Landsc Ecol (2026) 41:17
https://doi.org/10.1007/s10980-025-02274-y

RESEARCH ARTICLE

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

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Received: 2 October 2025 / Accepted: 1 December 2025

Abstract

Context Marine reserve networks designed to enhance larval dispersal provide important biodiversity benefits. Designs are commonly based on time-averaged means of dispersal estimates. It is unclear whether they capture the connectivity portfolio effect, by which temporal variation in individual reserve performance is buffered by the entire network.

Objectives To evaluate the implications of dispersal variability and derive general rules for network design.

Methods We modelled larval dispersal of four commercially important reef species for 20 years in Southeast Sulawesi, Indonesia. We built reserve network scenarios informed by temporal dispersal as either an interannual mean or dispersal for individual years. We then evaluated reserve network performance.

Results *Plectropomus leopardus* and *Siganus canaliculatus* experienced higher variability in interannual larval flow compared to *Lutjanus malabaricus* and *Octopus vulgaris*. We discover that using a single time-averaged mean dispersal estimate can create subpar reserve networks in highly variable systems. Mean dispersal was suitable for less variable species such as *O. vulgaris,* but not for more variable species where high larval flow was not protected over time. By explicitly identifying reefs contributing a high amount of larval flow in each of the 20 years, we were able to improve network designs and provide a more consistent protection of larval supply over time.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-025-02274-y.

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Conclusions We develop methods to improve network performance by protecting reefs with high larval flow contribution across years. The steps outlined here illustrate how information from multitemporal connectivity datasets can help inform a spatial prioritisation framework to accommodate larval dispersal volatility.

Keywords Larval dispersal · Marine conservation planning · Coral reef · Temporal variability

Introduction

Many marine fauna disperse predominantly during larval stages, creating demographic and genetic connectivity between subpopulations (Cowen and 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 and Jonsson 2012). As large-scale climate oscillations and interannual circulation patterns such as El Niño Southern Oscillation (ENSO) 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 and 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 (Manel et al. 2019).

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 and 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 with higher survivorship potential than larvae of smaller 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 (Fig. 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.

Methods

Larval dispersal models

We modelled the larval dispersal of four commercially important reef species: Leopard coralgrouper (*Plectropomus leopardus*), Malabar blood snapper (*Lutjanus malabaricus*), White-spotted spinefoot (*Siganus canaliculatus*), and common octopus (*Octopus vulgaris*), in the Indonesian province of Southeast Sulawesi using a coupled hydrodynamic and biological model (Fig. 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.

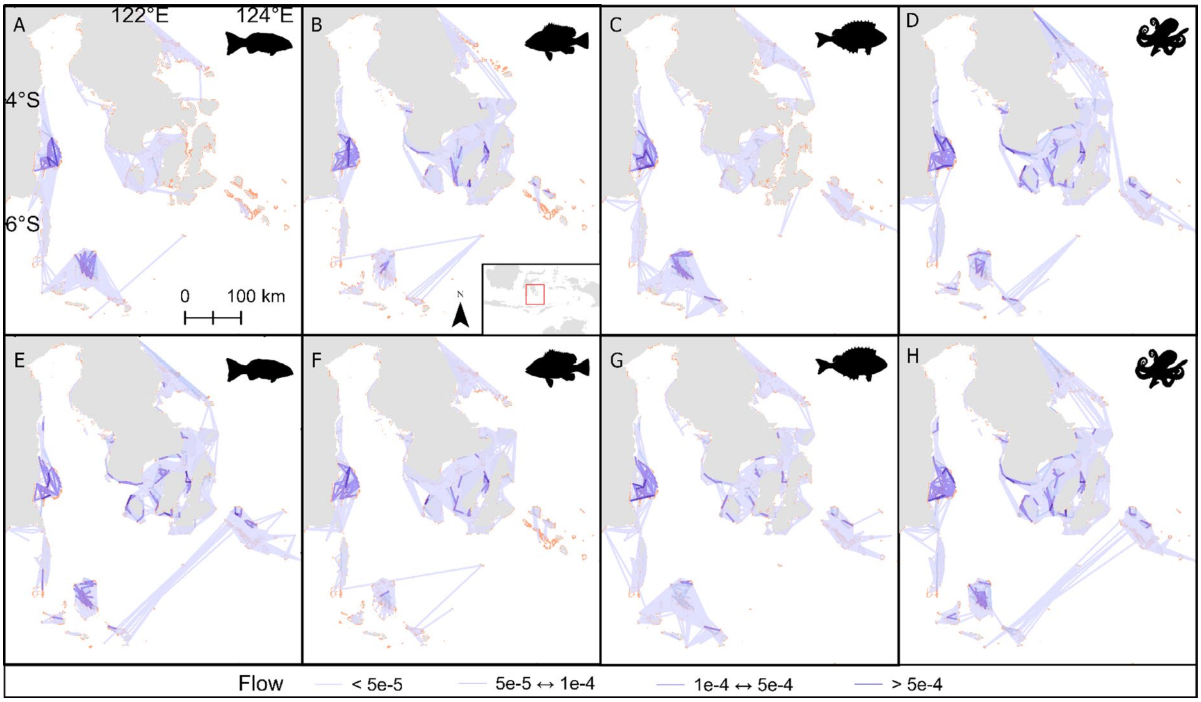

Fig. 1 Overview of larval dispersal in Southeast Sulawesi, Indonesia, for three fish and one invertebrate species with reef-shaped planning units shown by orange polygons. Larval flow in 1999 (**A–D**) and 2000 (**E–H**) for *Plectropomus leopardus* (**A, E**), *Lutjanus malabaricus* (**B, F**), *Siganus canaliculatus* (**C, G**), and *Octopus vulgaris* (**D, H**) estimated by coupled biological oceanographic dispersal models. Connections < 1e-6 are not shown

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 (SI Appendix, Table S1). All 487 reef patches were assumed to be suitable for recruitment and growth. Spawning windows were around the new moon, September–November, for *P. leopardus*, and daily between October-February for *L. malabaricus*, March-September for *S. canaliculatus,* and year-round for *O. vulgaris*. Due to a lack of species-specific life history data, we used *S. spinus* parameters in place of *S. canaliculatus* and *L. carponotatus* parameters in place of *L. malabaricus* (SI Appendix, Table S1). 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 maximum potential proportion of larvae arriving at a recipient planning unit. We used area of reef patch as a proxy for spawning population size, as larger reefs generally host larger fish populations.

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. Cost in spatial prioritisation is a measure of how expensive it is to protect a given area. The area-based cost used here assumes that larger areas are more expensive to protect, e.g. by incurring higher opportunity costs in lost fishing revenue. 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. The spatial dependency method does not use the diagonal of the matrix, in this case self-recruitment.

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 and 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).

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.

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 the scenarios which achieved the highest connectivity portfolio effects. 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 either the top 5, 10, or 15 designated planning units with highest larval flow contributions 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.

Results

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 (Fig. 2). 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 (Fig. 3). 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 (Fig. 3).

Similarities in the spatial prioritisation solutions correlated with different climatic indices, depending on the species (Fig. 4). 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* ($r^2 = 0.26$, $P = 0.001$), and *O. vulgaris* ($r^2 = 0.18$, $P = 0.001$), and Dipole Mode index for *S. canaliculatus* ($r^2 = 0.12$, $P = 0.001$). These results corresponded with an overlap between when these climate drivers were at their most influential and the spawning windows of each species (SI Appendix, Fig. S1), from September to November for *P. leopardus*, October to February for *L. malabaricus*, and

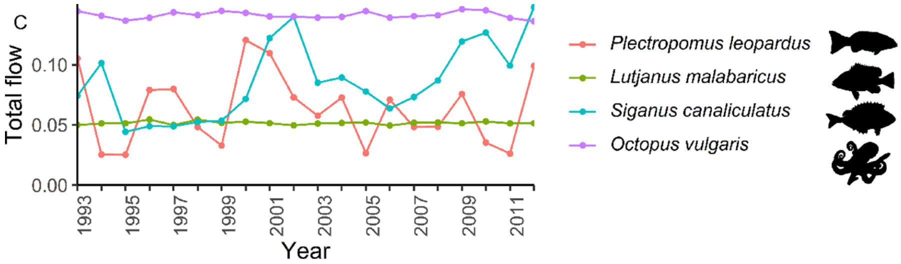

Fig. 2 Cumulative annual larval flow strength across all planning units from 1993 to 2012 for each of the four species

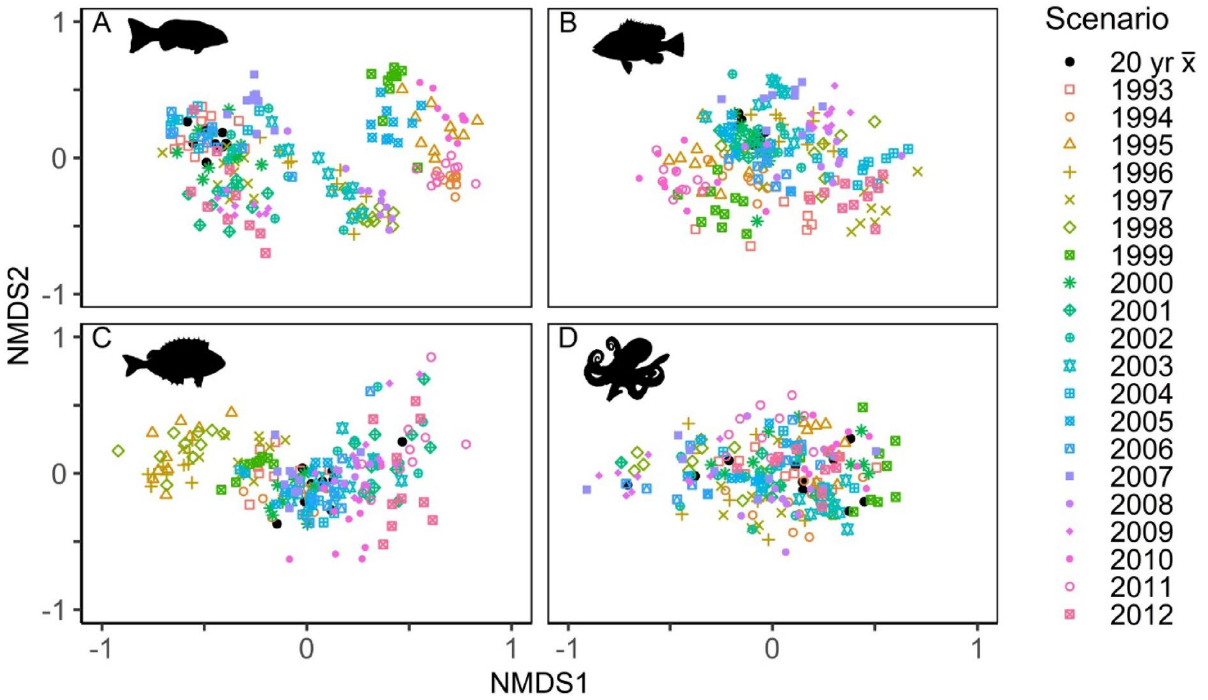

Fig. 3 Non-metric multi-dimensional scaling (nMDS) plot of the top ten Marxan solutions coloured by scenario based on a Jaccard resemblance matrix. Each scenario involves a reserve network designed using the larval dispersal of either a 20-year mean or individual years for **A** *P. leopardus*, **B** *L. malabaricus*, **C** *S. canaliculatus*, and **D** *O. vulgaris*

March to September for *S. canaliculatus* (SI Appendix, Table S1). In contrast, *O. vulgaris* with year-round spawning had lower r-square values overall compared to three fish species. ENSO-related indices modulate monsoon wind patterns and the strength and routing of the Indonesian Throughflow, while the Dipole Mode Index reflects Indian Ocean Dipole events that alter regional circulation and upwelling intensity (Li et al. 2023). Such changes modify current velocity and direction during species-specific spawning windows, thereby influencing the resulting larval trajectories and lowering or raising similarity among annual dispersal matrices. The significant correlations observed in the *envfit* analysis therefore reflect known mechanistic links between climatic forcing and larval transport pathways in this region.

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 (Fig. 5). 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 (Fig. 5, 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. In these modified’HiFlo target’

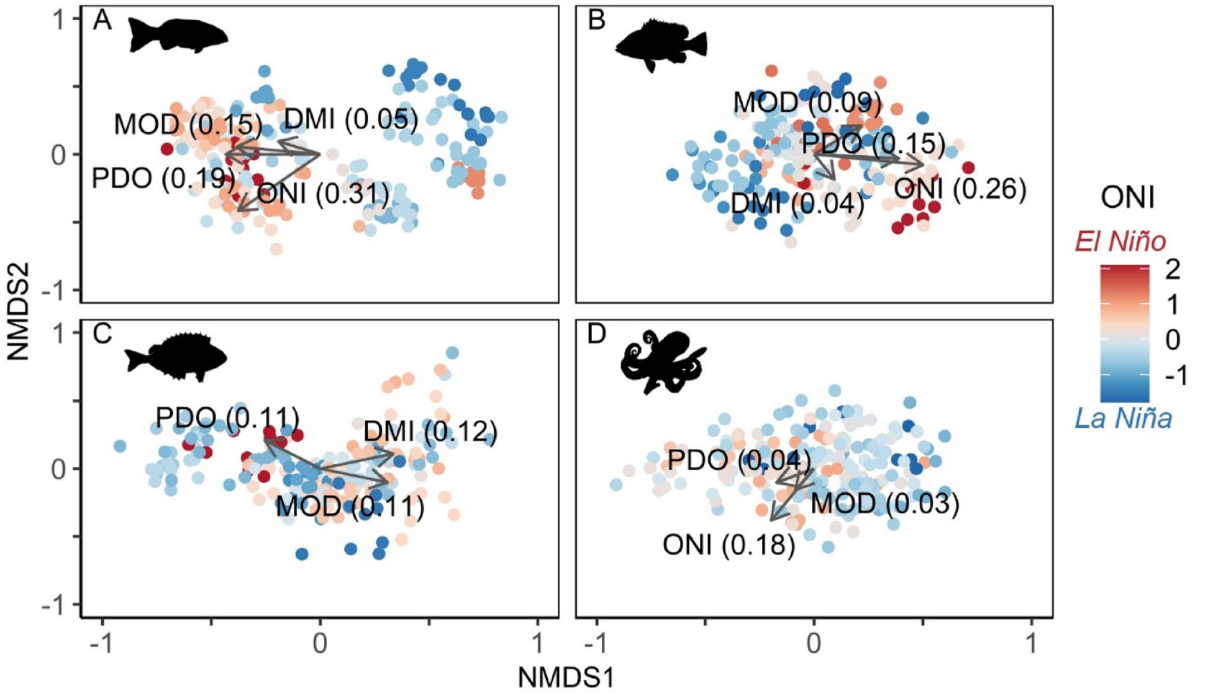

Fig. 4 Non-metric multi-dimensional scaling (nMDS) plot of the top ten Marxan solutions of the individual year and 20 year mean scenarios (Fig. 2) with colours indicating strength of the Oceanic Niño 3.4 Index for **A** *P. leopardus*, **B** *L. malabaricus*, **C** *S. canaliculatus*, and **D** *O. vulgaris*. 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)

scenarios, either one or both performance metrics could be improved beyond the 20 annual or 20-year mean scenarios (Fig. 5, black triangle). In *P. leopardus* and *S. canaliculatus*, modified scenarios scored highest portfolio effects and flow, whilst in *L. malabaricus* higher flow was achieved whilst portfolio effects remained comparable to the original scenarios without additional conservation features. In *O. vulgaris* the reserve performance could not be improved. The greatest increase in performance was achieved by setting 50% targets for the top 15 high larval flow contribution planning units in *P. leopardus* using the 1995 dispersal as the spatial dependency connectivity dataset, the top 10 in *L. malabaricus* using the 20-year mean dispersal dataset, and the top 5 in *S. canaliculatus* using the 2010 dispersal dataset.

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 instead dispersal connectivity of specific years to design reserve networks 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

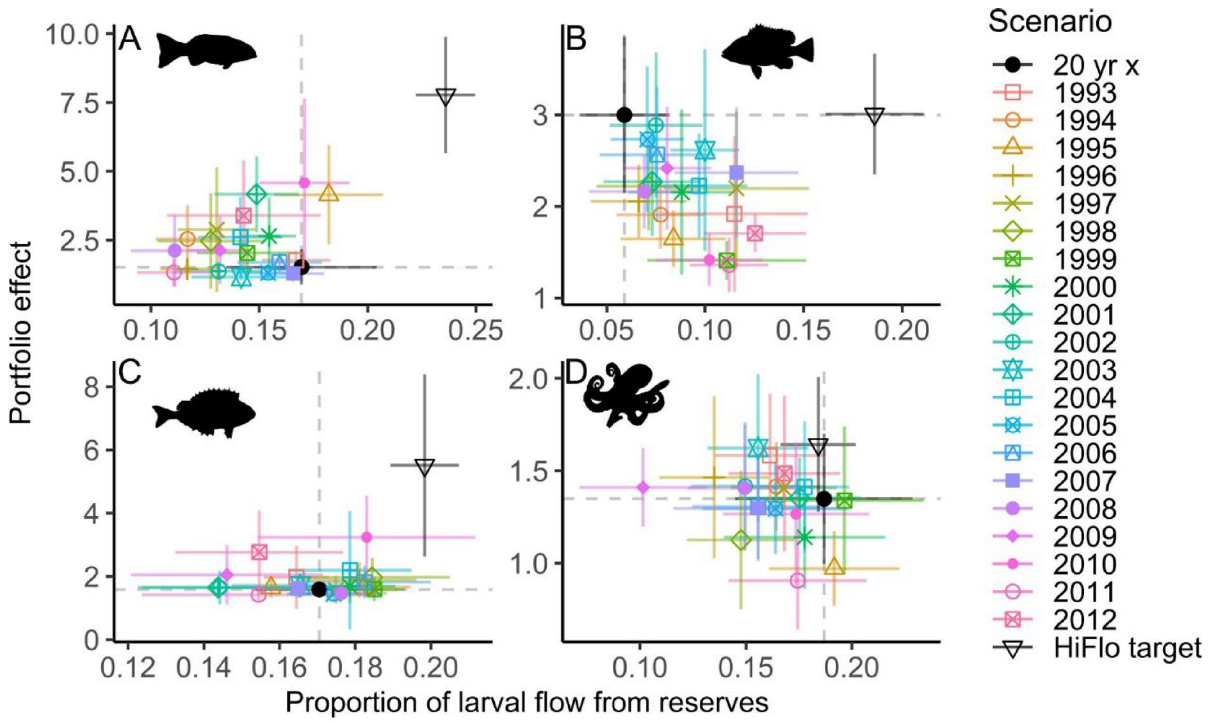

Fig. 5 Performance of reserve networks designed using either larval dispersal of individual years, a 20 year mean, or the scenario with highest portfolio effects with additional targets for highly contributing planning units (HiFlo target). Performance is measured as the proportion of total flow originating 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*

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, spawning frequency per reproductive cycle, and pelagic larval duration. 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 (SI Appendix, Fig. S1), 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). Multi-species optimisation would require explicit approaches for reconciling potentially conflicting spatial demands of different species, such as joint objective functions, multi-criteria prioritisation, or weightings informed by ecological or management priorities.

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 and 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. A combination of methodologies is likely to produce the best results, and ideally settlement, recruitment, and ontogenetic movement are verified and incorporated where possible.

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 also precludes the use of a dynamic dispersal benefit that is based on the previous year's values. This difficulty was evidenced in the large range of portfolio effect values across different solutions, including in the improved network scenarios (Fig. 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.

While our performance metric focuses on the cumulative larval flow originating from protected reefs, this does not imply that only high-flow pathways are ecologically relevant. Rare, weak long-distance dispersal events—although low in magnitude—contribute to functional connectivity by maintaining genetic connectivity and facilitating recolonisation after disturbance despite their small demographic effects (D'Aloia et al. 2022). In contrast, our approach focuses primarily on demographic connectivity, i.e. connections strong enough to influence population persistence through substantial larval exchange. Because the topography of the dispersal network shifts across years with changing oceanographic conditions, the identity of critical nodes influencing persistence is not static. The connectivity portfolio effect we quantify can therefore be interpreted as a network-level stabilisation mechanism, arising from asynchronous contributions of different nodes under different dispersal regimes. By prioritising reefs that hold high-flow positions across years, our improved scenarios implicitly protect the structural backbone of the metapopulation network, thereby enhancing long-term persistence under variable dispersal.

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 and 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. *P. leopardus*, for example, may be assumed to have low population abundance due to its fishery value and targeting in live reef fish trade (Khasanah et al. 2019). Third, our model does not incorporate larval behaviour, since species-specific data on this is scarce. Fourth, 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.

This highlights an important distinction between permanent and temporally adjusted, dynamic reserve configurations (Cashion et al. 2020). Even if specific connections weaken or shift over time, well-designed networks can continue to provide ecological benefits by protecting core habitats where biological processes are consistently tied to fixed locations—such as long-established spawning aggregation sites, nursery habitats, or reef structures that act as persistent larval sources. Protecting these sources is crucial, as the long-term viability of sink populations depends on the continued productivity of high-quality spawning habitats (Bode et al. 2006). More flexible spatial measures (e.g., periodically adjusted fisheries closures or dynamic spatial management) may complement permanent reserves in systems where dispersal shifts over time.

Connectivity is increasingly used to inform reserve system implementation (Balbar and 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.

Author contributions All authors contributed to the study conception and design. Larval dispersal modelling was performed by Kay Critchell and Eric A. Treml. Spatial prioritisation analysis was performed by Dominic Muenzel. The first draft of the manuscript was written by Dominic Muenzel and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This work was funded by University of Leeds School of Biology Doctoral Training Studentship, Bloomberg Philanthropies.

Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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