techniques to give a more comprehensive picture of biodiversity and its distribution across space. This is the first study to explore how this data can be used in conservation planning to protect greater functional and taxonomic space. Future applications of eDNA in marine conservation planning will benefit from efforts to expand the taxonomic coverage of reference databases and understand eDNA dispersion and decay in tropical marine environments.

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Chapter 6. Discussion

Following decades of conservation planning, analyses of protected area effectiveness show mixed results (Edgar et al. 2014). Two elements central to the effectiveness of conservation plans are achieving adequate persistence and representation (Sarkar et al. 2006). As larval dispersal underpins persistence of coral reef ecosystems, conservation outcomes can be improved by incorporating larval dispersal into MPA design (Olds et al. 2016). The importance of dispersal is acknowledged in the latest 2021-2030 draft of the Global Biodiversity Framework stating that "at least 30 per cent of… sea areas… are conserved through… well-connected systems of protected areas" (Convention on Biological Diversity 2021). In practice, however, the current adoption of connectivity in conservation planning is still limited and highly geographically biased due to barriers preventing wider uptake (Magris et al. 2014; Balbar & Metaxas 2019).

The first aim of this thesis was to address three knowledge gaps in using larval dispersal to inform MPA design. I approached this aim by combining spatial prioritisation analyses based on biodiversity and biophysical larval dispersal data with population models to assess MPA network performance. I found that incorporating larval dispersal generally improved performance of MPA networks compared to solutions omitting dispersal, although there were differences between species and in different contexts. The methods and analyses I describe are intended to help conservation researchers and practitioners work with the different spatial and temporal dimensions of larval dispersal to design MPA networks and provide guidelines on when different spatial prioritisation approaches should be used.

Objective 1: *Illustrate how larval dispersal information can inform conservation planning at multiple spatial scales*

In Chapter 2, I show how information on larval dispersal can inform conservation planning at two different spatial scales when designing and establishing an MPA network. Regional designs and local actions have complementary strengths and limitations, and both are necessary to achieve conservation goals (Pressey et al. 2013). At a local scale, I present simple metrics of incoming and outgoing connectivity which are used together with habitat quality information in consensus-based, stakeholder workshops to delineate reserve boundaries within districts. The benefits of working at this scale are that additional detailed data collection and direct stakeholder engagement are possible. This maximises conservation outcomes as reserve placement is based on accurate, verified data of live coral cover instead of less certain, remotely sensed coral reef datasets (Edgar et al. 2016). Compliance and enforcement is also strengthened as local community members are engaged in knowledge exchanges and directly involved in decision-making (Arias et al. 2015). Bottom-up, community-based implementation is particularly suited for the Coral Triangle region where MPAs are typically small and community reliance on coral reef resources is high (Ban et al. 2011).

At a regional scale, I use connectivity as a spatial dependency in spatial prioritisation to identify priority areas for subsequent reserve network expansion across the province. Regional prioritisation has the benefit of creating a functionally connected reserve network (Mills et al. 2010). Additionally, steps at both scales inform one another as regional prioritisation is updated once some local reserves are established. Integration of the two scales, local and regional, addresses the widespread research-implementation gap whereby regional assessments often fail to result in actions (Knight et al. 2008). Continual feedback between regional and local planning is important as developments occur in either (Cheok et al. 2018). Examples of this include losses in biodiversity during the incremental implementation of local actions (Visconti et al. 2010) or availability of new data on cost or biodiversity (Rouget 2003). Such adaptive planning is particularly important when protecting dynamic processes such as dispersal, as dispersal patterns and our understanding of them evolve over time (Ban et al. 2011).

Objective 2: *Determine conditions in which different methods of using connectivity in spatial prioritisation are more suitable*

In Chapter 3, I determine suitability of different approaches to using connectivity in conservation planning. I focus specifically on implementations available in the widely used decision support tool Marxan (Ball et al. 2009), although findings apply to similarly functioning tools using either a site- or spatial dependency-based formulation of connectivity. I identify four conditions which affect the performance of different methods: reproductive contributions of unprotected areas to the wider metapopulation, distance of larval dispersal, proportion of habitat protected, and distribution of dispersal characteristics across habitat patches or planning units. Selecting clusters of planning units for protection with a spatial dependency approach is appropriate when dispersal is limited, unprotected areas are highly degraded, or little habitat is protected. Instead, selecting individual sites for protection based on local properties of connectivity is appropriate when dispersal is greater, unprotected areas are less degraded, or more habitat is protected. These findings highlight that the performance of different methods is highly context dependent. Conservation practitioners should acknowledge these conditions in their local planning area for the species or habitat being protected to make an informed selection of methods.

These results also highlight that *post hoc* population viability analyses are crucial in the evaluation of expected conservation outcomes from incorporating larval dispersal into conservation planning. This is due to an inherent difficulty in translating dynamic processes such as dispersal into static, area-based spatial prioritisations, especially as to how prioritisation solutions relate to population persistence (Bode et al. 2016). Different prioritisation solutions and approaches can be compared using quantitative, evaluative models which balance available data with model complexity (García-Díaz et al. 2019). By reducing model complexity and being clear about underlying assumptions and model parameters, evaluations about reserve network performance are more likely to be accepted by end-users and avoid misinterpretation or misuse (Cartwright et al. 2016).

Objective 3: *Explore the implications of temporal variation in larval dispersal for MPA network design*

In Chapter 4, I explore the effect of temporal variability in larval dispersal on MPA network performance. I show that the common practice of using a time-averaged mean of dispersal may underachieve possible conservation benefits. MPA networks can instead be designed to produce more consistent larval benefits by using dispersal of individual years or by protecting habitat patches which have high larval contributions across different dispersal events. These findings suggest that although spatial prioritisation does not, at present, incorporate the temporal dimension of larval dispersal, there are benefits in doing so. As dispersal variability can change metapopulation growth rates and the ability of reef recovery following disturbance (Williams & Hastings 2013; Thompson et al. 2018), ignoring this additional layer may lead to unrealistic expectations of conservation benefits.

Including the temporal dimension of larval dispersal increases the realism captured by models. Our understanding of larval dispersal is evolving, and only recently has the large magnitude of seasonal and annual fluctuations in dispersal become apparent (Wilson et al. 2018; Catalano et al. 2021). Whether the additional effort and resources required to obtain temporal data are justifiable depends on how large the expected gains in reserve network performance would be. These findings suggest that species experiencing greater dispersal fluctuations benefit more when temporal variability is incorporated into MPA network design. In relatively stable systems, resources may instead be better used for other conservation activities.

Objective 4: *Compare conservation priorities identified by eDNA and traditional survey techniques*

The second aim of this thesis was to advance the goal of biodiversity representation in coral reef conservation planning using eDNA. I approached this aim in Chapter 5 by conducting biodiversity surveys of coral reefs in the Wallacea region using UVC and eDNA metabarcoding with COI and 18S primers. I used survey data to develop spatial models of species distributions and identify priority areas for conservation through spatial prioritisation. I show that although eDNA methods discovered a greater taxonomic diversity compared to UVC, both survey techniques identified unique taxonomic groups. The co-detection of shared taxonomic groups was relatively low, and different priority areas were identified depending on whether targets were set for species identified by UVC or eDNA. For these reasons, we suggest that both UVC and eDNA should be used as complementary survey techniques.

As eDNA can detect different functional groups and ecological niches compared to UVC, combining the two datasets to set conservation priorities would theoretically strengthen protection of ecosystem functioning (Aglieri et al. 2021). There is still much undocumented biodiversity in coral reefs, for example of fungi and molluscs (Milne & Griffiths 2014; Wainwright et al. 2019), which may nonetheless be providing important functional roles. Every survey technique has its own biases and limitations (Polanco Fernández et al. 2021), which the combined use of several different techniques can reduce. As taxon-specific primers are developed and reference databases are improved, eDNA metabarcoding will play a growing role in uncovering this hidden diversity so that it can be effectively managed through conservation planning.

Taken together, these research chapters describe how protected areas can be designed more effectively and efficiently to provide both societal and environmental benefits and minimise adverse impacts to other marine users. Both historically and to this day, many marine protected areas are criticised for top-down management in which placement is based on political expediency instead of scientific evidence (O'Leary et al. 2018). Here instead, we demonstrate protected area design which involves local people and is informed by ecological principles of key demographic processes. By implementing a two-scale approach, existing uses and values are considered by involving local people in decision-making. The perception of 'external elites' imposing management is reduced, and a sense of ownership and control over resources is created in communities instead (Tranter et al. 2022). As conservation planning continues to be implemented across the globe, a combination of top-down and bottom-up processes will be necessary to ensure success and equity (Cheok et al. 2020).

Explicitly incorporating larval dispersal and its impact on population dynamics forms a link between protected and unprotected areas, as protected areas have the dual function of supporting both fishery and conservation outcomes. This reinforces the shift in conservation thinking from treating protected areas as far away, undisturbed areas to treating them as integrated components of a system that provides ecosystem goods and services for people. Moreover, a lack of connection with nature is often cited as a driver of the anthropogenic degradation of ecosystems (Fletcher 2017). By understanding and describing how protecting larval dispersal can support fished populations, a sense of connection may be established between marine users and protected areas. Highlighting such connections can facilitate conflict management between conservation and other human activities, as finding solutions requires recognising problems as shared ones and having a transparent evidence base (Redpath et al. 2013).

Although protected areas are by definition area-based exclusionary tools in which some degree of user displacement is inevitable, we show how to minimise these adverse impacts. The advantage of using spatial prioritisation methods over manual selection of priority areas is that solutions are optimised to have the lowest cost. Methodical and targeted placement of protected areas is also helped by having comprehensive and detailed inventories of biodiversity occurrence from environmental DNA survey data. Incorporating larval dispersal and detailed survey data ensures that redundant or irrelevant areas are not designated for protection, which avoids inflating the total displacement cost of protected area systems. With these improved approaches and resulting outcomes, protected areas will hopefully be perceived as coupled human-environment systems which communities take ownership of.

6.1. Challenges in using larval dispersal end eDNA for coral reef conservation planning

There remain some challenges in achieving wider use of larval dispersal in conservation planning which were not addressed in this thesis. One major obstacle is that obtaining empirical measurements or models of larval dispersal requires substantial technical expertise and resources (Schill et al. 2015). The capacity of most conservation projects across the world to measure dispersal through tagging, genetics, or modelling is severely limited, particularly in developing nations where subsistence fishing and dependence on coral reef ecosystems are high (Barber et al. 2014). The long timescale generally needed to produce dispersal data may also conflict with the need for rapid actions to mitigate immediate threats. Bridging this gap requires interorganisational and international collaborations between conservation managers and scientists, as well as targeted, long-term conservation funding. Additionally, existing dispersal datasets should be made available in public repositories for others to use to minimise duplication of effort and increase access to planning with dispersal.

Certain aspects of larval dispersal are still poorly understood and create uncertainty around management. These include vertical and horizontal larval movement, sensory detection of suitable habitat, larval mortality, and processes occurring in the nearshore environment (Swearer et al. 2019). In Chapter 3 we suggest that the different resolutions of biophysical models impact their ability to correctly capture coastal boundary layers, which in turn may result in the identification of different priority areas. Some fundamental life history parameters used in biophysical modelling, such as pelagic larval duration, have been quantified for heavily studied species but are lacking for others. As species may exhibit geographic variation in larval traits, caution is needed when making generalisations across regions (Sotka 2012). We used life history parameters of closely related species where species-specific data was unavailable for dispersal modelling, but future applications would benefit from species-specific empirical measurements. When using genetic patterns to infer connectivity, disentangling dispersal effects from differential selective pressures on traits can prove difficult (White et al. 2019). Studies may circumvent some of these issues by using multiple, different methods of measuring dispersal to cross-validate dispersal estimates and minimise uncertainty (McCook et al. 2009).

The use of eDNA for coral reef biodiversity assessments and marine conservation planning can be refined in several ways. The effects of biotic and abiotic factors on eDNA generation, dispersion, and decay in tropical marine environments need to be better understood so that future sampling and survey methods can be improved (Harrison et al. 2019). For example, expected rates of false negative detection due to local conditions can inform the number of replicate samples required per site. The low detection of shared taxonomic groups in our surveyed sites indicated a high rate of negative detection, both by UVC and eDNA, which is problematic for managing species that are rare or of conservation concern. Our results also highlight the need for barcoding efforts for coral reef species, as a high proportion of Operational Taxonomic Units were not successfully assigned to known species (DiBattista et al. 2017).

6.1. Future advancements

There are several areas where the use of larval dispersal in conservation planning can be improved given that it is an evolving field. First, the design of MPA networks for multiple species with varying dispersal patterns is an ongoing area of research (Jonsson et al. 2016; Magris et al. 2016, 2018). Conservation management is increasingly moving from a single species focus to protecting entire communities, in recognition of important interspecific relationships. We found that species with diverse dispersal characteristics had little overlap in marine reserve placement (Chapter 2) and behaved differently with the two spatial prioritisation methods of using connectivity (Chapter 3). Species also exhibited different levels of temporal variability in larval dispersal and MPA network performance over time (Chapter 4). These results support the notion that MPA networks will only be effective if the design considers the full variety of life history traits (Magris et al. 2016). As spatial prioritisation tools such as Marxan involve a degree of user-defined balancing of different targets, penalties, and parameter settings, care is needed that contrasting species requirements are correctly captured.

Second, conservation planning should consider how larval dispersal patterns will change as a result of climate change. A number of studies have incorporated connectivity and climate change objectives into MPA design (Mumby et al. 2011; Beger et al. 2015; Magris et al. 2017), but few have explored climate-mediated changes in connectivity (Álvarez-Romero et al. 2018). Climate change will alter oceanographic current strength and direction, habitat availability, and biological traits such as calcification of larvae, pelagic larval duration, survival, behaviour, and spawning timing (Munday et al. 2009). Refining climate projections and establishing how species might respond to changing environments through genetic and phenotypic plasticity will help inform decision-making. By combining existing dispersal patterns with climate projections and expected species responses, future dispersal patterns can be predicted (Álvarez-Romero et al. 2018). Ideally, predictions would also be made about whether and how larval dispersal variability will change due to climate change to ensure stability of MPA network performance in the future (Chapter 4). Periodic monitoring and ground-truthing of larval dispersal patterns through empirical measurements or modelling and validation will be necessary, with findings used to strategically adapt MPA design and management.

Third, conservation planning should address possible unintended consequences and trade-offs when enhancing dispersal between MPAs. Changing environmental conditions are pushing invasive species and disease into new marine areas (Occhipinti-Ambrogi 2007; Byers 2021), which the placement of well-connected MPA networks may inadvertently facilitate. By studying the dispersal capability and predicted future distributions of invasive species and diseases, targeted management interventions could mitigate these unintended consequences. Additionally, the trade-off between connectivity and environmental covariance in light of climate change should be considered. Environmental covariance occurs when demographic responses to environmental disturbances are spatially correlated, for example, when nearby populations are subjected to the same cyclone or marine heatwave (Blowes & Connolly 2012). In Chapter 3 we found that spatial dependency methods generally produced more spatially aggregated MPA networks, suggesting that these methods may be more susceptible to such unintended consequences. As climate-driven disturbances continue to increase in both intensity and frequency (O'Leary et al. 2017), strategies which balance risk-spreading and enhanced connectivity must be developed.

We provided a first look at how eDNA can inform marine conservation planning of coral reefs, but there are other ways of using eDNA data to design MPA networks. The big data which eDNA metabarcoding produces is well-suited for new types of analyses such as joint species distribution models (Pichler & Hartig 2021). By explaining species occurrence as a function of both the environment and species interactions, predictions of rare species' distribution can be improved. Comparing such models with traditional single species models would determine the importance of biotic interactions compared to abiotic effects. eDNA data can also be used to uncover community-level attributes to be targeted by conservation planning, such as network complexity or trophic interactions (Bani et al. 2020).

6.2. Conclusions

MPA networks aim to achieve persistence and representation of coral reef ecosystems in a changing world. The integration of larval dispersal which underpins coral reef persistence is slowly becoming more widespread, but a number of knowledge gaps remain. This thesis explored how to use larval connectivity at multiple spatial scales of conservation planning and determined the conditions under which different approaches of using dispersal in spatial prioritisation are suitable. It also considered how temporal variability in dispersal can be accounted for in the design of MPA networks. In order to advance the goal of representation, this thesis explored how survey techniques based on eDNA metabarcoding can improve biodiversity assessments and setting of conservation priorities.

Ultimately, successful coral conservation will hinge on both spatial and non-spatial interventions such as regulation of resource-use, monitoring programmes, capacity building, and education. The success of MPA designs also depends on effective management, strict compliance, and political backing. However, by improving MPA designs to better achieve persistence and representation, demonstrable conservation benefits are more likely to occur and lead to wider support.

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List of abbreviations

AUC	Area under the curve
COI	Cytochrome c oxidase subunit I
CSM	Connectivity strength modifier
DHW	Degree Heating Week
eDNA	environmental DNA
GAM	Generalised additive model
GLM	Generalised linear model
LEP	Lifetime egg production
MAA	Managed Access Area
MPA	Marine protected area
nMDS	non-metric multidimensional scaling
PLD	Pelagic larval duration
PU	Planning unit
RF	Random forest
RMSE	Root mean square error
SDM	Species distribution model
SST	Sea surface temperature
UVC	Underwater visual census

Chapter 7. Appendix

7.1. Appendix 7.1 - Supplementary Material for chapter 2

7.1.1. Regional Marxan prioritisation as a first step

In our case study, the first iteration of MAA selection in our implementation was performed through assessments with partners. However, in other cases, a regional Marxan prioritisation may also be taken as a first step to first identify priority areas for protection (Figure S7.1.1). Using Marxan with Connectivity as spatial dependencies and targeting 20% of coral reef habitat, priority reefs for conservation can be identified. The larval dispersal models of relevant target species are used as an additional penalty element in the objective function of the spatial prioritisation, ensuring that selected reserves are connected to a wider reserve network. In Southeast Sulawesi, priority areas differ for each species, but Wakatobi, Buton, and the eastern coast of Sulawesi display high selection frequency for several species (Figure S7.1.1.).

The expected conservation benefits from these putative reserve networks can be assessed using a discrete-time, metapopulation model to assess biomass gain over 30 years after reserve implementation (Appendix 7.1.3.). Compared to randomly selecting a set of reefs for reserve designation, the reserve networks identified by Marxan are expected to achieve higher biomass across the province (Figure S7.1.2.).

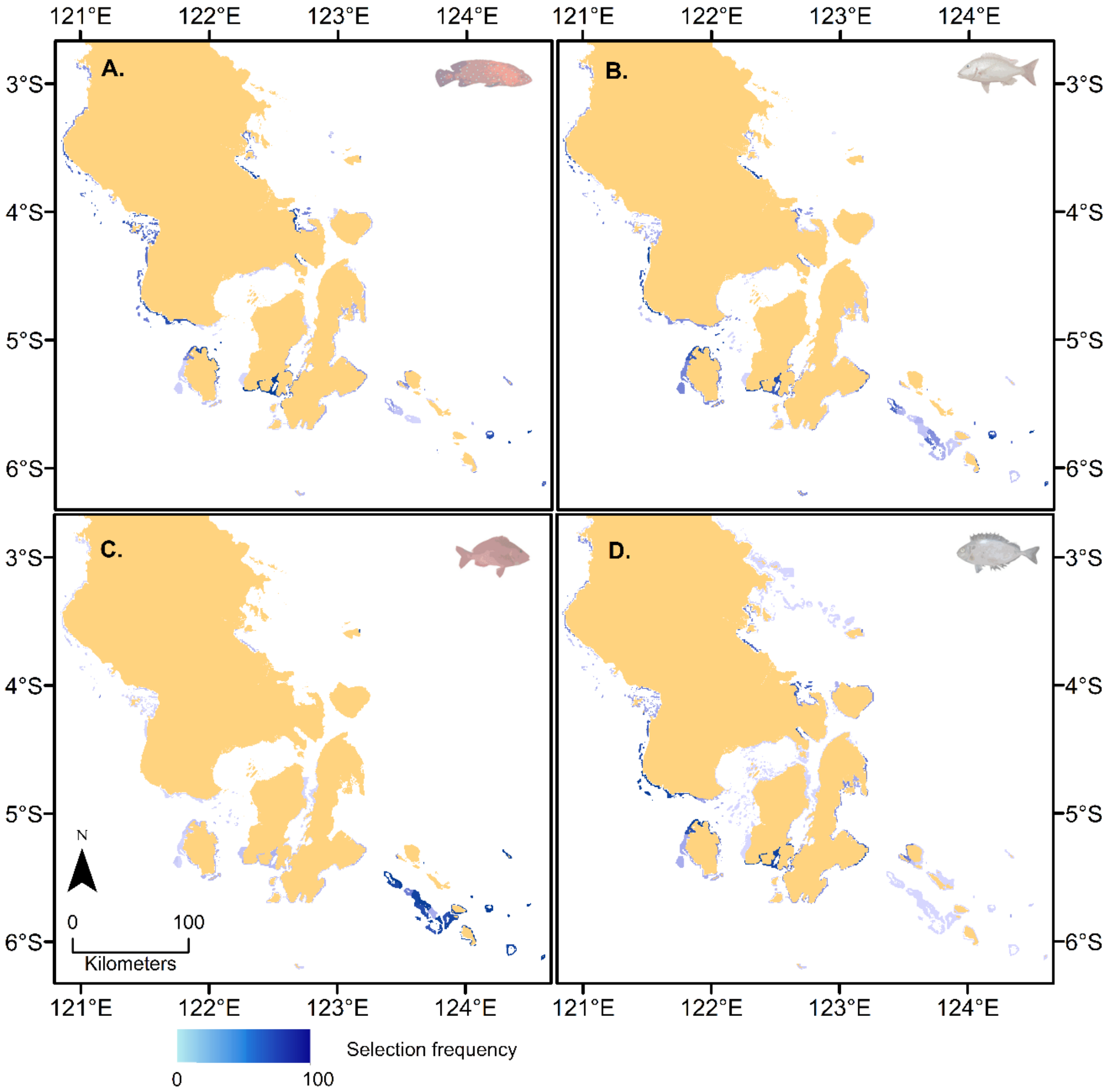

Figure S7.1.1. Map of planning unit selection frequency if Marxan regional prioritisation is used as a first step to identify a set of candidate reserve networks across the province.

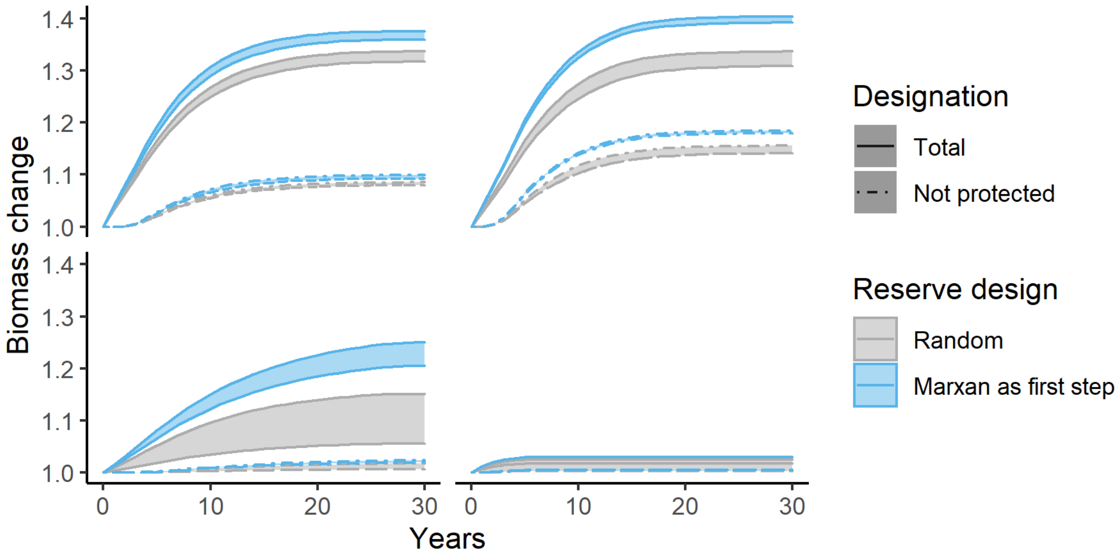

Figure S7.1.2. Biomass change across all planning units (solid line) and in fished areas (dotted lines) for the top five Marxan solutions of A. coral trout, B. emperor, C. snapper, and D. rabbitfish. Reserves are designed using either Marxan with Connectivity or through random selection. Reserves were implemented for 30 years after running models to equilibrium for 250 years. Biomass has been normalised on the y-axis.

7.1.2. Larval dispersal model

The biophysical model is a coupled hydrodynamic and biological model describing the dispersal dynamics of the population in the marine environment. We used the Delft3D-FLOW system (https://oss.deltares.nl/web/delft3d) to produce fine scale hydrodynamics for the model region from 1993 to 2012, the time period for which boundary conditions were available (average horizontal resolution of 500 m). Delft3D-FLOW is a finite mesh, terrain following, free surface, primitive equation model, which quantifies currents based on geostrophic, wind, and tidal forcing. Tidal boundary conditions on the open ocean boundaries were extracted from the TPXO China Sea model (Egbert & Erofeeva 2002), while non-tidal open boundary conditions were sourced from the global ocean circulation model HYCOM. NOAA's global NCEP reanalysis model (Kalnay et al. 1996) was used to provide spatially and temporally variable 10 m wind boundary conditions.

The hydrodynamic model was validated using sea level data from the Bau-Bau, Kendari and Palopo tide gauges, as no current data was readily available for the model domain. Data provided by the National Mapping Agency of Indonesia Badan Informasi Geospasial were available for 2012 for Kendari and Palopo and from 13/5/2012 until 1/1/2013 for Bau Bau. Comparison of the model to sea level data showed broadly good agreement between measured and modelled time series, although deviations were seen generally during spring tides. Linear regressions relating modelled to measured data had r^2 results of 0.91, 0.93 and 0.93 and root mean square errors of 0.16, 0.13, and 0.17 for Bau Bau, Kendari and Palopo, respectively.

The entire model domain extends for ~ 560 km in east-west direction and ~600 km in north-south direction. We used depth-averaged currents to 10 m deep to represent the water column where the vast majority of larvae are located. Larvae were assumed to be uniformly distributed across this 10m because data does not exist on whether they are positive or negatively buoyant. This is a common and conservative approach to these problems when the vertical movement is unknown or very uncertain. We used probability functions to determine when larvae settle. In short, larvae remain in the water column until they become competent to settle (using a species-specific parameterised Gamma function for gradual onset of competency). Larvae also have a daily settlement likelihood to control larval settlement if over suitable habitat. Together, these parameters accurately capture the biology and avoid problems associated with traditional particle tracking approaches (where 100% of particles instantly settle creating artefacts). Simply, modelled larvae only 'stop' if they settle to suitable habitat (as above) or if they are advected out of the domain (at open ocean boundaries) or if the simulation is stopped (max larval duration).

The power and precision of our dispersal model (described in detail in Treml et al. 2012, including a sensitivity analysis) is down to 1/100,000,000 per row of the connectivity matrix. This is for each source patch for each simulation in the ensemble. Using our advective transport scheme, we are not bound by traditional limitations of classic particle models. Larval dispersal simulations were initiated from the centroid of each reef patch (Figure S7.1.3.) in months appropriate for each species' life history (Table S7.1.1.).

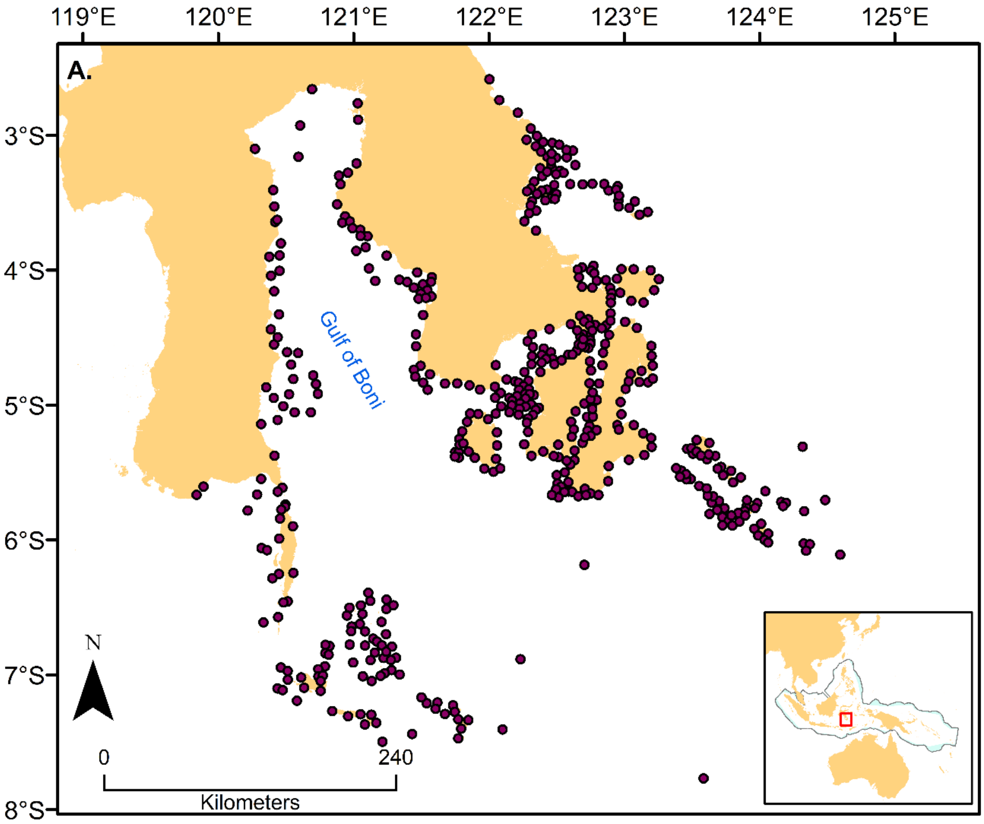

Figure S7.1.3. Location of 487 seeding locations, taken from the centroids of the coral reef habitat patches.

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Table S7.1.1. Larval life history traits used in the simulations.

Species	Competency (days)	Ref.	Larval duration (days)	maxPLD (days)	Ref.	Spawning window	Ref.	Habitat	Ref.
Coral trout	15	1	19-31	31	1	New moon, Sep-Nov	2	Reefs	2, 3
Emperor	24[a]	4	33.5 ± 5.9	40[b]	5	Mar-May	2	Reefs	2, 3
Snapper	25	6	33-40	40[c]	7	Summer months (Oct-Feb)[c]	7	Reefs	2, 3
Rabbitfish	10	6	17 ± 2[d]	19	8	Mar-Sep[d]	8	Reefs	2, 3

[a] Based on measurements of Lethrinidae from temperate coasts of Japan

[b] Based on values for Lethrinidae family from literature

[c] Based on Lutjanus carponotatus

[d] Based on Siganus spinus

References and notes

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6 Estimate

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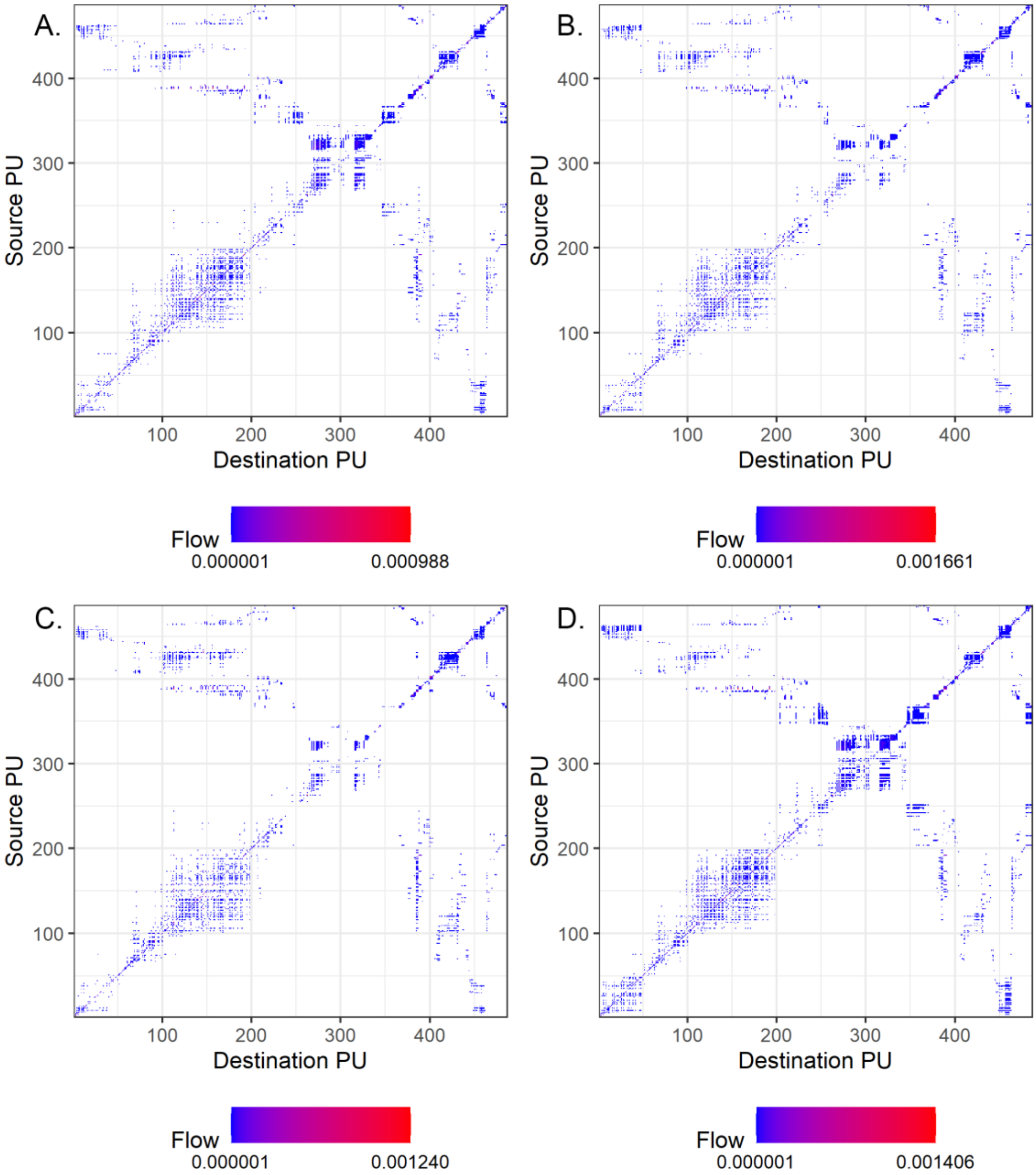

Figure S7.1.4. Larval dispersal flow matrix for A. coral trout, B. emperor, C. snapper, and D. rabbitfish. Flow was calculated as the dispersal probability scaled by relative amount of coral reef habitat in each of the 487 patches.

7.1.3. Metapopulation model

We used a discrete time, age-structured, single species, spatially explicit population model based on one developed by White et al. (2013) and Garavelli et al. (2018).

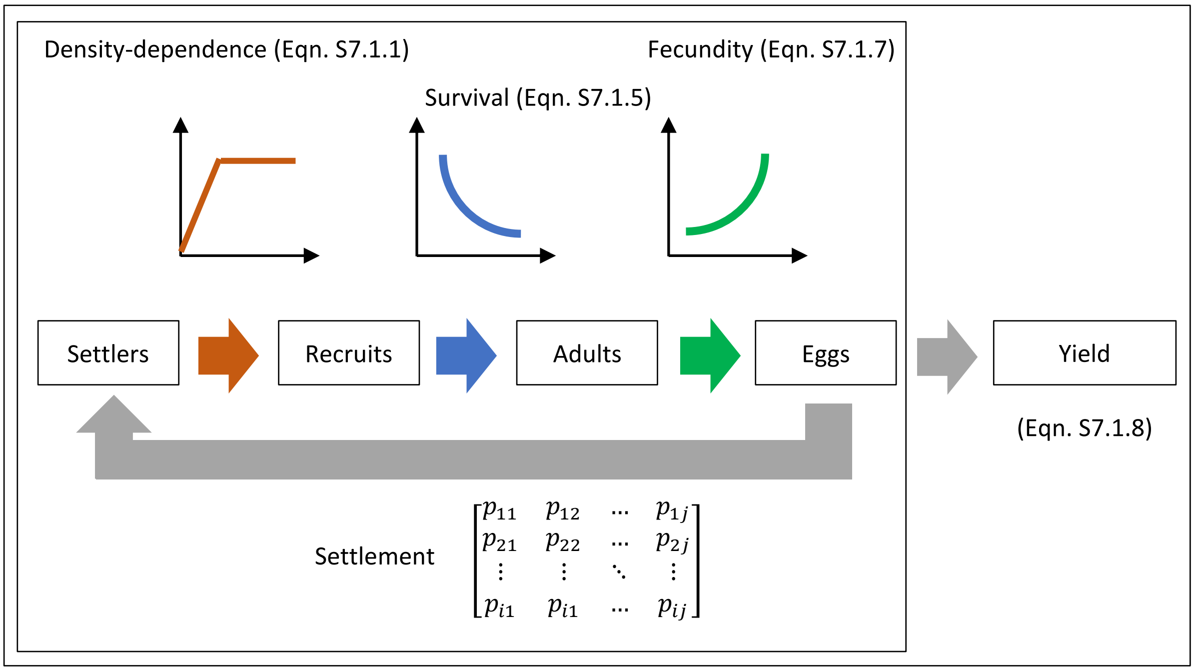

Figure S7.1.5. Summary of the metapopulation model. The square matrix used to calculate settlement refers to the probability matrix of the larval dispersal models.

Each time step, settlers undergo density-dependent survival, adults are exposed to natural and fishing mortality, adults produce eggs, and eggs are distributed across planning units following the larval dispersal probability matrix.

The number of recruits (R_i) from settlers (S_i) in each planning unit *i* was determined from a Beverton-Holt survivorship function

$$R_i = \frac{\alpha}{1 + \frac{\alpha}{\beta_i} S_i} S_i \qquad \text{(Eqn. S7.1.1)}$$

where α describes survival at low densities and β_i describes the maximum density of recruits in a planning unit.

Following Garavelli et al. (2018) and White (2010), α was calculated as the inverse of the biomass at which the population collapses

$$\alpha = \frac{1}{LEP \times FLEP \ \times \lambda_P} \qquad \text{(Eqn. S7.1.2)}$$

where *LEP* is the un-fished maximum lifetime egg production, *FLEP* is the fraction of natural *LEP* at which collapse occurs, and λ_P is the dominant eigenvalue of the larval dispersal probability matrix *P*.

LEP, which approximates to the spawning stock biomass per recruit, was calculated from fecundity (f_a) and survival (l_a) of all age classes

$$LEP = \sum l_a f_a \qquad \text{(Eqn. S7.1.3)}$$

The parameter β_i was considered to vary in space, being related to the habitat area within each planning unit

$$\beta_i = \ A_i \varepsilon \qquad \text{(Eqn. S7.1.4)}$$

where A_i is the habitat area and ε is the maximum density of recruits per km^2.

Survival of adults at different ages (l_a) was calculated using natural mortality (*N*) and fishing mortality (*F*) for individuals above age at first capture (t_c) following Goodyear (1993)

$$l_a = \begin{cases} e^{-M} \, for \ a \ < t_c \\ e^{-(N+F)} \, for \ a \ \geq t_c \end{cases} \qquad \text{(Eqn. S7.1.5)}$$

Fecundity of adults (f_a) was calculated from relationships between length and age. Length of an adult (L_a) was determined using von Bertalanffy parameters for asymptotic length (L_∞), growth rate (*K*), and age at which individual would be length 0 (t_0).

$$L_a = \ L_\infty(1 - e^{-K(a-t_0)}) \qquad \text{(Eqn. S7.1.6)}$$

From length we calculated egg production using α and β fecundity-at-length relationships which vary with species (Table S7.1.2.).

$$f_a = \ \alpha \, L_a{}^{\beta} \qquad \text{(Eqn. S7.1.7a)}$$

$$f_a = \ \alpha \, L_a + \beta \qquad \text{(Eqn. S7.1.7b)}$$

Equation S7.1.7a is for coral trout, snapper, and rabbitfish, while equation S7.1.7b is for emperor which has a linear relationship of fecundity to length (Toor 1964).

To estimate yield, we transformed population abundance to biomass using weight at length relationships

$$W_a = \gamma L_a \delta \qquad \text{(Eqn. S7.1.8)}$$

where γ and δ are parameters of weight at length.

Models were initially run to equilibrium for 250 years with an arbitrary starting population size with constant fishing pressure, after which a number of planning units were designated as reserves and fishing pressure was removed in these. Short-term patterns of biomass change were assessed after 30 years (250-280 years).

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Table S7.1.2. Population parameters for species modelled

Parameter	Coral trout	Ref.	Emperor	Ref.	Snapper	Ref.	Rabbitfish	Ref.
Fishing mortality (*F*)	0.65	1	0.8	1	0.64	1	0.48	1
Natural mortality (*N*)	0.2	2	0.22	4	0.112	31	0.61	17
Maximum age (years)	26	3	19	5	31	5	7.8	16
Age at maturity (years)	3	21	3	23	3.5	24	2	14
Age at first capture (years) (t_c)	3	6	3	6	3.5	6	2	6
Proportion of mature per year class	0≤3 1>3	21	0≤3 1>3	23	0≤3 1>3	24	0≤2 1>2	14
Fecundity at length (α)	4.7559	22	7308.44	23	314296	25	1.914	14
Fecundity at length (β)	2.6399	22	-207107.33	23	NA	25	3.663	14
Asymptotic von Bertalanffy length (L_∞)	80.6	1	33.9	9	72.8	5	25.2	13
Von Bertalanffy growth parameter (*K*)	0.521	1	0.7	9	0.3	5	1.872	13
Age at which individual is length 0 (t_0)	0	1	-0.04	9	0	5	0.02	13
Parameter of weight-at-length (γ)	0.0117	5	0.0251	5	0.0209	12	0.0234	15
Parameter weight-at-length (δ)	3.11	5	2.88	5	2.93	12	2.93	15
Fraction of natural LEP at which collapse occurs	0.35	20	0.35	20	0.35	20	0.35	20
Maximum density of recruits (per km^2) (ε)	4000	28	2000	29	1000	30	56000	27

1 Calculated from field data.

2 Average for species within genus in Frisch, A.J., Cameron, D.S., Pratchett, M.S., Williamson, D.H., Williams, A.J., Reynolds, A.D., Hoey, A.S., Rizzari, J.R., Evans, L., Kerrigan B. and G. Muldoon, 2016. Key aspects of the biology, fisheries and management of Coral grouper. Reviews in Fish Biology and Fisheries. 26(3):303-25.

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6 This parameter is unknown for the area of study. Therefore it was assumed that age of first capture=age of maturity

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27 Calculated from 2017 ecological survey data. S. canalicultus recruit data was not available. Counts of S. vermiculatus 7.5 cm in length were used as a proxy for S. canalicultus recruit density.

28 Calculated from 2017 ecological survey data. Counts of individuals 15 cm in length were used to calculate recruit density.

29 Calculated from 2017 ecological survey data. Counts of individuals 16 cm in length were used to calculate recruit density.

30 Calculated from 2017 ecological survey data. Counts of individuals 20 cm in length were used to calculate recruit density.

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7.1.4. Results of manta tow benthic surveys

Across all surveyed planning units, the most common substrate type was live hard coral (30% ± 16, mean and sd), followed by sand (26% ± 20), dead hard coral (14% ± 13), rubble (12% ± 10), rock (8% ± 9), soft coral (4% ± 7), and macroalgae (4% ± 5).

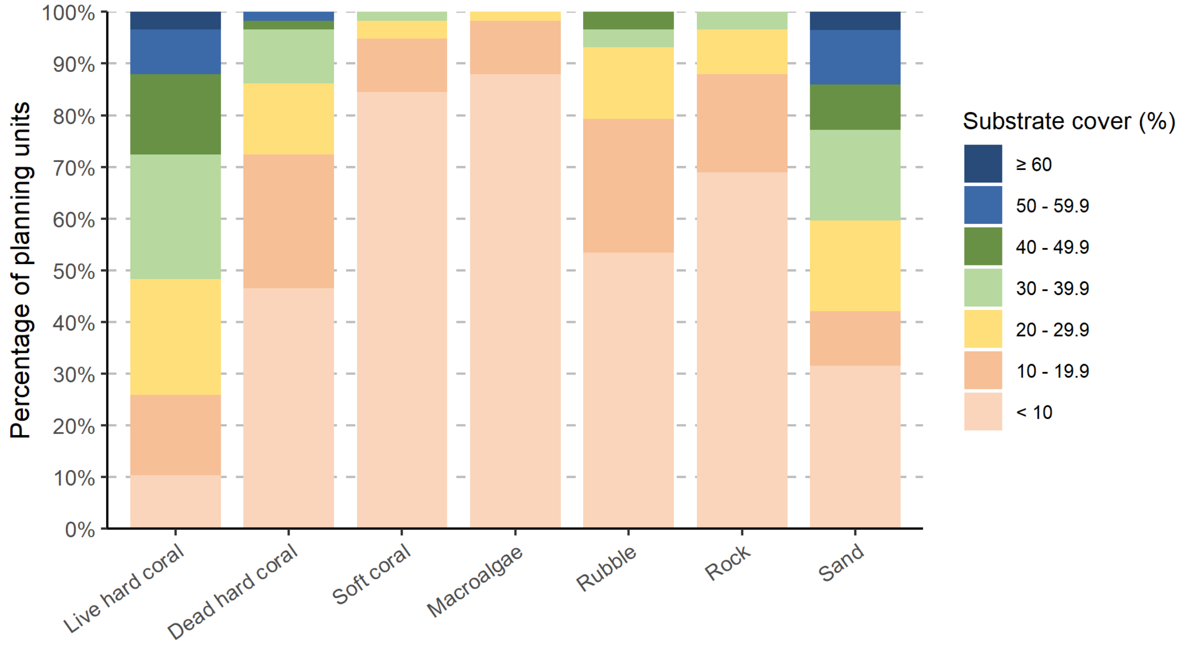

Figure S7.1.6. Proportion of substrate cover in planning units recorded in manta tows in Southeast Sulawesi. Each column on the x-axis is a different substrate type. Different colours show the proportion of cover in a given planning unit (PU). For example for live hard coral cover, 10% of all PUs had <10% cover, 26% of all PUs had <20% cover, and 48% of PUs had <30% cover.

7.1.5. Overlap in selection frequencies from 89 reserves + spatial dependency networks

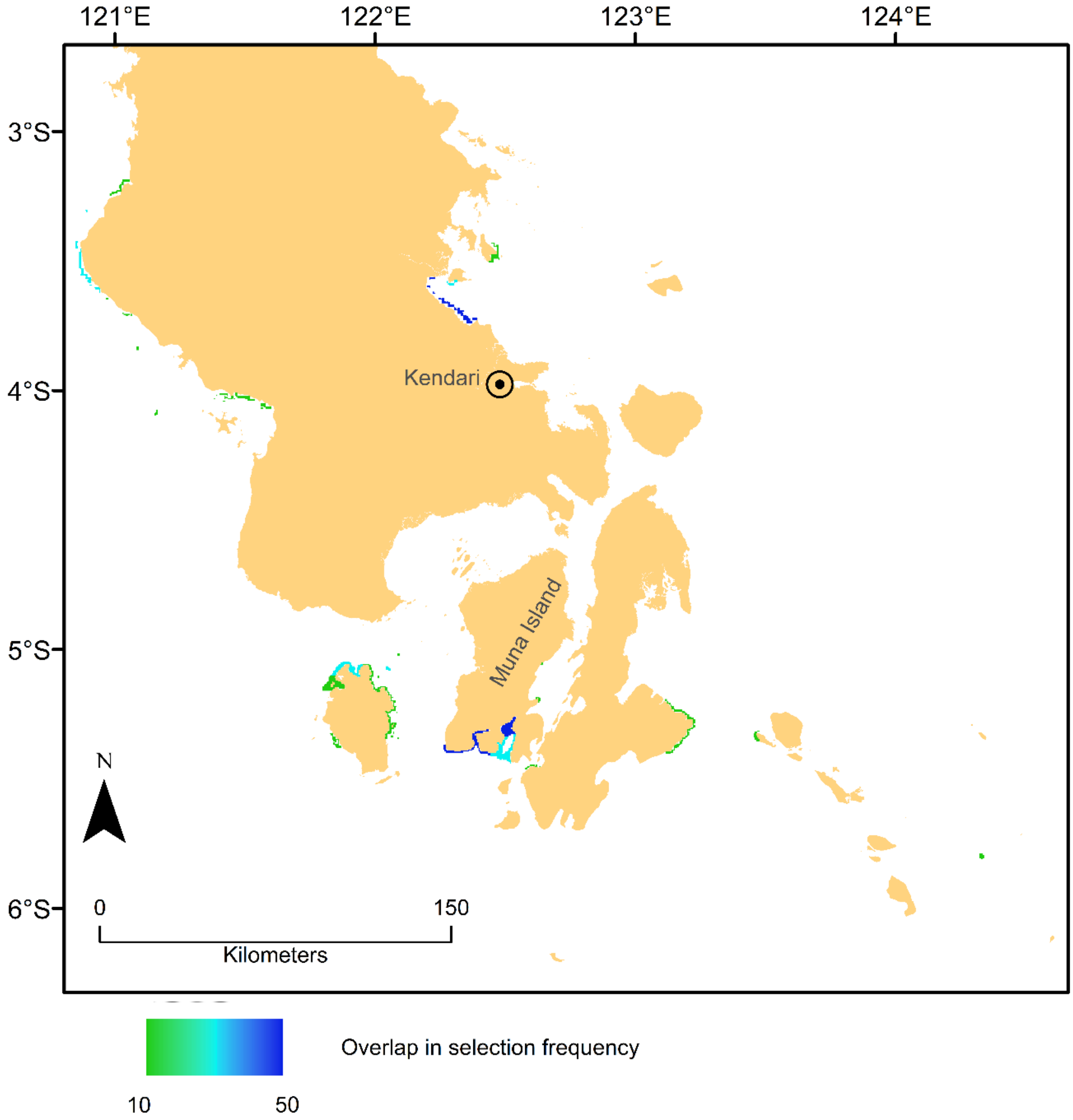

Figure S7.1.7. Map showing planning units where the Marxan solutions for all four species (Figure 2.4.) had high selection frequencies. Marxan with Connectivity as spatial dependencies was used to generate reserve networks based on expanding the 89 reserves established by stakeholder-driven selection. Dark blue planning units are those selected at least 50 times over the 100 Marxan repeat runs for all four species.

7.2. Appendix 7.2 – Supplementary Material for chapter 3

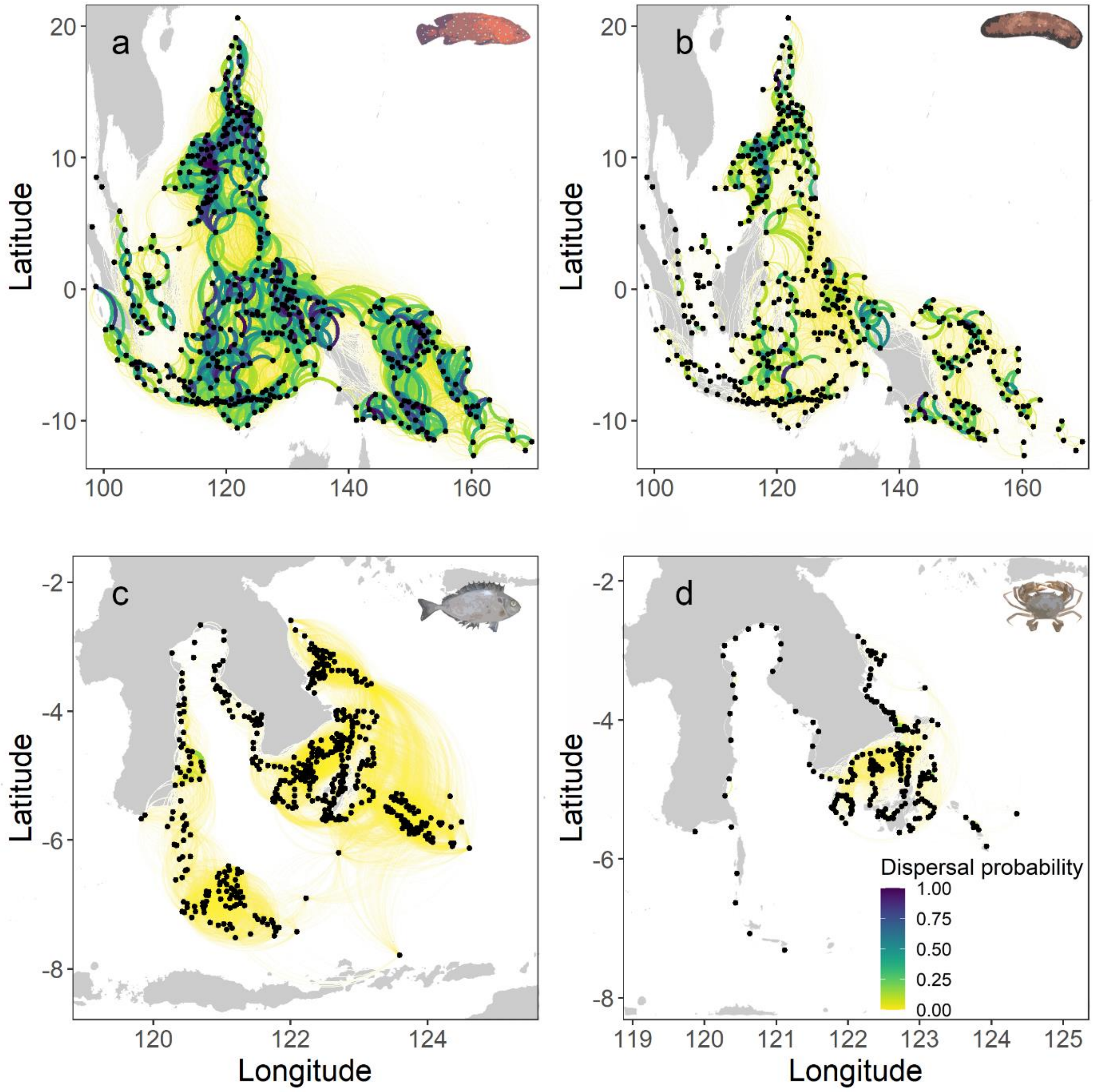

Figure S7.2.1. Representation of the case studies as network graphs. Nodes are the habitat centroids from which dispersal was initiated. Arcs show the probability of dispersal between different habitat patches, coloured by weight. Panels are for coral trout (a), sea cucumber (b), rabbitfish (c), and mudcrab (d).

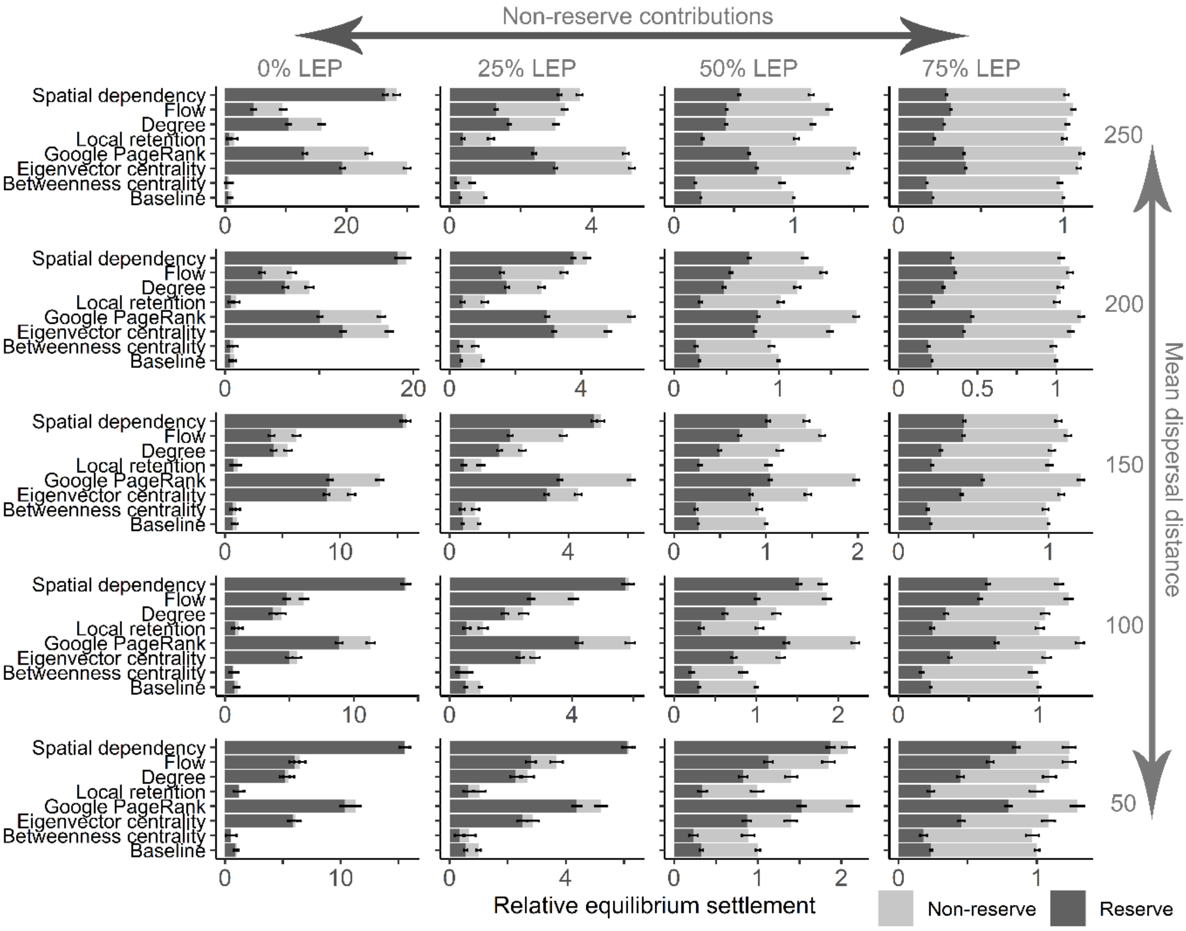

Figure S7.2.2. Performance of reserve networks protecting 20% of habitat designed using different connectivity methods for simulated seascapes with a near neighbour pattern. Each panel shows the mean of 100 seascapes for a given mean larval dispersal distance (rows) and assumption about non-reserve contributions (columns). A worst-case, scorched earth assumption outside reserves is represented by 0% lifetime egg production (LEP) relative to 100% inside reserves. Equilibrium settlement consists of settlement inside (dark grey) and outside (light grey) reserves and is relative to a baseline of 1 where reserves are designed with no connectivity. For example, relative equilibrium settlement of 2 is twice as much as that achieved by the baseline. Error bars indicate 89% confidence intervals of Bayesian linear models.

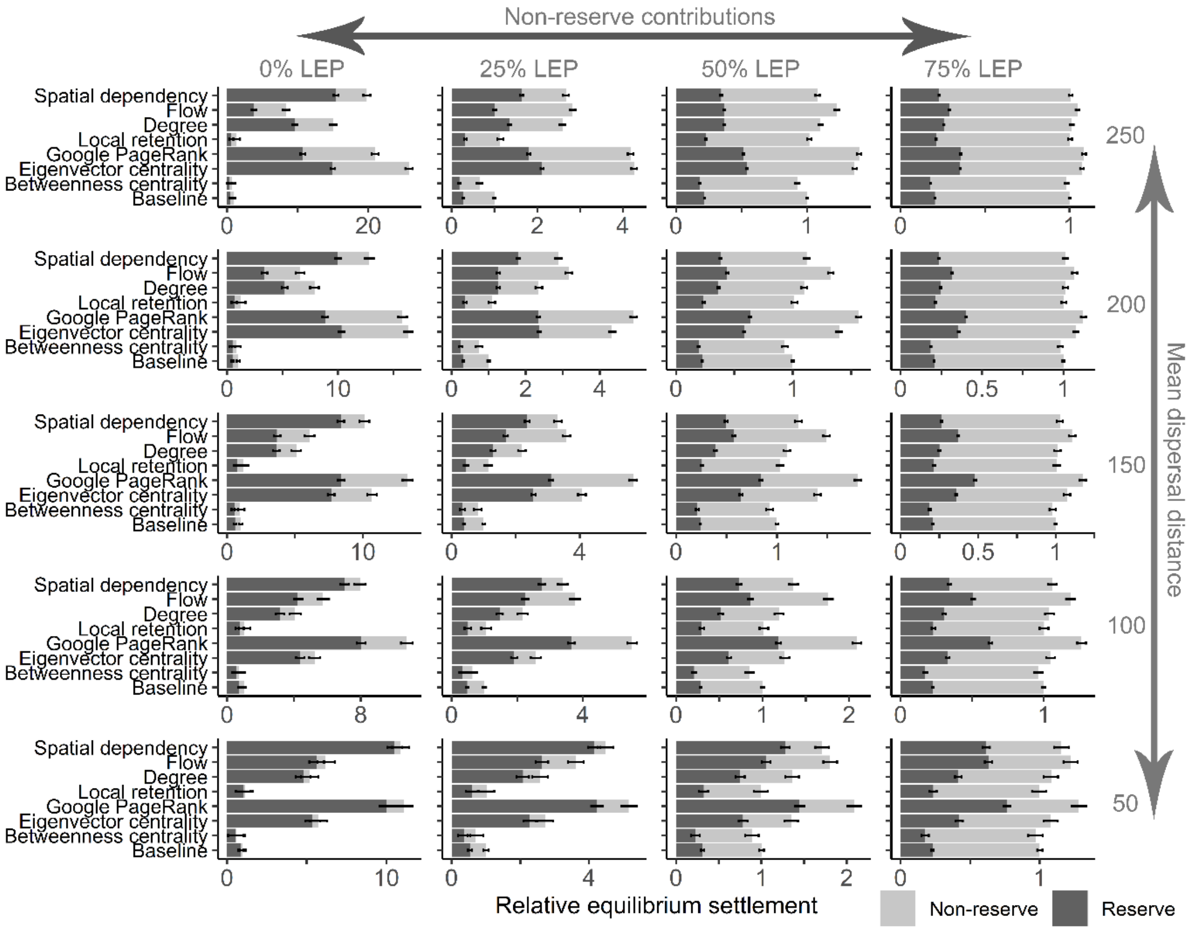

Figure S7.2.3. Performance of reserve networks protecting 20% of habitat designed using different connectivity methods for simulated seascapes with a small-world links pattern. Each panel shows the mean of 100 seascapes for a given mean larval dispersal distance (rows) and assumption about non-reserve contributions (columns). A worst-case, scorched earth assumption outside reserves is represented by 0% lifetime egg production (LEP) relative to 100% inside reserves. Equilibrium settlement consists of settlement inside (dark grey) and outside (light grey) reserves and is relative to a baseline of 1 where reserves are designed with no connectivity. For example, relative equilibrium settlement of 2 is twice as much as that achieved by the baseline. Error bars indicate 89% confidence intervals of Bayesian linear models.

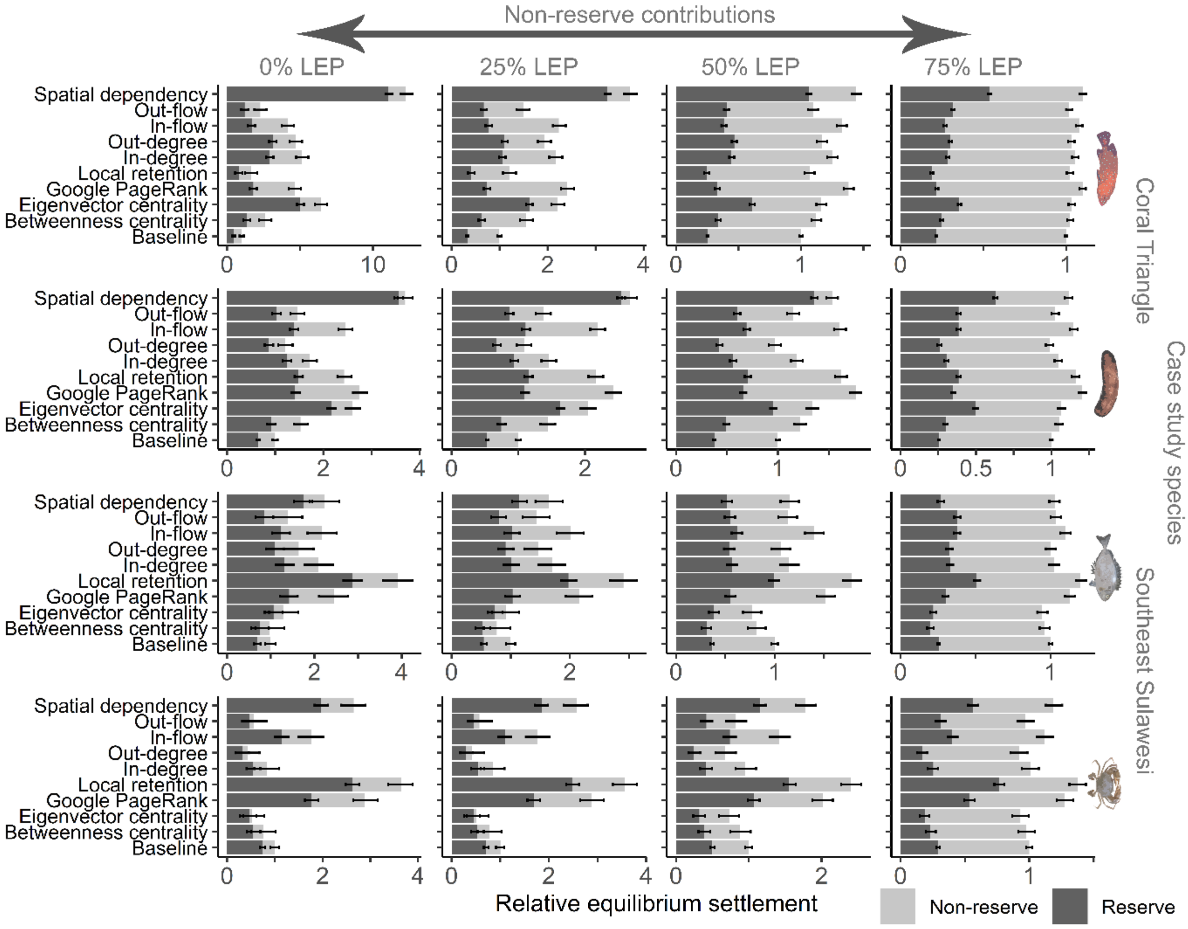

Figure S7.2.4. Performance of reserve networks protecting 20% of habitat designed using different connectivity methods for coral trout, sea cucumber, rabbitfish, and mud crab, from top to bottom. Columns represent different assumptions about non-reserve contributions, where 0% lifetime egg production (LEP) outside reserves represents a worst-case, scorched earth assumption. Equilibrium settlement consists of settlement inside (dark grey) and outside (light grey) reserves and is relative to a baseline of 1 where reserves are designed with no connectivity. For example, relative equilibrium settlement of 2 is twice as much as that achieved by the baseline. Error bars indicate 89% confidence intervals of Bayesian linear models.

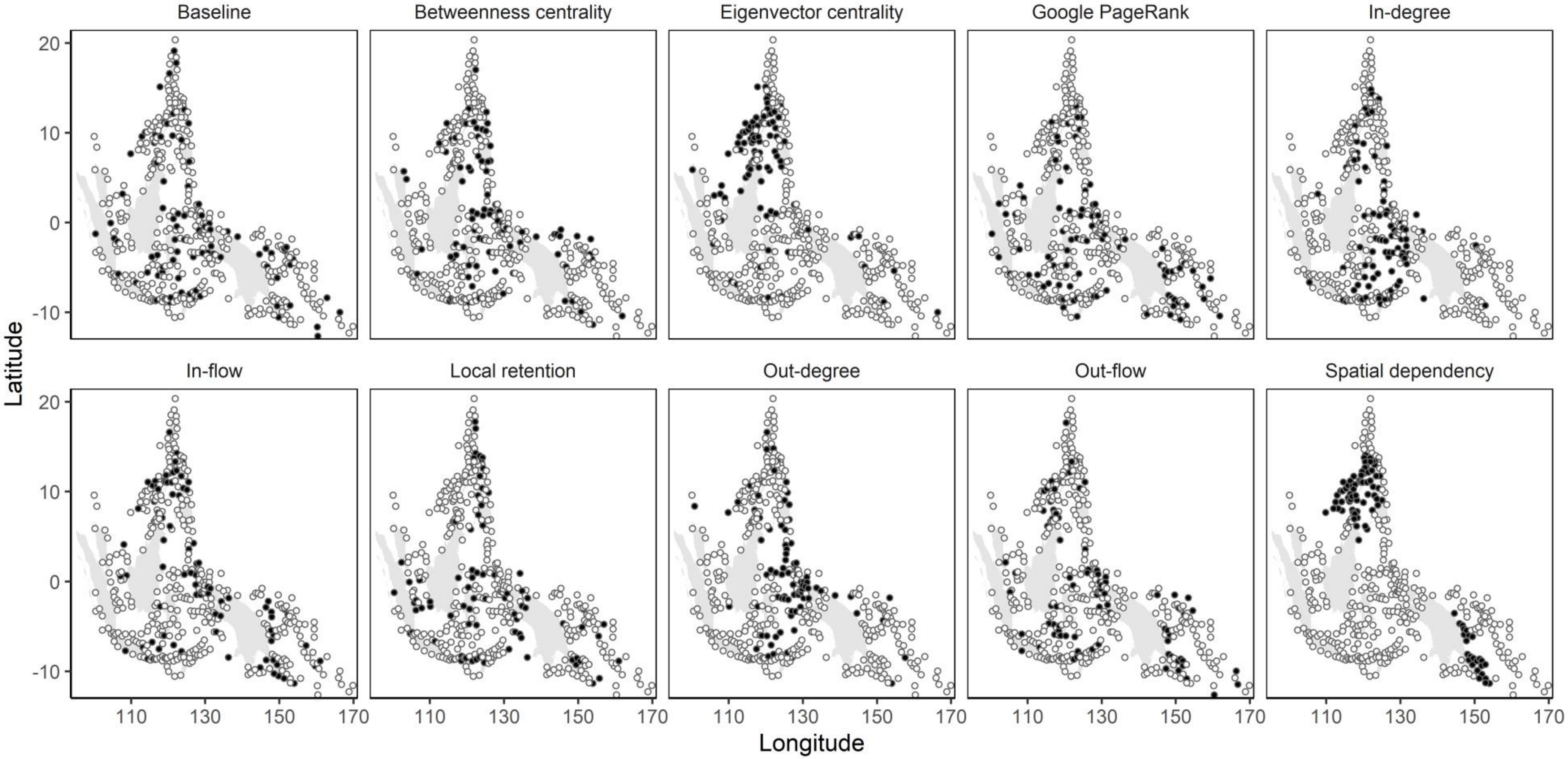

Figure S7.2.5. Top Marxan solution for coral trout in the Coral Triangle case study showing reserves (filled circles) and non-reserves (open circles) with a 20% habitat target. Panels show a baseline run not using any connectivity information, the connectivity-based features methods where targets are set for planning units scoring highly in a given metric, and the spatial dependency method.

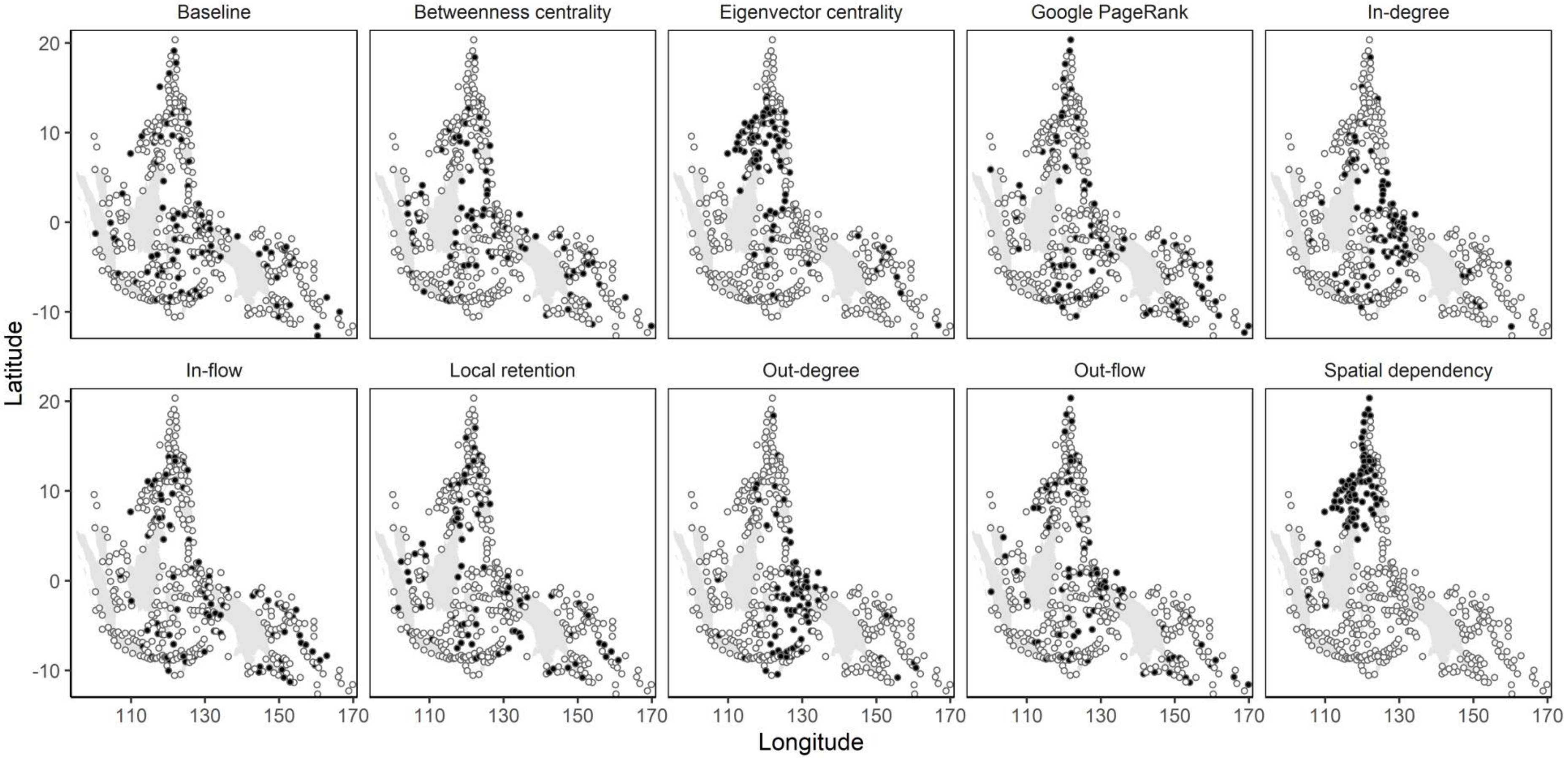

Figure S7.2.6. Top Marxan solution for sea cucumber in the Coral Triangle case study showing reserves (filled circles) and non-reserves (open circles) with a 20% habitat target. Panels show a baseline run not using any connectivity information, the connectivity-based features methods where targets are set for planning units scoring highly in a given metric, and the spatial dependency method.

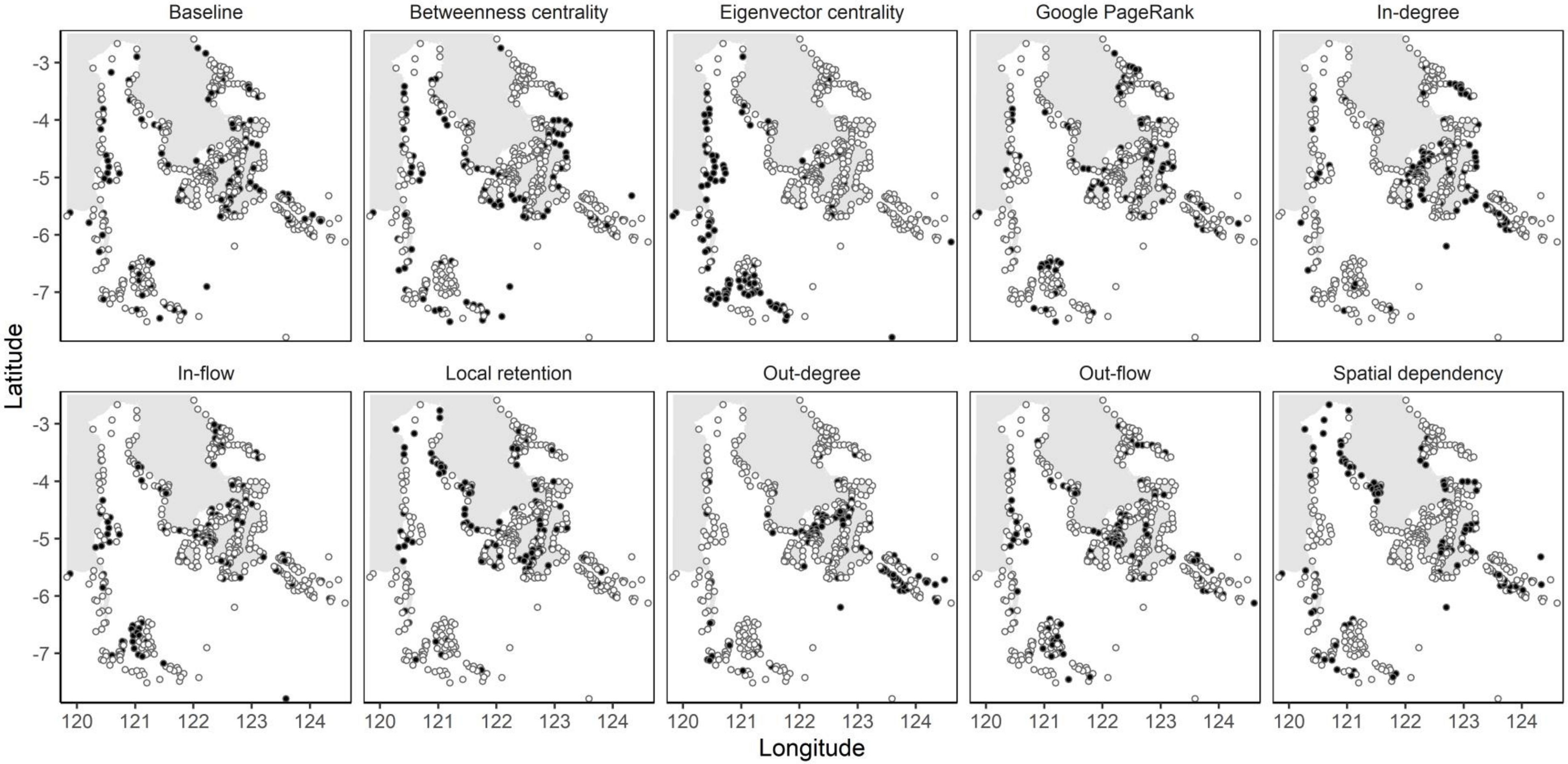

Figure S7.2.7. Top Marxan solution for rabbitfish in the Southeast Sulawesi case study showing reserves (filled circles) and non-reserves (open circles) with a 20% habitat target. Panels show a baseline run not using any connectivity information, the connectivity-based features methods where targets are set for planning units scoring highly in a given metric, and the spatial dependency method.

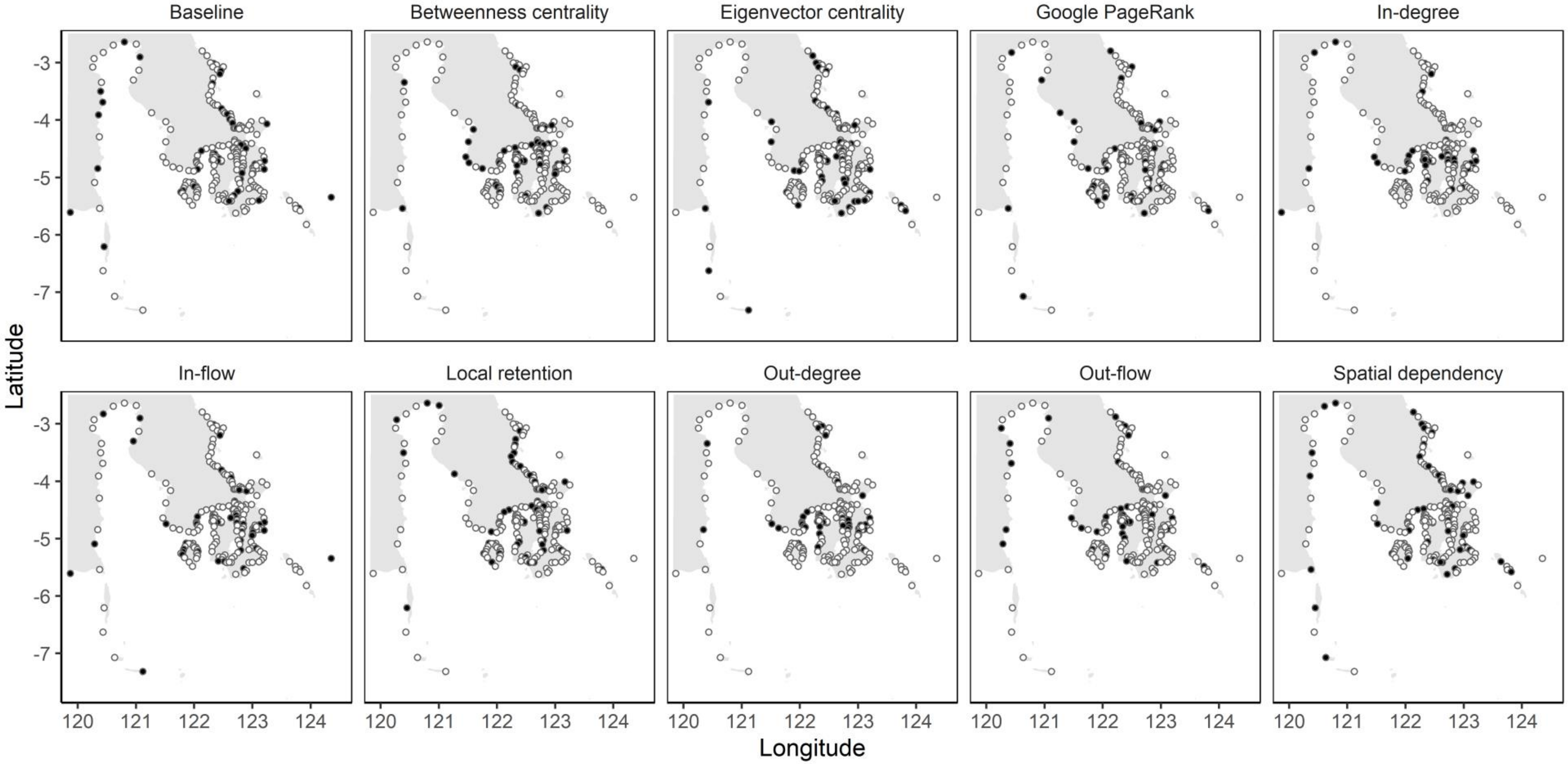

Figure S7.2.8. Top Marxan solution for mud crab in the Southeast Sulawesi case study showing reserves (filled circles) and non-reserves (open circles) with a 20% habitat target. Panels show a baseline run not using any connectivity information, the connectivity-based features methods where targets are set for planning units scoring highly in a given metric, and the spatial dependency method.

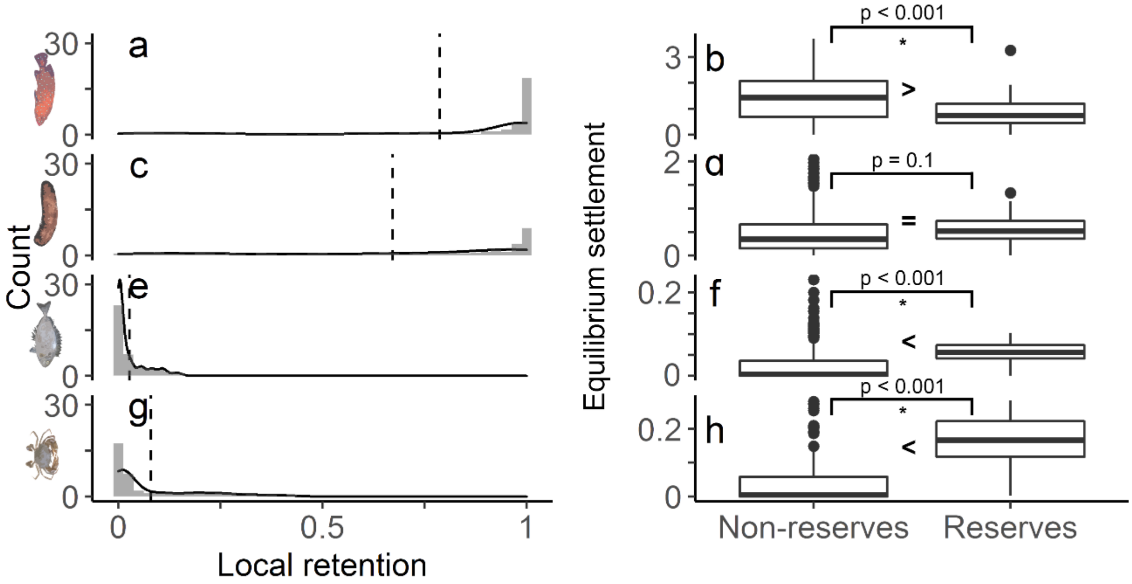

Figure S7.2.9. (a, c, e, g) Histograms of local retention of habitat patches with dashed lines giving the mean. (b, d, f, h) Boxplots comparing the equilibrium settlement in habitat patches before solutions have been implemented, divided into reserves which are designated when 20% of habitat is protected and patches that are not. Welch two-samples t-test showed equilibrium settlement in non-reserves was significantly lower than in reserves for mud crab and rabbitfish and reversed for coral trout, with no difference for mud crab. Rows correspond to coral trout and sea cucumber in the Coral Triangle case study and rabbitfish and mud crab in the Southeast Sulawesi case study, in descending order.

Table S7.2.1. General characteristics of the dispersal simulations for Southeast Sulawesi and the Coral Triangle.

a. Details of dispersal models

Location	**Spatial scale**	**Temporal scale**	**Horizontal resolution**	**Oceanographic model**	**Details**
Southeast Sulawesi	119.8°E to 124.9°E and 2.4°S to 8°S	1993-2012	~500 m	Delft3D-FLOW system (https://oss.deltares.nl/web/delft3d)	Finite mesh, terrain following, free surface, primitive equation model which quantifies currents based on geostrophic, wind, and tidal forcing. Models were validated using sea level data from tide gauges.
Coral Triangle	100°E to 170°E and 30°N to 30°S	2004-2012	~10 km	HYCOM GLBa0.08 (https://www.hycom.org/data/glba0pt08)	Hybrid isopycnal-sigma-pressure coordinate ocean model available as open-source.

b. Species life history parameters

Location	**Species**	**Competency (days)**	**Ref.**	**Larval duration (days)**	**maxPLD (days)**	**Ref.**	**Spawning window**	**Ref.**	**Habitat**	**Ref.**
Southeast Sulawesi	Rabbitfish	10	1	17 ± 2	19	2	Mar-Sep	2	Reefs	3, 4
Southeast Sulawesi	Mud crab	16 ± 5	5	38	38	5	April-June, Sept-Oct	5	Mangroves	5
Coral Triangle	Coral trout	10	6	35	35	6	Sept-Nov	6,7	Reefs	3,4
Coral Triangle	Sea cucumber	3	8,9	15	15	10,11,12	April, June	8	Reefs	3,4

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1. Estimate
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12. Uthicke, S. & Benzie, J. A. H. (2002). A genetic fingerprint recapture technique for measuring growth in ‘unmarkable’ invertebrates: negative growth in commercially fished holothurians (Holothuria nobilis). Mar. Ecol. Prog. Ser. 241, 221-226.

R Code used in the analysis of this study and underlying data can be found at https://github.com/dominicmuenzel/ComparingPrioritisationMethods.

7.3. Appendix 7.3 – Supplementary Material for chapter 4

Table S7.3.1. Larval life history traits used in the simulations.

Species	Competency (days)	Ref.	Larval duration (days)	maxPLD (days)	Ref.	Spawning window	Ref.	Habitat	Ref.
Coral trout	15	1	19-31	31	1	New moon, Sep-Nov	2	Reefs	2, 3
Snapper	25	4	33-40	40	5	Summer months (Oct-Feb)	5	Reefs	2, 3
Rabbitfish	10	4	17 ± 2	19	6	Mar-Sep	6	Reefs	2, 3
Octopus	15	7	30-35	35	8	Year-round	8	Reefs	9

References

1. Doherty, P.J., Fowler, A.J., Samoilys, M.A. & Harris, D.A. (1994). Monitoring the replenishment of coral trout (Pisces: Serranidae) populations. Bull. Mar. Sci., 54, 343–355.
2. SCRFA. Science and Conservation of Fish Aggregations Database. https://www.scrfa.org/database/ (12/2019)
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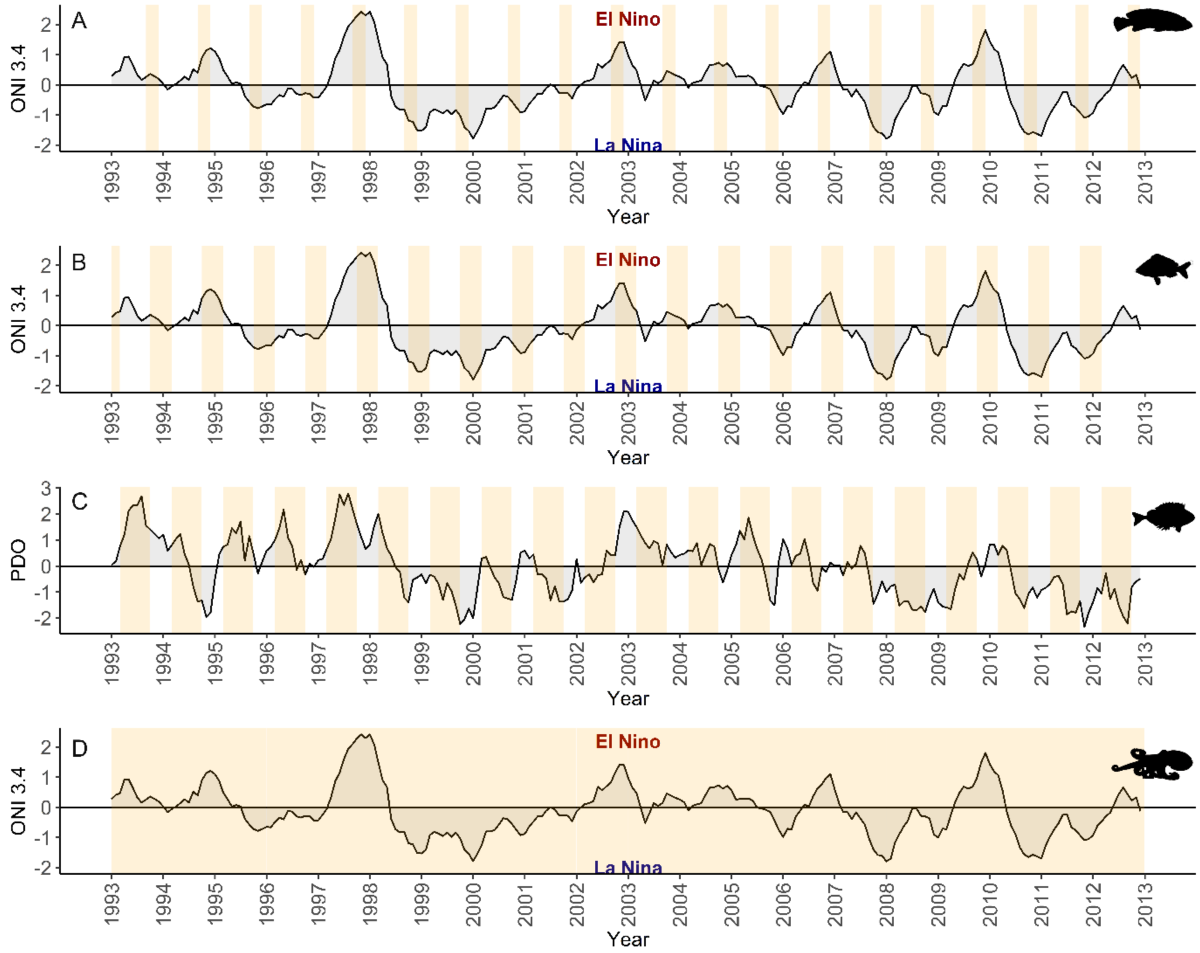

Figure S7.3.1. Spawning windows of species in each of the 20 modelled years (yellow rectangles) overlaid on the climatic indices having the highest correlation with solution ordinations (Figure 4.3.). In (A) *P. leopardus*, (B) *L. malabaricus*, and (D) *O. vulgaris* the index is the Oceanic Niño 3.4 Index, where large positive and negative values indicate strong El Niño and La Niña years, respectively. In (C) *S. canaliculatus* the index is the Pacific Decadal Oscillation.

7.4. Appendix 7.4 – Supplementary Material for chapter 5

Table S7.4.1. Species recorded by underwater visual census (UVC) and eDNA metabarcoding at coral reefs in the Wallacea region for which species distribution models were successfully built. Ensemble models were a combination of random forest (RF), generalised linear model (GLM), and generalised additive model (GAM). x indicates which environmental variables were used as predictors.

					Species recorded by UVC							
Species	**Model**	**SST mean**	**SST range**	**DHW>4**	**DHW max**	**Mean pH**	**Mean Salinity**	**Mean chlorophyll a**	**Mean O2**	**Mean PAR**	**Human pressure**	**Wave energy**
Acanthochromis polyacanthus	Ensemble		x		x	x			x			
Acanthurus mata	GLM					x	x		x		x	
Acanthurus pyroferus	Ensemble	x				x	x	x				
Acropora granulosa	GLM			x		x				x		x
Acropora hyacinthus	Ensemble				x		x	x	x			
Acropora nasuta	RF			x		x		x				x
Amanses scopas	Ensemble	x			x	x						x
Amblyglyphidodon aureus	RF		x				x	x			x	
Amblyglyphidodon curacao	Ensemble			x			x	x				x
Amblyglyphidodon leucogaster	Ensemble	x		x	x		x					
Amphiprion clarkii	GLM				x		x	x			x	
Arothron nigropunctatus	GAM	x			x			x			x	
Balistapus undulatus	Ensemble			x	x			x				x
Bodianus mesothorax	Ensemble	x				x				x	x	
Caesio teres	GLM					x	x		x		x	
Centropyge tibicen	Ensemble	x			x	x					x	
Centropyge vroliki	GLM				x	x		x				x
Cephalopholis cyanostigma	GLM	x						x		x		x
Cephalopholis urodeta	GLM			x			x	x			x	

Chaetodon baronessa	Ensemble				x			x	x			x
Chaetodon kleinii	Ensemble				x		x	x				x
Chaetodon lunulatus	Ensemble	x			x		x					x
Chaetodon rafflesi	GLM		x		x			x			x	
Chaetodon vagabundus	Ensemble			x	x					x	x	
Cheilinus fasciatus	Ensemble			x			x	x	x			
Chlorurus bleekeri	Ensemble			x	x	x	x					
Chlorurus sordidus	Ensemble		x	x					x			x
Chromis amboinensis	GLM			x	x		x				x	
Chromis atripes	Ensemble		x		x			x			x	
Chromis lepidolepis	Ensemble		x				x	x		x		
Chromis margaritifer	Ensemble	x				x				x		x
Chromis retrofasciata	Ensemble			x	x		x	x				
Chromis ternatensis	RF				x	x					x	x
Chromis viridis	GLM	x	x								x	x
Chromis weberi	Ensemble		x	x			x		x			
Chromis xanthura	Ensemble	x	x							x	x	
Chrysiptera rollandi	Ensemble		x	x	x				x			
Chrysiptera talboti	Ensemble	x						x	x	x		
Ctenochaetus binotatus	Ensemble			x		x	x		x			
Ctenochaetus cyanocheilus	Ensemble		x				x		x	x		
Ctenochaetus striatus	Ensemble	x	x		x			x				
Danafungia horrida	Ensemble	x	x	x						x		
Dascyllus reticulatus	Ensemble	x				x	x		x			
Dascyllus trimaculatus	GLM		x			x			x			x
Diproctacanthus xanthurus	Ensemble		x		x			x	x			
Echinopora gemmacea	GLM	x	x		x					x		
Favites abdita	Ensemble		x		x	x			x			
Favites pentagona	GLM			x		x		x	x			
Forcipiger flavissimus	Ensemble	x					x	x		x		

Fungia fungites	Ensemble			x			x	x		x		
Galaxea fascicularis	Ensemble				x		x	x	x			
Goniastrea edwardsi	GLM					x	x		x	x		
Halichoeres chrysus	GLM	x		x		x			x			
Halichoeres hortulanus	Ensemble	x						x			x	x
Halichoeres leucurus	Ensemble	x		x					x	x		
Halichoeres melanurus	Ensemble					x	x		x		x	
Halichoeres prosopeion	Ensemble		x	x		x		x				
Heniochus chrysostomus	Ensemble				x		x	x	x			
Heniochus varius	Ensemble					x		x	x		x	
Hydnophora rigida	Ensemble			x	x			x	x			
Labrichthys unilineatus	Ensemble				x		x	x	x			
Labroides bicolor	Ensemble	x		x						x		x
Labroides dimidiatus	Ensemble	x	x			x		x				
Labroides pectoralis	Ensemble			x			x	x			x	
Leptastrea pruinosa	Ensemble					x		x	x		x	
Lithophyllon repanda	Ensemble			x			x			x	x	
Lobophora sp.	Ensemble			x				x		x	x	
Lobophyllia recta	Ensemble	x				x	x				x	
Lutjanus bohar	Ensemble	x					x			x		x
Lutjanus decussatus	Ensemble		x	x		x	x					
Melichthys vidua	Ensemble					x		x	x		x	
Merulina ampliata	Ensemble	x		x				x			x	
Merulina scabricula	Ensemble		x	x					x	x		
Millepora dichotoma	GLM	x				x	x		x			
Monotaxis grandoculis	Ensemble			x	x		x			x		
Montipora aequituberculata	Ensemble			x		x	x	x				
Montipora confusa	Ensemble	x	x			x	x					
Mycedium elephantotus	Ensemble		x	x		x	x					
Neoglyphidodon melas	GLM			x				x	x		x	

Neoglyphidodon nigroris	GLM	x						x	x	x		
Odonus niger	GLM	x		x				x			x	
Ostorhinchus compressus	GLM	x		x	x		x					
Oxycheilinus digramma	GLM		x	x				x	x			
Oxypora lacera	Ensemble		x	x					x	x		
Paracirrhites forsteri	Ensemble	x						x	x	x		
Parupeneus barberinus	Ensemble							x	x	x	x	
Parupeneus crassilabris	Ensemble							x	x	x		x
Parupeneus multifasciatus	Ensemble			x		x			x	x		
Peyssonnelia sp.	Ensemble			x		x		x	x			
Platygyra pini	Ensemble		x						x	x		x
Pleuractis paumotensis	Ensemble			x			x			x	x	
Pocillopora verrucosa	Ensemble	x		x				x	x			
Pomacentrus amboinensis	Ensemble				x	x			x		x	
Pomacentrus auriventris	Ensemble	x	x			x			x			
Pomacentrus brachialis	Ensemble	x				x	x		x			
Pomacentrus lepidogenys	GLM		x		x			x				x
Pomacentrus moluccensis	GLM		x	x			x					x
Pomacentrus reidi	Ensemble				x	x		x		x		
Porites cylindrica	Ensemble	x			x				x	x		
Porites lobata	Ensemble				x				x		x	x
Porites lutea	Ensemble	x				x			x	x		
Pseudanthias huchtii	Ensemble				x		x	x			x	
Pseudocheilinus hexataenia	Ensemble	x						x	x	x		
Pterocaesio pisang	Ensemble							x	x	x	x	
Pterocaesio tile	Ensemble	x					x			x	x	
Pygoplites diacanthus	Ensemble	x				x	x	x				
Sargocentron caudimaculatum	Ensemble	x	x							x		x
Scarus niger	Ensemble							x	x	x		x
Scolopsis bilineatus	Ensemble	x	x	x	x							

Siganus puellus	GLM		x		x		x		x			
Siganus vulpinus	Ensemble		x					x			x	x
Stethojulis interrupta	Ensemble		x			x		x				x
Sufflamen bursa	Ensemble	x				x			x	x		
Thalassoma lunare	Ensemble	x	x			x		x				
Zanclus cornutus	Ensemble		x					x		x		x
Zebrasoma scopas	Ensemble					x	x	x				x

Species recorded by eDNA

Species	Model	SST mean	SST range	DHW>4	DHW max	Mean pH	Mean Salinity	Mean chlorophyll a	Mean O2	Mean PAR	Human pressure	Wave energy
Acanthaster planci	GAM				x		x	x			x	
Achlya bisexualis	Ensemble		x	x		x			x			
Acrossota amboinensis	GAM		x			x			x	x		
Agarum clathratum	Ensemble				x	x		x			x	
Aglaophenia tubiformis	Ensemble	x	x	x			x					
Akashiwo sanguinea	Ensemble	x					x	x	x			
Alexandrium fundyense	Ensemble				x		x	x		x		
Alexandrium ostenfeldii	GLM	x	x					x			x	
Alexandrium tamarense	Ensemble				x	x	x					x
Amathia vidovici	GLM		x	x	x			x				
Amphicorina mobilis	GLM				x		x		x	x		
Amphistegina lobifera	GLM		x		x	x				x		
Aphanomyces astaci	Ensemble		x				x		x	x		
Artemisina tubulosa	GLM	x	x		x				x			
Arthropoda environmental	GAM					x	x	x		x		
Atrina pectinata	Ensemble						x	x	x	x		
Aureococcus anophagefferens	Ensemble	x			x				x	x		
Auxis thazard	Ensemble					x	x	x				x
Azumapecten farreri	GLM			x		x			x	x		
Barranca multiflagellata	Ensemble	x			x			x	x			

Besnoitia besnoiti	Ensemble	x			x			x		x		
Bestioina similis	Ensemble	x					x	x		x		
Bestiolina brasiliensis	GLM			x		x					x	x
Bodianus mesothorax	GAM	x	x		x		x					
Boeckella gracilis	GLM				x		x	x				x
Botrydiopsis alpina	Ensemble	x				x	x	x				
Botryochytrium radiatum	GLM	x	x			x			x			
Breviturma brevipes	Ensemble		x			x			x	x		
Bulinus globosus	GLM		x		x	x			x			
Caesio cuning	GLM					x	x		x			x
Callianax biplicata	Ensemble	x		x					x	x		
Calocalanus styliremis	Ensemble	x					x				x	x
Caryophyllia smithii	GAM	x							x	x	x	
Cavolinia uncinata	Ensemble		x				x			x		x
Cerithium coralium	GAM		x		x		x			x		
Chaetoceros costatus	Ensemble	x			x	x						x
Chaetoceros diadema	Ensemble				x		x	x	x			
Chaetoceros socialis	Ensemble	x	x		x		x					
Cheilinus chlorourus	GLM		x				x	x	x			
Chromis scotochiloptera	Ensemble	x	x			x		x				
Chromis xanthochira	GLM			x			x		x	x		
Chrysiptera rollandi	Ensemble					x	x	x			x	
Ciliophrys infusionum	Ensemble	x		x			x	x				
Clarkcomanthus littoralis	Ensemble				x			x	x			x
Coeloseris mayeri	GLM		x	x			x			x		
Colpomenia sinuosa	Ensemble	x						x	x	x		
Cominella nassoides	Ensemble				x		x	x			x	
Conqueria laevis	GAM		x		x			x				x
Conticribra weissflogii	Ensemble	x			x	x				x		
Copilia mirabilis	Ensemble	x	x		x				x			

Cornirostra pellucida	Ensemble		x			x			x		x	
Cosmocalanus darwinii	Ensemble	x	x		x		x					
Creseis acicula	Ensemble			x	x	x	x					
Creseis virgula	Ensemble	x	x				x	x				
Crithidia expoeki	Ensemble	x					x			x	x	
Cunea thuwala	Ensemble		x	x	x	x						
Cyanea tzetlinii	Ensemble		x				x			x		x
Dascyllus reticulatus	GLM	x						x		x		x
Dascyllus trimaculatus	Ensemble		x					x		x	x	
Desmarestia japonica	Ensemble		x			x	x				x	
Desmarestia menziesii	GLM			x			x	x			x	
Diacronema vlkianum	Ensemble	x	x			x			x			
Dictyocha octonaria	GAM	x						x	x	x		
Dictyonella incisa	Ensemble				x	x				x		x
Dictyosiphon foeniculaceus	RF	x				x	x	x				
Dictyota linearis	Ensemble	x			x	x	x					
Dinobryon divergens	Ensemble	x				x					x	x
Dioithona oculata	Ensemble	x				x				x		x
Dioithona rigida	Ensemble	x			x	x	x					
Diphyes chamissonis	Ensemble		x	x			x			x		
Ectocarpus fasciculatus	Ensemble	x		x		x		x				
Effrenium voratum	Ensemble			x			x		x	x		
Encrasicholina eheteroloba	GAM	x			x		x	x				
Endectyon fruticosum	Ensemble							x	x	x		x
Eucalanus pseudattenuatus	Ensemble	x	x				x			x		
Euchirella pulchra	Ensemble		x	x	x						x	
Euthora cristata	GLM	x	x			x					x	
Flexammina islandica	GLM	x	x		x		x					
Fucus vesiculosus	Ensemble	x		x		x				x		
Galaxea fascicularis	GLM			x	x		x		x			

Geminigera cryophila	Ensemble				x			x	x	x		
Globigerinita glutinata	Ensemble			x	x			x		x		
Globoquadrina conglomerata	Ensemble	x						x	x	x		
Gonyaulax elongata	Ensemble	x	x				x	x				
Gymnodinium microreticulatum	Ensemble			x				x	x	x		
Gyraulus soritai	Ensemble	x		x			x			x		
Haliclona amboinensis	GAM		x			x	x			x		
Halophytophthora vesicula	Ensemble	x					x	x		x		
Halopsis ocellata	GAM				x		x		x	x		
Harpacticus flexus	Ensemble				x	x	x	x				
Haslea ostrearia	GLM		x				x	x		x		
Heliconoides inflatus	Ensemble		x	x	x		x					
Helkesimastix marina	Ensemble				x	x	x				x	
Herposiphonia tenella	Ensemble			x				x		x		x
Hippocrepinella hirudinea	GLM	x	x	x				x				
Hormosira banksii	Ensemble				x		x	x	x			
Hymenena kylinii	GAM		x						x	x	x	
Iasis cylindrica	Ensemble							x	x	x		x
Isochrysis galbana	GLM		x				x			x	x	
Jassa marmorata	Ensemble	x	x				x		x			
Korotnevella heteracantha	GAM				x	x				x	x	
labyrinthulid quahog	GLM	x	x			x			x			
Laminariocolax aecidioides	Ensemble						x	x	x	x		
Liriope tetraphylla	Ensemble	x	x		x				x			
Livoneca redmanii	Ensemble						x	x	x			x
Lobophora declerckii	Ensemble	x	x				x	x				
Longipedia ulleungensis	GAM	x	x	x					x			
Macropharyngodon ornatus	Ensemble	x				x		x		x		
Margalefidinium fulvescens	Ensemble	x				x	x		x			
Melichthys niger	GLM	x	x		x			x				

Melosira nummuloides	Ensemble	x	x			x	x					
Montipora aequituberculata	Ensemble			x	x	x				x		
Mutimo cylindricus	Ensemble	x	x					x			x	
Neofibularia hartmani	Ensemble					x	x			x		x
Neogloboquadrina dutertrei	GLM	x				x	x			x		
Oithona dissimilis	Ensemble			x		x			x	x		
Opecarcinus hypostegus	Ensemble		x	x		x	x					
Ophiocoma erinaceus	Ensemble			x			x	x		x		
Ophionereis porrecta	GLM				x		x	x		x		
Ophionereis schayeri	Ensemble	x				x			x			x
Ophiothrix trilineata	Ensemble						x	x	x		x	
Pandora neoaphidis	Ensemble		x		x	x	x					
Paracalanus parvus	Ensemble	x	x			x					x	
Paralecudina anankea	Ensemble			x		x				x	x	
Paramoeba pemaquidensis	Ensemble			x			x	x	x			
Parupeneus multifasciatus	Ensemble			x	x			x		x		
Parvocalanus crassirostris	Ensemble	x	x					x		x		
Pavlova gyrans	Ensemble		x	x		x			x			
Peripatopsis moseleyi	GAM								x	x	x	x
Perkinsus olseni	GLM					x	x		x	x		
Phaeostroma pustulosum	Ensemble	x			x					x	x	
Phainogullmia aurata	Ensemble	x							x		x	x
Phakellia tropicalis	GAM			x	x		x	x				
Phallusia nigra	Ensemble	x	x				x	x				
Pleurobranchus forskalii	GAM						x	x		x	x	
Pluteus cervinus	Ensemble					x	x	x		x		
Pomacentrus amboinensis	GAM			x		x	x				x	
Pomacentrus bankanensis	Ensemble	x					x	x	x			
Pomacentrus brachialis	GLM	x	x			x						x
Procambarus clarkii	Ensemble						x	x			x	x

Prorocentrum lima	GLM			x		x			x	x		
Prototheca blaschkeae	Ensemble					x	x			x	x	
Pseudancylastrum frolikhae	GLM		x	x		x	x					
Pseudoparamoeba garorimi	Ensemble				x		x	x			x	
Pseudopedinella elastica	Ensemble	x	x					x		x		
Pterocaesio chrysozona	GLM			x					x		x	x
Pterocaesio tessellata	GLM						x	x		x		x
Ptilocaulis walpersi	Ensemble		x			x			x	x		
Pulleniatina obliquiloculata	Ensemble		x			x				x	x	
Pyramimonas parkeae	GLM		x		x			x			x	
Pythium inflatum	Ensemble	x		x		x					x	
Rastrelliger kanagurta	Ensemble							x	x		x	x
Salarias fasciatus	Ensemble	x	x		x		x					
Sarcocystis fulicae	Ensemble		x			x	x			x		
Sarcocystis sinensis	Ensemble	x		x			x			x		
Sarcocystis zamani	Ensemble					x	x			x		x
Sarcophyton trocheliophorum	Ensemble				x	x		x			x	
Scolopsis monogramma	GAM		x			x	x		x			
Scomberoides lysan	Ensemble		x	x	x						x	
Scytosiphon promiscuus	Ensemble				x	x				x	x	
Scytosiphon shibazakiorum	GAM		x						x	x	x	
Selar crumenophthalmus	GAM		x		x	x		x				
Sicyopterus stimpsoni	Ensemble		x			x	x		x			
Skeletonema potamos	Ensemble		x	x				x	x			
Sorogena stoianovitchae	GAM	x				x		x			x	
Spirastrella hartmani	Ensemble			x			x		x		x	
Splanchnotrophus angulatus	Ensemble			x			x	x	x			
Stictyosiphon soriferus	GAM						x			x	x	x
Stylocheilus striatus	Ensemble	x		x			x		x			
Subeucalanus pileatus	Ensemble				x			x		x		x

Synchaeta pectinata	Ensemble	x					x	x		x		
Temora discaudata	Ensemble		x	x			x			x		
Temora stylifera	Ensemble	x	x		x		x					
Terpios hoshinota	Ensemble			x	x		x					x
Thrinacophora cervicornis	Ensemble			x	x	x						x
Torodinium teredo	Ensemble		x	x					x	x		
Triconia minuta	Ensemble				x		x	x				x
Trochus maculatus	Ensemble		x			x	x				x	
Tubipora musica	Ensemble	x							x	x	x	
Ulua mentalis	Ensemble			x	x		x	x				
uncultured Jaminaea	GLM				x	x		x		x		
uncultured Jiaozhou	Ensemble			x	x	x				x		
Vermamoeba vermiformis	Ensemble	x	x		x			x				
Virgulinella fragilis	Ensemble				x		x			x		x
Vulsella vulsella	GLM		x		x		x	x				
Xcellia lamelliphila	GLM		x	x					x		x	

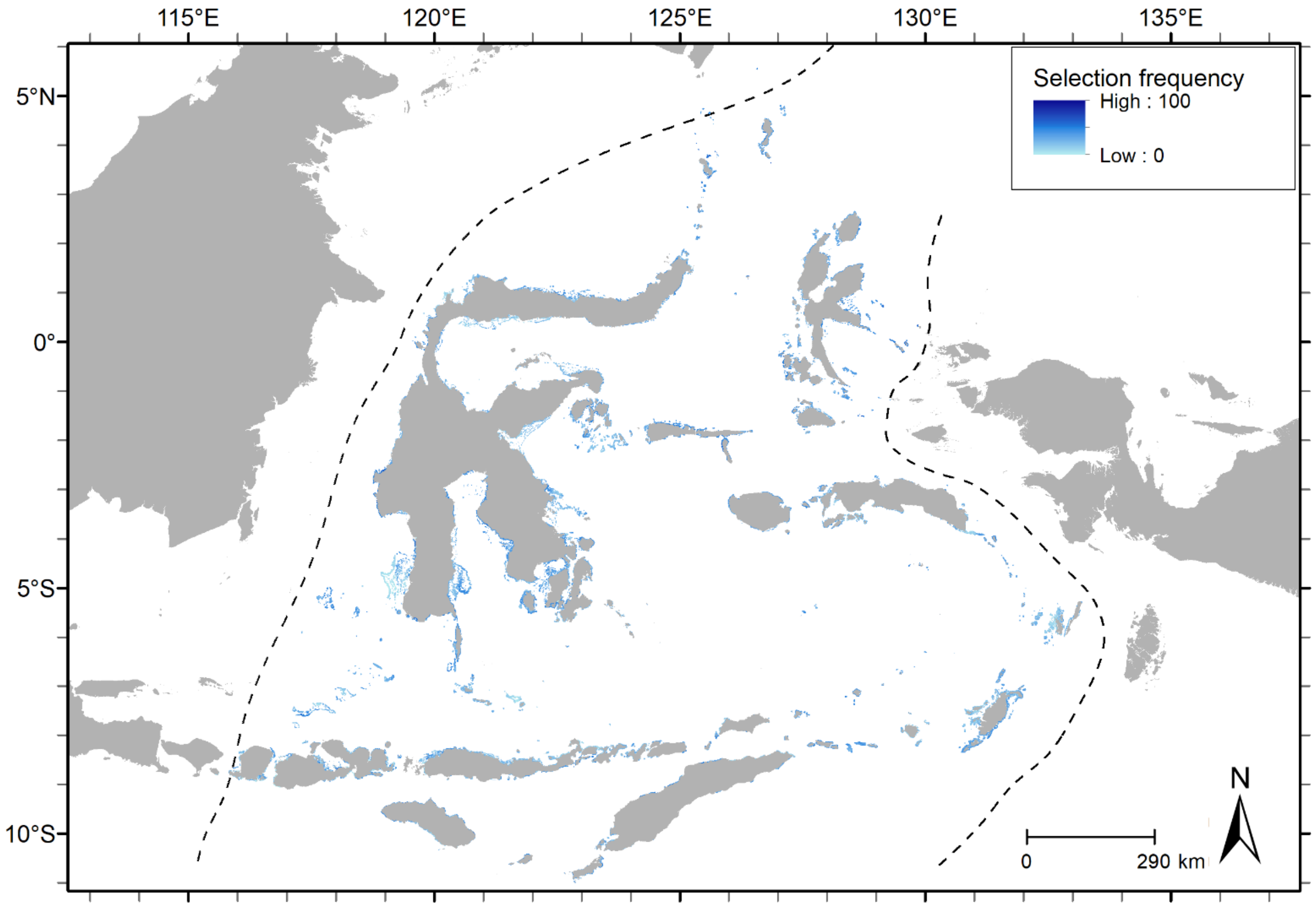

Figure S7.4.1. Map of planning unit selection frequency for Marxan spatial prioritisation where targets are set for species identified by UVC surveys. Selection frequency is how often planning units are selected in solutions across 100 runs.

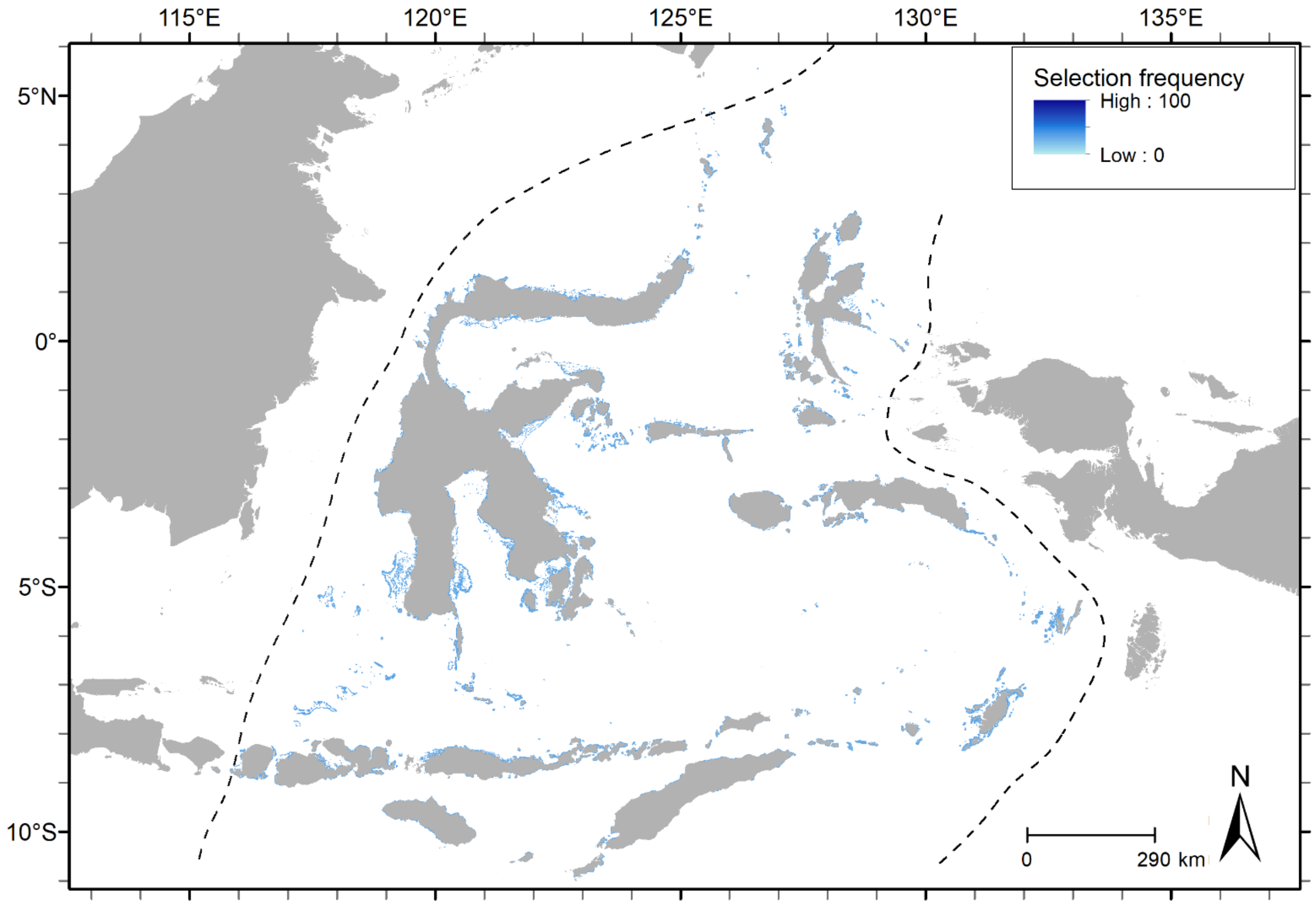

Figure S7.4.2. Map of planning unit selection frequency for Marxan spatial prioritisation where targets are set for species identified by eDNA metabarcoding. Selection frequency is how often planning units are selected in solutions across 100 runs.

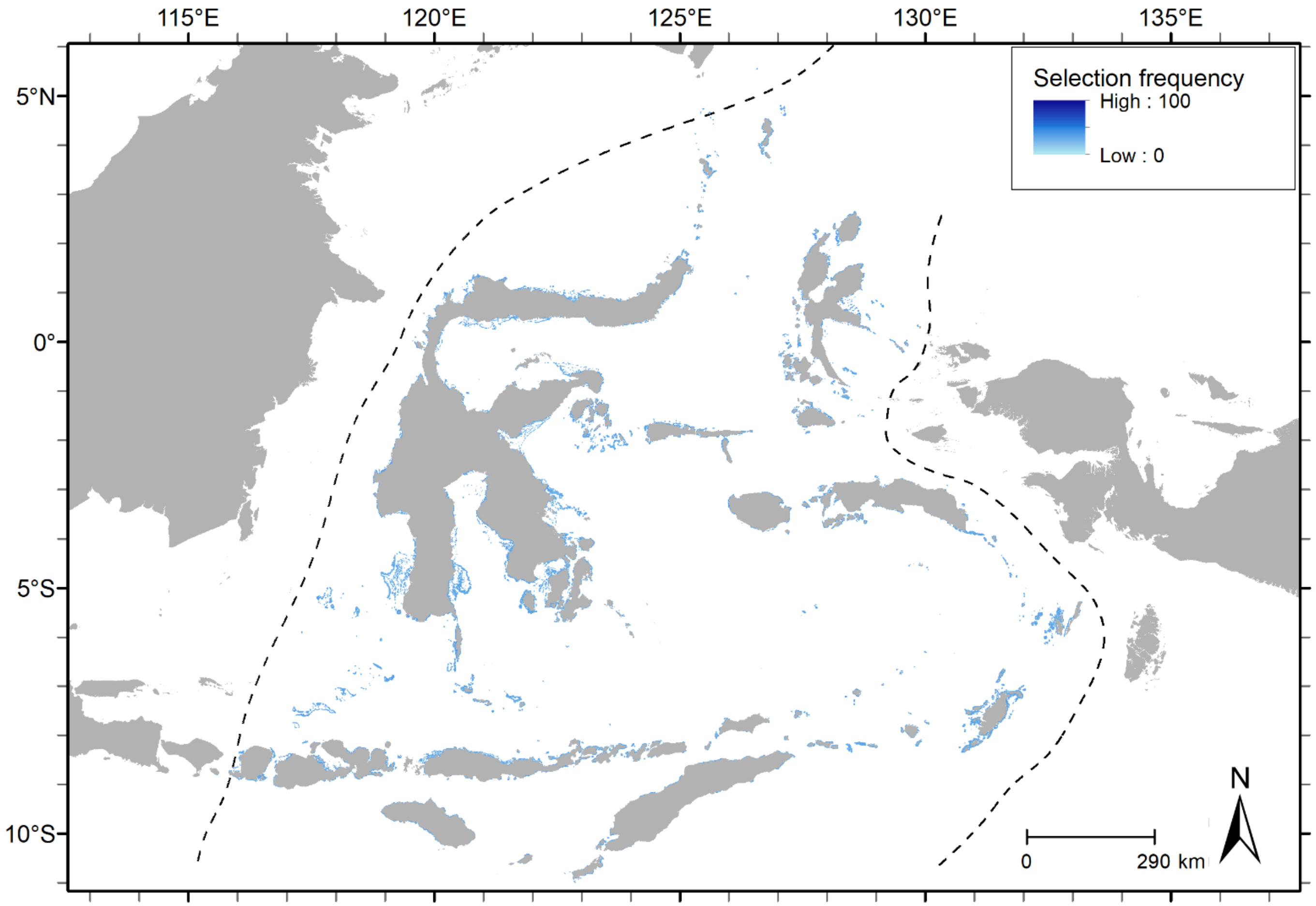

Figure S7.4.3. Map of planning unit selection frequency for Marxan spatial prioritisation where targets are set for species identified by both UVC and eDNA metabarcoding. Selection frequency is how often planning units are selected in solutions across 100 runs.