Received: 3 March 2022 | Revised: 20 September 2022 | Accepted: 1 October 2022

DOI: 10.1111/cobi.14038

Conservation Biology

CONTRIBUTED PAPERS

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

Dominic Muenzel[1] | Kay Critchell[2] | Courtney Cox[3] | Stuart J. Campbell[3,4] | Raymond Jakub[3,4] | Wahid Suherfian[4] | La Sara[5] | Iliana Chollett[6] | Eric A. Treml[2] | Maria Beger[1,7]

[1]School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

[2]School of Life and Environmental Sciences, Centre for Integrative Ecology, Deakin University, Geelong, Victoria, Australia

[3]Rare, Arlington, Virginia, USA

[4]Rare Indonesia, Kota Bogor, Indonesia

[5]Department of Aquatic Resources Management, Faculty of Fisheries and Marine Science, Haluoleo University, Kendari, Indonesia

[6]Sea Cottage, Louisburgh, Ireland

[7]Centre for Biodiversity and Conservation Science, School of Biological Sciences, University of Queensland, Brisbane, Queensland, Australia

Correspondence
Dominic Muenzel, School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK.
Email: bsdkm@leeds.ac.uk

Article impact statement: Larval dispersal can inform the design of no-take reserve networks in regional planning and fine-scale local decision-making.

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. We used larval dispersal connectivity at regional (hundreds of kilometers) and local (tens of kilometers) scales to aid in design of networks of no-take reserves in Southeast Sulawesi, Indonesia. We used Marxan with Connectivity informed by biophysical larval dispersal models and remotely sensed coral reef habitat data to design marine reserve networks for 4 commercially important reef species across the region. We complemented regional spatial prioritization with decision trees that combined network-based connectivity metrics and habitat quality to design reserve boundaries locally. Decision trees were used in consensus-based workshops with stakeholders to qualitatively assess site desirability, and Marxan was used to identify areas for subsequent network expansion. Priority areas for protection and expected benefits differed among species, with little overlap in reserve network solutions. Because reef quality varied considerably across reefs, we suggest reef degradation must inform the interpretation of larval dispersal patterns and the conservation benefits achievable from protecting reefs. Our methods can be readily applied by conservation practitioners, in this region and elsewhere, to integrate connectivity data across multiple spatial scales.

KEYWORDS
conservation planning, larval dispersal, marine reserve networks, Marxan, spatial prioritization

Integración de la conectividad larval al proceso de toma de decisiones en la conservación marina en escalas espaciales

Resumen: Comúnmente se integra la conectividad de la dispersión larval a las decisiones de conservación espacial a escalas regionales o nacionales, pero las agencias de implementación luchan con la transferencia de estos métodos a las escalas locales. Usamos la conectividad de la dispersión larval a escalas regionales (cientos de kilómetros) y locales (decenas de kilómetros) para ayudar en el diseño de redes de reservas con protección total en Sulawesi Sudoriental, Indonesia. Usamos Marxan con la conectividad guiada por los modelos biofísicos de dispersión larval y detectamos a distancia los datos de hábitat de los arrecifes de coral para diseñar redes de reservas marinas para cuatro especies de importancia comercial en la región. Complementamos la priorización espacial regional con árboles de decisión que combinaron medidas de conectividad basadas en las redes y la calidad del hábitat para diseñar localmente los límites de la reserva. Usamos los árboles de decisión con los actores en talleres basados en el consenso para evaluar cualitativamente la conveniencia del sitio. También usamos Marxan para identificar áreas para la expansión subsecuente de la red. Las áreas prioritarias para la protección y los beneficios esperados difirieron entre especies, con un traslape reducido en las soluciones de la red de reservas. Ya que la calidad del arrecife varió considerablemente entre los arrecifes, sugerimos que la degradación de estos debe orientar la interpretación de los patrones de dispersión larval y los beneficios de conservación alcanzables con la protección de los arrecifes. Los practicantes de la conservación pueden aplicar nuestros métodos inmediatamente, en esta región o en cualquier otra, para integrar los datos de conectividad en varias escalas espaciales.

PALABRAS CLAVE
dispersión larval, Marxan, planeación de la conservación, priorización espacial, redes de reservas marinas

【摘要】
幼体扩散的连接度常常被纳入区域或国家尺度的空间保护决策中，但保护执行机构在将这些方法转化到局部尺度时却经常遇到困难。本研究在区域(几百公里)和局部(几十公里)范围内，利用幼体扩散连接度来帮助设计了印度尼西亚东南苏拉威西的禁捕保护区网络。我们在幼体扩散的生物物理学模型和珊瑚礁生境遥感数据的指导下，利用Marxan软件的连接度方法，为该地区四个具有商业价值的珊瑚礁物种设计了海洋保护区网络。接下来，我们以结合基于网络的连接度指标与生境质量来设计局部保护区边界的决策树作为补充，确定了该区域的空间优先保护地区。研究者在与利益相关者的共识研讨会中用决策树定性评估了位点的可取性，并用Marxan软件确定了后续网络扩展的区域。不同物种间的优先保护区域和预期效益有所不同，且在保护区网络解决方案中几乎没有重叠。由于不同珊瑚礁的质量差异很大，我们建议在理解幼体扩散模式和珊瑚礁保护的预期效益时必须考虑珊瑚礁的退化。保护工作者可以将我们的方法很好地用于该地区及其他地区，来整合多个空间尺度的连接度数据。**【翻译:胡怡思;审校:聂永刚】**

关键词: 保护规划，幼体扩散，Marxan软件，海洋保护区网络，空间优先保护

INTRODUCTION

The exchange of larvae between subpopulations is a fundamental ecological process in many marine ecosystems (Almany et al., 2009). Recent technological advancements have popularized the adoption of larval connectivity into the design of no-take marine reserves (Magris et al., 2014), aiming to make metapopulations more resilient to localized disturbances (Almany et al., 2009) and to provide adjacent unprotected areas biodiversity and fishery benefits via spillover (Harrison et al., 2012). Methods to incorporate larval connectivity in reserve design range from complex mechanistic metapopulation models (Bode et al., 2016; Chollett et al., 2017) to simpler static optimizations performed with software, such as Marxan (White et al., 2014; Beger et al., 2015; Daigle et al., 2020), to basic rule of thumb 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); spatial prioritization incorporating connectivity is often used at regional scales (Beger et al., 2015); and rules of thumb, such as reserve sizing, are 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 problem is particularly relevant in tropical coral reef ecosystems, characterized by fragmented habitat patches that host fish species with relatively sedentary adult stages (Almany et al., 2009) and larvae that can disperse tens of meters to tens or hundreds of kilometers (Green et al., 2015). Although 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, multiscale planning where governance and actions at different scales inform one another is required to improve conservation outcomes and minimize scale mismatches (Cheok et al., 2020).

A further challenge is that reefs vary from semipristine 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 based on 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.

We integrated connectivity in marine spatial planning at regional and local scales to demonstrate a connectivity-based planning and consultation process of no-take reserve networks that occurred in the province of Southeast Sulawesi, Indonesia. The conservation organization Rare's Fish Forever program 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 4 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 kilometers). In the subsequent expansion of the reserve network at the regional, provincial scale (hundreds of kilometers), we used Marxan, a spatial prioritization tool, to identify connected priority areas for protection. Methods were specifically chosen to be easily communicable in nonspecialist, community consultations.

METHODS

Planning region

The province of Southeast Sulawesi in central Indonesia is in the heart of the Coral Triangle biodiversity hotspot (Figure 1a). 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 MAAs (defined above), inside of which smaller no-take marine reserves are established. Joint village management bodies are formed from joint village and fishing community groups and allocated comanagement rights to manage MAA resources and develop 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 were obtained from local habitat surveys and the publicly available Global Distribution of Coral Reefs data set (UNEP-WCMC et al., 2018). Due to time and resource constraints, 20% of reefs will not be protected at once; rather, they will be protected 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).

An initial system of 22 MAAs was established in 2019 through assessments with government partners and community inputs (Figure 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 behavior campaigns to build stakeholder support and policy development. This was followed by no-take reserve delineation undertaken at the local scale that combined additional habitat quality data available only locally with measures of larval import and export (Figure 3). Following reserve establishment in the 22 MAAs, we used Marxan with Connectivity to identify potential priority areas for expanding the reserve networks across the province.

The sociopolitical 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 2-scale process, the initial selection of reserves may be carried out through regional conservation prioritization (Figure 2, step 1B; Appendix S1).

Larval dispersal modeling

We modeled larval dispersal for the commercially important fishery species of coral trout (*Plectropomus leopardus*), emperor (*Lethrinus lentjan*), snapper (*Lutjanus malabaricus*), and rabbitfish (*Siganus canaliculatus*) with 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 the literature. When specific data were unavailable, we used the most similar species and closest location. Reef habitat was divided into 487 discrete patches ranging in size from 0.25 to 122.75 km^2 with natural clustering of habitat and geomorphological attributes of the coastlines. A nearest-neighbor and overwater distance algorithm was used for initial clustering of reef habitat in 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 (PUs), 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 interpatch 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 (details in Appendix S2).

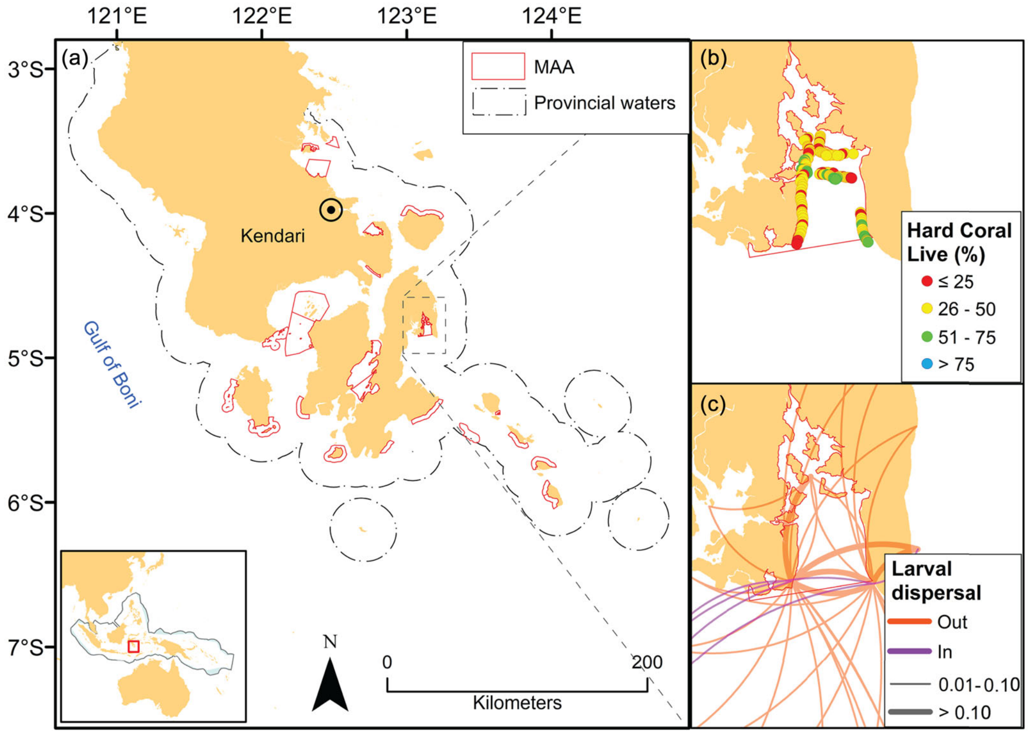

FIGURE 1 (a) Map of the planning area of Southeast Sulawesi, Indonesia, showing provincial waters and the 22 managed access areas (MAAs) identified through government consultations (inset, location of the province in the wider Coral Triangle region); (b) example of one of the MAAs with benthic data on habitat quality; and (c) incoming and outgoing coral trout larval connectivity as proportion of larvae arriving at a reef originating from a donor reef (connection proportions <0.01 have been omitted for ease of visualization)

Local reserve placement

The small number of PUs in each of the 22 MAAs precluded the use of software-driven spatial prioritization for local decision support. Although smaller PUs could be used by downscaling the connectivity matrix (Beger et al., 2015), this would overstate data quality (Mills et al., 2010). There are advantages to using PUs that follow habitat patch delineations (Nhancale & Smith, 2011). Instead, we identified priority areas for reserve designation through consensus-based workshops with stakeholders, based on maps of habitat quality and larval flow, and simple decision trees to qualitatively assess site desirability (Figure 3). Workshops 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 in the MAA, women from villages, and workers in various fishery-related roles in the community (e.g., fishers, buyers).

Habitat quality in MAAs was assessed using manta tow surveys (Figures 1b & 3b). Trained snorkel divers were towed behind a boat and recorded benthic cover for 250- to 300-m stretches, after which the boat stopped to allow divers time to record their quantitative assessment of substrate cover. Habitat quality was recorded in percentages as 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):

$$k_i^{\text{in}} = \sum_j^N \mathbf{x}_{ji} \text{ for } j \neq i \tag{1}$$

and

$$s_i^{\text{in}} = \sum_j^N \mathbf{M}_{ji} \text{ for } j \neq i, \tag{2}$$

where the in degree k_i^{in} is the column sum of an adjacency matrix $\mathbf{x}$ and the sum of incoming weights s_i^{in} is the column sum of the migration matrix $\mathbf{M}$. The i refers to rows and j refers to columns of both $\mathbf{x}$ and $\mathbf{M}$, and N is the total number of PUs. These were combined into weighted in degree with an $\alpha = 0.5$ to balance the number of incoming connections (k_i^{in}) with their weight (s_i^{in}) to ensure a diversity of larval sources for offsetting risks:

$$C_{\text{D-in}}^{\text{w}\alpha}(i) = k_i^{\text{in}} \times \left(\frac{s_i^{\text{in}}}{k_i^{\text{in}}}\right)^{\alpha}. \tag{3}$$

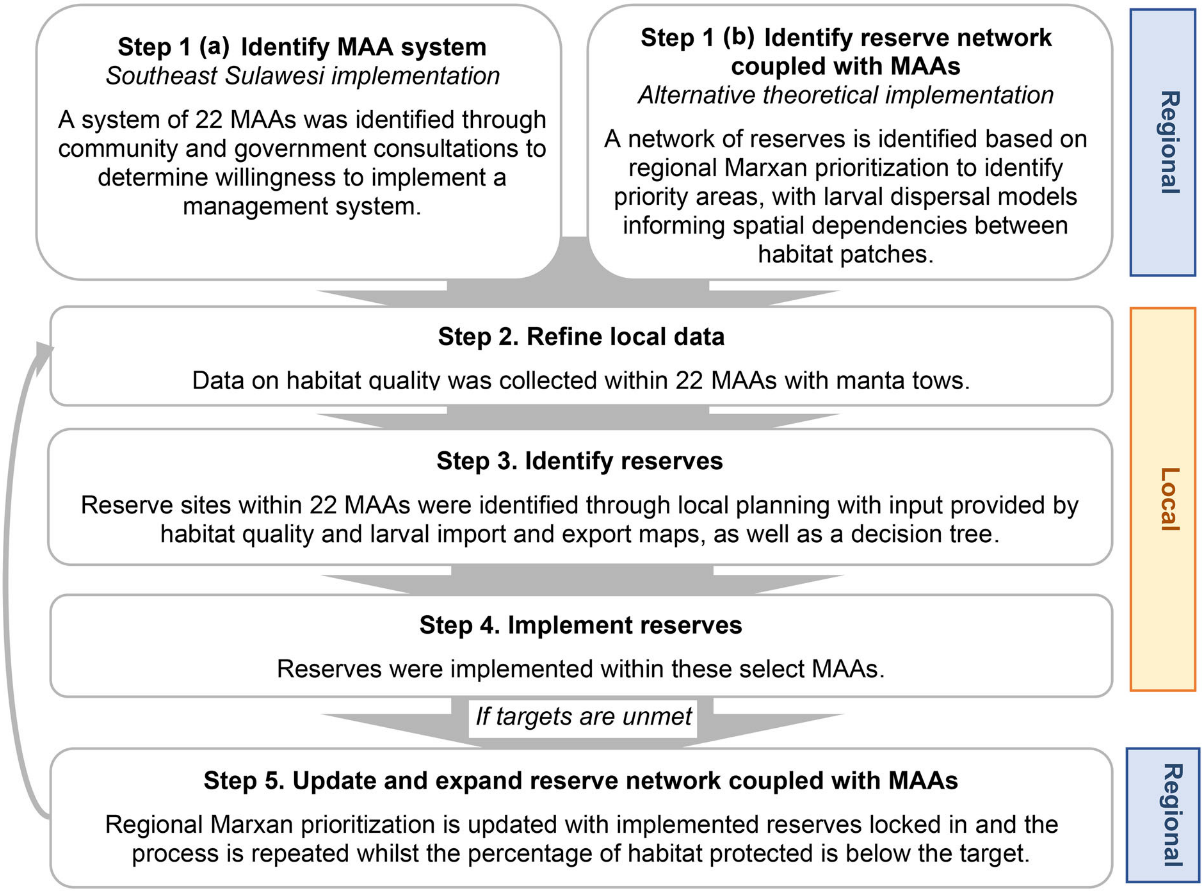

FIGURE 2 Steps in the iterative workflow to establish a network of marine reserves and managed access areas (MAAs) through combined regional and local planning processes

Larval export was calculated as source influence (Roberts et al., 2021), a measure of export contribution of a patch to downstream patches, as the row sum of **M**:

$$\mathrm{SrcInf}\,(i) = \sum_{j}^{N} \mathbf{M}_{ij} \text{ for } j \neq i. \tag{4}$$

Integrated regional spatial prioritization

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 maximize larval flow between reserves. Marxan solves a minimum set problem of identifying efficient spatial reserve configurations that meet a target for habitat representation while minimizing overall socioeconomic cost based on the following objective function:

$$\overbrace{\sum\nolimits_{\mathrm{PUs}} \mathrm{cost}}^{a} + \overbrace{\sum\nolimits_{\mathrm{ConValue}} \mathrm{SPF} \times \mathrm{penalty}}^{b} + \overbrace{\mathrm{CSM} \sum\nolimits_{\mathrm{PUs}} \mathrm{connectivity}}^{c} = \text{Marxan score} \tag{5}$$

Each of the 487 PUs contained a certain amount of coral reef conservation feature calculated from the regional data (UNEP-WCMC et al., 2018) and was assigned PU size as a proxy for cost (Ardron et al., 2010). The PUs are the potential sites or spatial management units that are either selected or not selected for protection in prioritization solutions. Because larger PUs contained more habitat area, the use of size as a proxy for cost ensured that solutions did not exclusively pick the biggest PUs. The objective function minimized the cumulative cost (Equation 5a) and the penalty associated with failing to protect conservation features (Equation 5b) weighed by a species penalty factor. Dispersal connectivity (connectivity) was

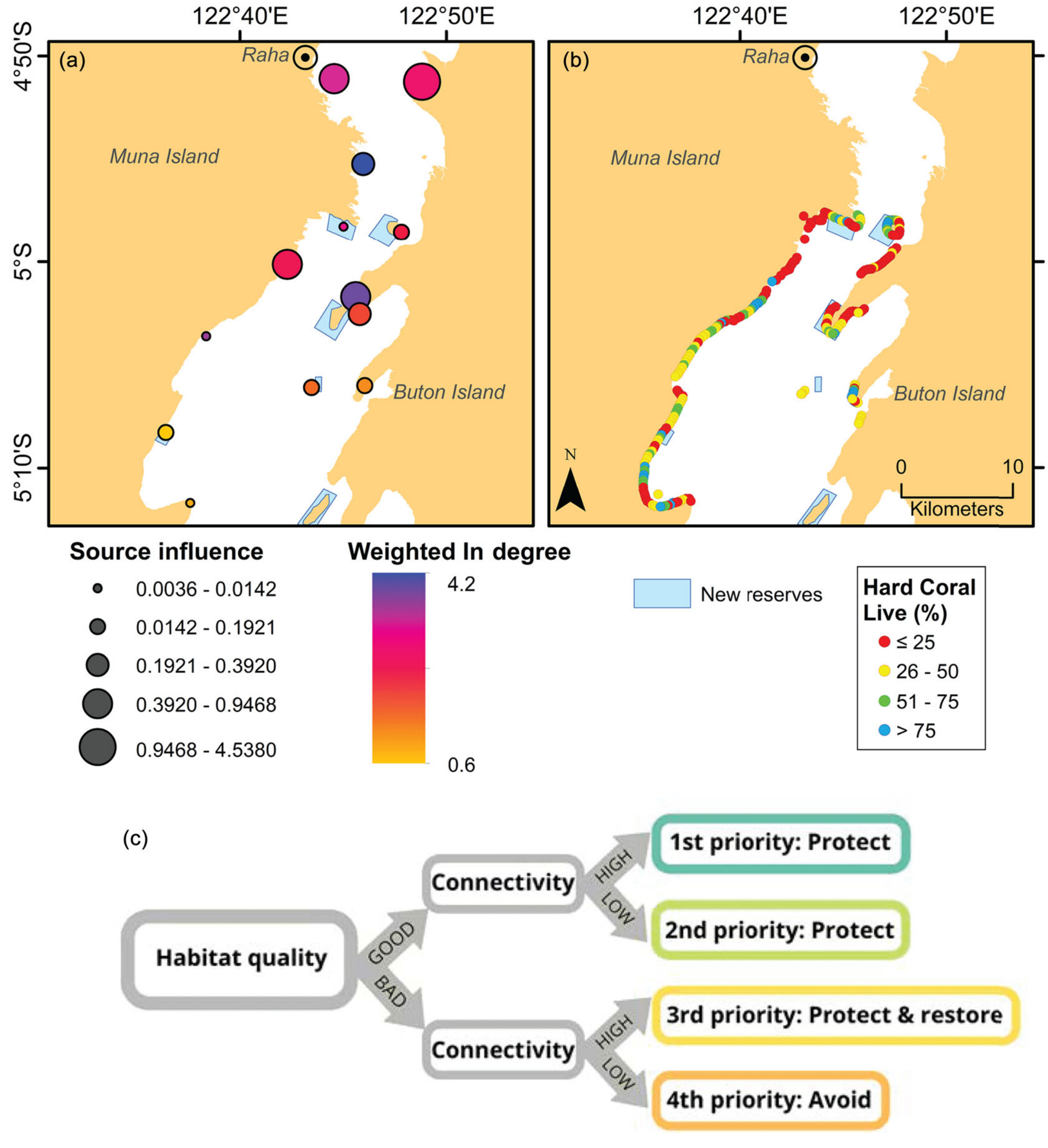

FIGURE 3 Inputs used in local decision-making for reserve delineation in Pasi Kolaga, one of the 22 managed access areas in Southeast Sulawesi: (a) coral trout larval import metric of weighted in degree and export metric of source influence, (b) percent live hard coral cover from benthic surveys (blue, newly designated reserves following community consultations), and (c) simple decision tree to rank the desirability of planning units in managed access areas for reserve designation

incorporated as an additional penalty to be minimized (Equation 5c); a high penalty was incurred if only 1 of a pair of strongly connected PUs was selected (Beger et al., 2010). This connectivity penalty replaced the traditional boundary.dat file used in Marxan to describe physical boundary lengths between PUs to create spatially compact solutions. The connectivity weighting factor 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 established in the 22 MAAs were locked in to solutions, and the spatial dependency component ensured that subsequently selected PUs 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 with discrete time, age-structured, single-species metapopulation models to assess biomass change of the fish species over 30 years after reserve implementation based on an assumption of total compliance with no fishing inside reserves (Appendix S3) (Garavelli et al., 2018). At each 1-year time step, settling larvae undergo density-dependent survival and adults are exposed to natural and fishing mortality and produce eggs that are distributed across PUs following the larval dispersal probabilities. We compared the performance of reserve networks with 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 normalized so a baseline of 1 represented biomass before any reserve designation.

RESULTS

Local reserve placement

The 22 MAAs ranged in size from 17 to 511 km^2; individual areas contained 2–14 larval dispersal PUs. Live coral cover varied between PUs; roughly 50% of PUs contained <30% live hard coral and 10% of PUs contained >50% live hard coral cover (Appendix S4).

The scientific inputs used in the workshops (Figure 3) were negotiated and traded off to achieve the best ecological result while accommodating community fishing practices. The decision tree illustrated that first priorities for reserve placement were areas of high-quality reef and high import and export. High-quality reefs with low connectivity were prioritized 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 could be taken. In general, the connectivity data were well-received by communities and used in the reserve design with socioeconomic factors complementing this decision-making and habitat quality data used in combination with local understanding.

Integrated regional prioritization

Following the community consultations for reserve delineation, 89 reserves were designated locally within the 22 MAAs by November 2020 that would protect 59 km^2 of coral reef and reached 15% of the regional habitat protection target (Figure 4). The Marxan regional prioritization identified potential areas for subsequent reserve network expansion to protect 20% of reef across the province (Figure 4). These reserve networks generated greater expected benefits in biomass gain compared with a random selection of reserves for protection, with variation across species (Figure 5). Removal of fishing pressure from designated PUs resulted in an immediate biomass increase inside reserves and a delayed increase outside reserves, during which the adult population in reserves built up, which increased larval export to unreserved areas. Coral trout and emperor had greatest expected biomass increase, followed by snapper and rabbitfish. Certain runs of random selection achieved nearly similar benefits in 3 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 S5).

DISCUSSION

In a 2-pronged approach, we used larval dispersal patterns to inform 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 2 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 recognize 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 prioritization, locally selected reserves were connected to a wider reserve network to maximize larval exchange. Metapopulation models verified that explicitly designed, connected networks generated greater potential benefits than randomly placed reserves (Figure 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) because highly degraded sites hosting small fish populations would not realize 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 on 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 modeling 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.

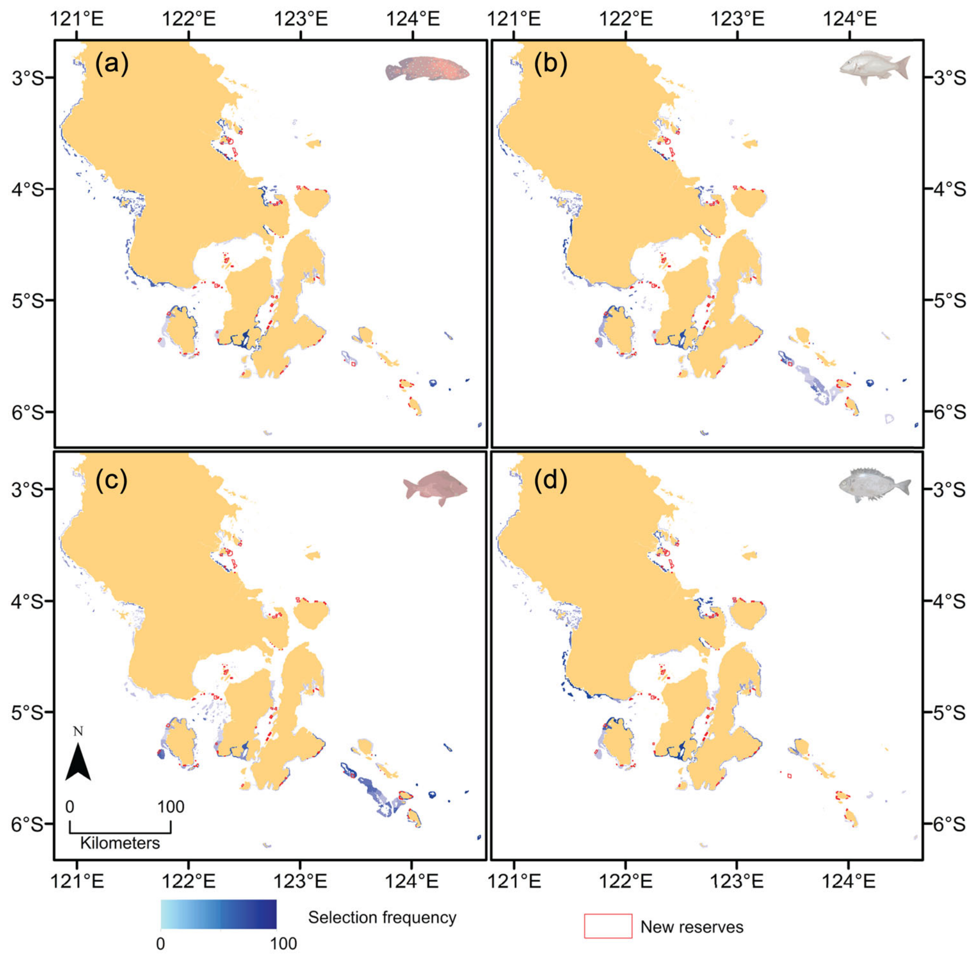

FIGURE 4 Selection frequency of planning units for reserve designation when Marxan prioritization is run with the 89 new reserves established in November 2020 locked in for (a) coral trout, (b) emperor, (c) snapper, and (d) rabbitfish

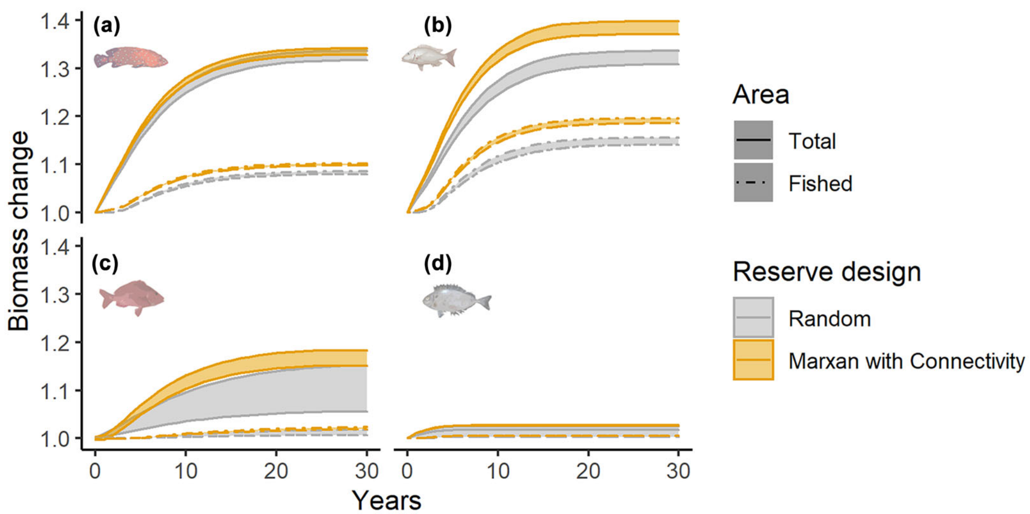

FIGURE 5 Biomass change across all reserved planning units and in fished areas for the top 5 Marxan priority conservation area solutions for (a) coral trout, (b) emperor, (c) snapper, and (d) rabbitfish (yellow, performance of reserve networks designed from the stakeholder-driven selection of 89 reserves in 22 managed access areas and expanded to cover 20% of habitat identified with Marxan with Connectivity; gray, results of randomly generated reserve systems with similar levels of protection)

Because it was logistically infeasible 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 based on coarse data risk underestimating site irreplaceability (Rouget, 2003) and increase uncertainty regarding species occurrences and the success of conservation actions (Hermoso & Kennard, 2012). 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 2-scale approach we used provides a 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 prioritization used the mean larval connectivity over 20 years, but whether using such a mean achieves temporal stability needs to be explored. We chose not to communicate this additional complexity in community consultations because we did not quantify the variability in expected reserve benefits. Marxan accepts only static connectivity information, but more complex implementations may become possible in the future.

A core assumption behind the decision tree we used in local planning was that reefs with high 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 high-risk sites if reserves accelerate recovery after habitat disturbance (Game et al., 2008). However, this presupposes that the region is generally not 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, although moderately affected sites may be candidates for restorative conservation actions, such actions have high implementation costs making widespread adoption difficult (Vercammen et al., 2019).

Our methods can be applied to other countries with some caveats. Public data repositories (UNEP-WCMC et al., 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 the best available data for the relevant species, it is likely that unquantified variability remains; therefore, there is uncertainty in our modeling output. For these reasons, decision-making should be realistic about uncertainty (Milner-Gulland & Shea, 2017), and outputs within a larger decision-making process should be informed by many data sources. Where larval dispersal modeling 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. 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, we found that effective conservation approaches can be centered on local stakeholder needs. Our approach was designed to inform community-based decision-making processes that combined methods at 2 spatial scales based on straightforward concepts. Our approach successfully fostered community buy-in and stakeholder participation and is predicted to generate positive conservation and fisheries benefits.

ACKNOWLEDGMENTS

D.M. was funded by the University of Leeds School of Biology Doctoral Training Studentship. We thank Bloomberg Philanthropies for funding the larval dispersal modeling in Southeast Sulawesi.

ORCID

Dominic Muenzel https://orcid.org/0000-0002-7158-7748
Iliana Chollett https://orcid.org/0000-0003-0536-499X

REFERENCES

Almany, G. R., Connolly, S. R., Heath, D. D., Hogan, J. D., Jones, G. P., McCook, L. J., Mills, M., Pressey, R. L., & Williamson, D H. (2009). Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs*, *28*, 339–351.

Ardron, J. A., Possingham, H. P., & Klein, C J. (2010). *Marxan good practices handbook: Version 2*. Pacific Marine Analysis and Research Association. https://www.pacmara.org

Arias, A. (2015). Understanding and managing compliance in the nature conservation context. *Journal of Environmental Management*, *153*, 134–143.

Beger, M., Linke, S., Watts, M. E., Game, E. T., Treml, E. A., Ball, I., & Possingham, H P. (2010). Incorporating asymmetric connectivity into spatial decision making for conservation. *Conservation Letters*, *3*, 359–368.

Beger, M., McGowan, J., Treml, E. A., Green, A. L., White, A. T., Wolff, N. H., Klein, C. J., Mumby, P. J., & Possingham, H P. (2015). Integrating regional conservation priorities for multiple objectives into national policy. *Nature Communications*, *6*, 1–8.

Berglund, M., Nilsson Jacobi, M., & Jonsson, P. R. (2012). Optimal selection of marine protected areas based on connectivity and habitat quality. *Ecological Modelling*, *240*, 105–112.

Bode, M., Williamson, D. H., Weeks, R., Jones, G. P., Almany, G. R., Harrison, H. B., Hopf, J. K., & Pressey, R L. (2016). Planning marine reserve networks for both feature representation and demographic persistence using connectivity patterns. *PLoS ONE*, *11*, 1–23.

Boschetti, F., Babcock, R. C., Doropoulos, C., Thomson, D. P., Feng, M., Slawinski, D., Berry, O., & Vanderklift, M. A. (2020). Setting priorities for conservation at the interface between ocean circulation, connectivity, and population dynamics. *Ecological Applications*, *30*, 1–13.

Burke, L., Reytar, K., Spalding, M., & Perry, A. (2012). *Reefs at risk: Revisited in the coral triangle*. World Resources Institute. https://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3150666&tool=pmcentrez&rendertype=abstract

Cabral, R. B., Gaines, S. D., Lim, M. T., Atrigenio, M. P., Mamauag, S. S., Pedemonte, G. C., & Aliño, P. M. (2016). Siting marine protected areas based on habitat quality and extent provides the greatest benefit to spatially structured metapopulations. *Ecosphere*, *7*, e01533.

Caswell, H. (2014). Matrix population models. In N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri, & J. L. Teugels (Eds.), *Wiley StatsRef: Statistics reference online*. John Wiley & Sons. https://doi.org/10.1002/9781118445112.stat07481

Cheok, J., Pressey, R. L., Weeks, R., VanDerWal, J., & Storlie, C. (2018). The plans they are a-changin': More frequent iterative adjustment of regional priorities in the transition to local actions can benefit implementation. *Diversity and Distributions*, *24*, 48–57.

Cheok, J., Weeks, R., Morrison, T. H., & Pressey, R. L. (2020). Scalar capital as ingredient of success in conservation governance: Evidence from Melanesia. *Global Environmental Change*, *62*, 102057.

Chollett, I., Garavelli, L., O'Farrell, S., Cherubin, L., Matthews, T. R., Mumby, P. J., & Box, S. J. (2017). A genuine win-win: Resolving the "conserve or catch" conflict in marine reserve network design. *Conservation Letters*, *10*, 555–563.

D'Aloia, C. C., Daigle, R. M., Côté, I. M., Curtis, J. M. R., Guichard, F., & Fortin, M. J. (2017). A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. *Biological Conservation*, *216*, 93–100.

Daigle, R. M., Metaxas, A., Balbar, A. C., McGowan, J., Treml, E. A., Kuempel, C. D., Possingham, H. P., & Beger, M. (2020). Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. *Methods in Ecology and Evolution*, *11*, 570–579.

Drew, J. A. (2005). Use of traditional ecological knowledge in marine conservation. *Conservation Biology*, *19*, 1286–1293.

Fontoura, L., D'Agata, S., Gamoyo, M., Barneche, D. R., Luiz, O. J., Madin, E. M. P., Eggertsen, L., & Maina, J. M. (2022). Protecting connectivity promotes successful biodiversity and fisheries conservation. *Science*, *375*, 336–340.

Game, E. T., McDonald-Madden, E., Puotinen, M. L., & Possingham, H. P. (2008). Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. *Conservation Biology*, *22*, 1619–1629.

Garavelli, L., White, J. W., Chollett, I., & Chérubin, L. M. (2018). Population models reveal unexpected patterns of local persistence despite widespread larval dispersal in a highly exploited species. *Conservation Letters*, *11*, 1–8.

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., Gleason, M. G., Mumby, P. J., & White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, *90*, 1215–1247.

Guerrero, A. M., Allister, R., Corcoran, J., & Wilson, K. A. (2013). Scale mismatches, conservation planning, and the value of social-network analyses. *Conservation Biology*, *27*, 35–44.

Harrison, H. B., Williamson, D. H., Evans, R. D., Almany, G. R., Thorrold, S. R., Russ, G. R., Feldheim, K. A., van Herwerden, L., Planes, S., Srinivasan, M., Berumen, M. L., & Jones, G. P. (2012). Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology*, *22*, 1023–1028.

Harrison, H. B., Bode, M., Williamson, D. H., Berumen, M. L., & Jones, G. P. (2020). A connectivity portfolio effect stabilizes marine reserve performance. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 25595–25600.

Hermoso, V., & Kennard, M. J. (2012). Uncertainty in coarse conservation assessments hinders the efficient achievement of conservation goals. *Biological Conservation*, *147*, 52–59.

Hock, K., Wolff, N. H., Ortiz, J. C., Condie, S. A., Anthony, K. R. N., Blackwell, P. G., & Mumby, P J. (2017). Connectivity and systemic resilience of the Great Barrier Reef. *PLoS Biology*, *15*, 1–23.

Huber, P. R., Greco, S. E., & Thorne, J. H. (2010). Spatial scale effects on conservation network design: Trade-offs and omissions in regional versus local scale planning. *Landscape Ecology*, *25*, 683–695.

Jones, G. P., McCormick, M. I., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 8251–8253.

Krueck, N. C., Legrand, C., Ahmadia, G. N., Green, A. L., Jones, G. P., Riginos, C., Treml, E. A., & Mumby, P. J. (2017). Reserve sizes needed to protect coral reef fishes. *Conservation Letters*, *11*, 1–9.

Magris, R. A., Pressey, R. L., Weeks, R., & Ban, N C. (2014). Integrating connectivity and climate change into marine conservation planning. *Biological Conservation*, *170*, 207–221.

Magris, R. A., Treml, E. A., Pressey, R. L., & Weeks, R. (2016). Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. *Ecography*, *39*, 649–664.

McCook, L. J., Almany, G. R., Berumen, M. L., Day, J. C., Green, A. L., Jones, G. P., Leis, J. M., Planes, S., Russ, G. R., Sale, P. F., & Thorrold, S. R. (2009). Management under uncertainty: Guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs*, *28*, 353–366.

Mills, M., Pressey, R. L., Weeks, R., Foale, S., & Ban, N. C. (2010). A mismatch of scales: Challenges in planning for implementation of marine protected areas in the Coral Triangle. *Conservation Letters*, *3*, 291–303.

Milner-Gulland, E. J., & Shea, K. (2017). Embracing uncertainty in applied ecology. *Journal of Applied Ecology*, *54*, 2063–2068.

Nhancale, B. A., & Smith, R J. (2011). The influence of planning unit characteristics on the efficiency and spatial pattern of systematic conservation planning assessments. *Biodiversity Conservation*, *20*, 1821–1835.

Nolan, M. K. B., Kim, C. J. S., Hoegh-Guldberg, O., & Beger, M. (2021). The benefits of heterogeneity in spatial prioritisation within coral reef environments. *Biological Conservation*, *258*, 109155.

Norström, A V., Nyström, M., Jouffray, J. B., Folke, C., Graham, N. A. J., Moberg, F., Olsson, P., & Williams, G. J. (2016). Guiding coral reef futures in the Anthropocene. *Frontiers in Ecology and the Environment*, *14*, 490–498.

Opsahl, T., Agneessens, F., & Skvoretz, J. (2010). Node centrality in weighted networks: Generalizing degree and shortest paths. *Social Networks*, *32*, 245–251.

Roberts, K. E., Cook, C. N., Beher, J., & Treml, E. A. (2021). Assessing the current state of ecological connectivity in a large marine protected area system. *Conservation Biology*, *35*, 699–710.

Rouget, M. (2003). Measuring conservation value at fine and broad scales: Implications for a diverse and fragmented region, the Agulhas Plain. *Biological Conservation*, *112*, 217–232.

Smith, J., & Metaxas, A. (2018). A decision tree that can address connectivity in the design of Marine Protected Area Networks (MPAn). *Marine Policy*, *88*, 269–278.

Sterling, E. J., Betley, E., Sigouin, A., Gomez, A., Toomey, A., Cullman, G., Malone, C., Pekor, A., Arengo, F., Blair, M., Filardi, C., Landrigan, K., & Porzecanski, A. L. (2017). Assessing the evidence for stakeholder engagement in biodiversity conservation. *Biological Conservation*, *209*, 159–171.

Treml, E. A., Ford, J. R., Black, K. P., & Swearer, S. E. (2015). Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. *Movement Ecology*, *3*, 1–16.

Treml, E. A., Roberts, J. J., Chao, Y., Halpin, P. N., Possingham, H. P., & Riginos, C. (2012). Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integrative and Comparative Biology*, *52*, 525–537.

UNEP-WCMC, WorldFishCentre, WRI, & TNC. (2018). *Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project: Version 4.0*. UN Environment World Conservation Monitoring Centre. https://data.unep-wcmc.org/datasets/1

Vercammen, A., McGowan, J., Knight, A. T., Pardede, S., Muttaqin, E., Harris, J., Ahmadia, G., Estradivari, Dallison, T., Selig, E., & Beger, M. (2019). Evaluating the impact of accounting for coral cover in large-scale

Conservation Biology

marine conservation prioritizations. *Diversity and Distributions*, *25*, 1564–1574.

White, J. W., Schroeger, J., Drake, P. T., & Edwards, C. A. (2014). The value of larval connectivity information in the static optimization of marine reserve design. *Conservation Letters*, *7*, 533–544.

Wilson, S. K., Fisher, R., Pratchett, M. S., Graham, N. A. J., Dulvy, N. K., Turner, R. A., Cakacaka, A., & Polunin, N V C. (2010). Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecological Applications*, *20*, 442–451.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Muenzel, D., Critchell, K., Cox, C., Campbell, S. J., Jakub, R., Suherfian, W., Sara, L., Chollett, I., Treml, E. A., & Beger, M. (2022). Integrating larval connectivity into the marine conservation decision-making process across spatial scales. *Conservation Biology*, e14038. https://doi.org/10.1111/cobi.14038