



## Benefits of measurable population connectivity metrics for area-based marine management

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### ABSTRACT

The dispersal of larvae by ocean currents is likely to represent an increasingly important driver of marine population dynamics across fragmented habitats. A boost in availability of larval dispersal data from biophysical simulations has therefore led to routine calculations of population connectivity metrics that are used for area-based management decision support, including the placement of Marine Protected Areas (MPAs). However, connectivity-based decision support for area-based management is often complex, highly uncertain, and the associated conservation impact rarely if ever evaluated. In combination, these challenges risk stakeholder engagement, compliance, and overall management effectiveness. Here we use a case study representing multiple key fishery species on coral reefs in Indonesia to demonstrate that consideration of larval dispersal for MPA placement decision support could be critical to recover both fish populations and fisheries from depletion, thereby mitigating potentially severe impacts on coastal communities. Importantly, we further show that MPA placement decisions can be effective even if based on comparatively simple and empirically measurable dispersal characteristics. Maximizing larval export, expressed as the contribution of larvae from MPA candidate sites to total larval settlement in surrounding areas, for example, was found to be a broadly beneficial MPA placement prioritization approach. Across investigated fish families with diverse life histories, this strategy resulted in MPA network designs that increased catches by a factor of  $1.3 \pm 0.3$  (mean  $\pm$  SD) and total fish biomass by a factor of  $3.2 \pm 0.3$  ( $9.7 \pm 1.2$  in no-fishing areas and  $1.4 \pm 0.3$  in fished areas) compared to conditions without effectively managed or protected areas. Our findings are relevant for both the implementation and impact evaluation of global marine conservation policies, specifically in tropical biodiversity hotspots, such as Indonesia, where coral reefs are often overfished and increasingly threatened but local communities highly dependent on sustainable fisheries.

### 1. Introduction

Most countries worldwide are committed to marine conservation initiatives that meet an increasingly ambitious set of targets defined by

the Convention on Biological Diversity (CBD) [1] and its currently negotiated post-2020 Global Biodiversity Framework. One critical component of CBD conservation goals is the enforcement of area-based management, including the expansion of Marine Protected Areas

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(MPAs) and Other Effective Conservation Measures (OECMs), in which fishing is “effectively” restricted [2–4]. Area-based management is widely recognized as an important tool whenever broad-scale regulations, such as catch limits, are difficult to implement, for example, because the management infrastructure is poorly developed or fishing activities are highly complex [5,6]. This situation is common in tropical coastal waters worldwide, which harbor much of the planet’s marine biodiversity. The Coral Triangle region in Southeast Asia typifies the associated dual challenge to (1) conserve exceptionally rich but threatened biodiversity while at the same time (2) ensuring sustainable fisheries production for highly dependent communities with a limited resource management capacity [7–9].

Area-based management is expected to be least effective where both marine resources and fishers are highly mobile [5,10]. However, on coral reefs throughout Southeast Asia fishing activities and associated impacts tend to be localized and severe. In this situation, the expansion of systematically placed MPAs (which are loosely defined here as areas where some regulations of fishing are enforced) is expected to help support both biodiversity conservation and sustainable fisheries production, as manifested in regional initiatives, such as the Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security [6, 11–13]. MPAs can be simpler to enforce than broad-scale fishery regulations (but see [14]), help effectively rebuild depleted reef fish populations [15–17], and can then export both adults [18–21] and larvae [22–24] to more heavily targeted fishing grounds nearby. The export of larvae is of particular interest in this context because it is spatially extensive [24, 25], and in contrast to adult movements out of managed or protected areas, unlikely to undermine the recovery potential of local populations [26,27]. More generally, larval replenishment is the central mechanism of species persistence and likely to be an increasingly important driver of population dynamics on coral reefs. This is due to a combination of both global and local human impacts on coral reef habitat and reef fish biomass [28–32], which are likely to reduce larval supply across fewer and more isolated patches of functional reef ecosystems.

Area-based management can help mitigate this problem by focusing on reefs where the rebuilding of fish biomass has the greatest potential to facilitate larval supply and the associated recovery of adult populations not only on local but multiple other reefs [33–35]. In theory, identifying such reefs with a high impact on metapopulation dynamics is now feasible, because data on larval dispersal among reefs can readily be generated by using ocean current data for biophysical modelling [36–39]. In practice, however, spatial prioritization based on metapopulation connectivity (or simply connectivity) remains challenging. For example, meeting the real-world need to achieve multiple potentially conflicting management objectives under global conservation policy commitments tends to result in complex site prioritization procedures, which integrate multiple data layers and/or metrics of connectivity [33, 40–43]. This situation prevents rigorous impact evaluations of resulting MPA network designs because only certain, comparatively simple, metrics of larval dispersal can be measured empirically. Furthermore, the rationale behind individual priority locations for management and protection based on complex combinations of connectivity metrics can be difficult or impossible to understand and thus explain to stakeholders. An associated lack of stakeholder engagement and support alone might then jeopardize the success of MPAs even though they could be ecologically effective [44–47].

Here we build on existing theory to calculate MPA network design performance based on various plausible metrics of connectivity derived from larval dispersal simulations for four key fish families targeted by fishers on coral reefs in Indonesia. We then use these connectivity metrics for spatial prioritization of management and protection, and to test associated outcomes against three commonly stated objectives: (1) population recovery within managed or protected areas, (2) metapopulation recovery beyond managed and protected area boundaries, and (3) fishery benefits. The key aims of our study are (1) to quantify the potential benefits of considering connectivity for area-based

management with multiple objectives, and (2) to clarify the potential trade-offs between biodiversity conservation and fishery outcomes based on spatial planning approaches that use comparatively simple and empirically measurable connectivity metrics vs complex approaches that use multiple balanced and weighted connectivity metrics. Simple and measurable connectivity metrics were conservatively hypothesized to result in substantial trade-offs among multiple management objectives.

## 2. Materials and methods

Our study was initiated by an expert workshop that focused on MPA placement decision support based on larval dispersal simulations for Southeast Sulawesi, Indonesia. The Southeast Sulawesi province is home to around 2.2 million people, many of whom depend on healthy coastal ecosystems for their food security and income. The Provincial government has authority over 11 million hectares of coastal waters (0–12 nm), which includes 10 formally implemented MPAs under the Provincial Government Marine Affairs and Fisheries Agency, totaling 455,065 ha. These areas target the protection and sustainable use of reef based nearshore marine habitats, adjacent habitats, and associated resources, including nearshore fisheries species. Multiple environmental initiatives in the region, including Rare’s Fish Forever program, are partnering with the Provincial Government Marine Affairs and Fisheries Agency, District government and local communities to establish networks of Managed Access with Reserve areas (MARs). MARs, which are equivalent to zoned or partially fished MPAs, already encompass 301,972 ha of provincial waters in Southeast Sulawesi, and place about 13% of the province’s critical habitat under full protection in no-take reserves while building local capacity to manage protected systems more sustainably.

Participants of the expert workshop hypothesized that there is a likely need to balance multiple metrics of population connectivity to maximize benefits from MPA networks in the region, but explicit strategies required to achieve management objectives for both biodiversity conservation and fisheries management were highly uncertain. Addressing this uncertainty and associated debates during the workshop, we started by specifying key MPA network performance indicators that we could test based on spatial fisheries modelling: (1) total fish biomass recovery; (2) fish biomass recovery in MPAs; (3) fish biomass recovery in fished areas; and (4) catch in fished areas. We then initiated a case study to test alternative connectivity parameterization strategies for spatial prioritization based on these performance indicators. In line with community priorities in the Southeast Sulawesi province, our study was focused on coastal (0–4 nm) small-scale fisheries, which account for on average 73% of household income in the region [48]. Small-scale fisheries in Southeast Sulawesi are broadly representative of fishing communities across Indonesia and the wider Coral Triangle region [49]. While fisheries governance may differ among provinces, including for example customary laws, most small-scale fisheries in Southeast Sulawesi and elsewhere practice long-held traditional fishing practices from boats that are generally less than 5 GT (4–6 m in length) and are used to operate non-mechanized fishing gears, including handline, speargun, traps and small nets [48]. Small-scale fishing operations in Southeast Sulawesi are commonly managed at the household level, with the catches generally sold to local buyers in the villages where catches are landed. Depending on the species, size, quality and thus value of individual fish, these are then transported to local and regional markets in Indonesia. Some high value fishes, including for example live grouper, emperor and snapper, are exported to markets across Southeast Asia [48].

Key target species of the nearshore coastal fishery in Southeast Sulawesi are represented by 31 families of teleost fishes in addition to octopus and mangrove crab, comprising a total of 171 species [48]. Our case study focused on four families of coral reef fishes among these: (1) groupers (Serranidae), (2) emperors (Lethrinidae), (3) snappers (Lutjanidae), and (4) rabbitfishes (Siganidae). These four families (1) have

been identified as key fishery targets by local fishing communities in Southeast Sulawesi [48,50], and (2) represented a diverse range of reproductive behaviors that were captured in our quantitative estimates of larval dispersal to help advance widely applicable spatial prioritization strategies. In combination, our four selected families represent some of the most highly valued fishery species across the wider Coral Triangle region, where reef-associated fishes account for more than 30% of total fisheries production [51]. Across the entire Southeast Sulawesi province, the average daily landed catch per fishing trip from July to December 2019 was 69 kg for emperors (10 species), 18 kg for snappers (27 species), 17 kg for groupers (31 species), and 9 kg for rabbitfishes (8 species). For comparison, the estimated annual per capita consumption of fish is just 20 kg [52]. Sale prices for live groupers, for example, range between IDR 100,000 and IDR 600,000/kg, depending on the size, quality and species [48]. Thus, groupers, emperors, snappers, and rabbitfishes are a significant source of protein and income for coastal communities in the region.

### 2.1. Larval dispersal simulations

To represent the four selected families in simulations of larval dispersal, we used a generic modelling framework that has been widely tested for similar applications and detailed in multiple previous studies [37–39]. Key biological parameters of the model include the spawning period, timing of settlement competency, maximum pelagic larval duration (PLD) and larval mortality rate. Gathering this information for multiple individual species of the four families of reef fishes was hindered by a general lack of data on the early life stages of marine fishes. In consequence, we chose to capture key characteristics in spawning and dispersal periods of selected families based on family-wide estimates or robust data on one or a few representative species (see summary in Supplementary Table S1). Groupers, for example, were assumed to spawn between September and November [53], releasing larvae that reach maximum settlement competency at 15 days over a maximum PLD of 31 days. These assumptions were informed by empirical data on two key species of coral trout (see [54,55] on *Plectropomus areolatus* and *P. leopardus*, which are among the most important target species for fishing communities across the Indo-Pacific region, including Southeast Sulawesi [50]). Due to a combination of their high value and vulnerability while aggregating to spawn, groupers tend to be heavily depleted [56]. Our data on catch rates in the study area is thus likely to under-represent their value because the composition of catches from heavily fished systems might feature less vulnerable species more prominently. Nevertheless, catch rates from Southeast Sulawesi indicated that emperors represent the recently most productive family of highly valued reef species. In our dispersal simulations, this similarly important family was represented by assuming a spawning period from March to May, with peak settlement competency of larvae assumed to be attained at 24 days over a maximum PLD of 40 days (see family-wide estimates of maximum PLDs in [57]). The third most productive family in terms of regional catch rates were snappers, which were assumed to spawn between October and February [58,59] and attain maximum settlement competency at 25 days over a maximum PLD of 40 days [57]. Finally, rabbitfishes, which are likely to be more resilient but less valuable than member of other families, were assumed to spawn from March to September and have a comparatively short maximum settlement competency period of 10 days and maximum PLD of 19 days (about three weeks [60]). The larval mortality rate during the dispersal period was assumed to be 5% per day for all families (see [61] for comparison).

The physical forcing of larval dispersal was quantified using a circulation model developed in the Delft3D modelling system. The Delft3D modelling system was assumed to best represent the seascape in the study area and provide for an accurate representation of processes acting in the region, capturing hydrodynamics that included forcing from temperature, salinity, tides, wind, atmospheric pressure, and Stokes drift from waves. The model was forced with tidal and geostrophic open

boundary conditions. The non-tidal boundary conditions were informed by the global ocean circulation model HYCOM, which is a well-validated model that is widely used for this purpose [62]. The tidal constituents were driven by the regional tidal model China Sea TPXO. The wave data was derived from a separate model (SWAN, at 5 km x 5 km resolution) to calculate Stokes drift and interpolate it onto the circulation model grid. The bathymetry used to derive the model grid was from the global GEBCO bathymetric dataset [63]. The native model output had an unstructured variable resolution ranging from 500 m near the high-priority communities to around 15 km near the open ocean boundaries. These data were then interpolated to our 1 km horizontal resolution biophysical model structure.

The distribution of coral reef habitat throughout the modelling environment was sourced from UNEP-WCMC. These coral reef layer data were used as a baseline to define the modelling environment for our spatially explicit dispersal model, allowing us to separate the seascape into 322 representative coral reef patches across Sulawesi (Fig. 1). Reef patches were identified based on natural breaks in reef topography, resulting in patches with areas ranging between 0.1 and 358.9 km<sup>2</sup> (mean ± SD: 11.9 ± 34.6 km<sup>2</sup>).

Based on this framework, the modelling process simulated the dispersal kernel (2-D surface) as a ‘cloud’ of larvae as it moves through time and space, allowing it to be concentrated or dispersed as defined by the biophysical parameters. An advection transport algorithm (4th order accurate) was used for moving larvae within the flow fields [64]. Larval density, settlement competency, mortality and habitat availability determined where, when, and how many larvae settled in different reef patches at each time step. The resulting simulation data were saved in the form of a 3-D dispersal matrix, representing the probability of larvae released from each source patch to settle at each destination patch at each time step (1 day). From these probability matrices (**P**), we calculated two other types of connectivity matrices: (1) the flow matrix (**F**), which quantified the (relative) number of larvae released from each habitat patch that survived to settle on downstream habitat patches; and (2) the migration matrix (**M**), which quantified the proportion of settlers from each source to the total settlement at each destination [65]. These three matrices provided the basis for calculating alternative metrics of use for MPA placement decision support.

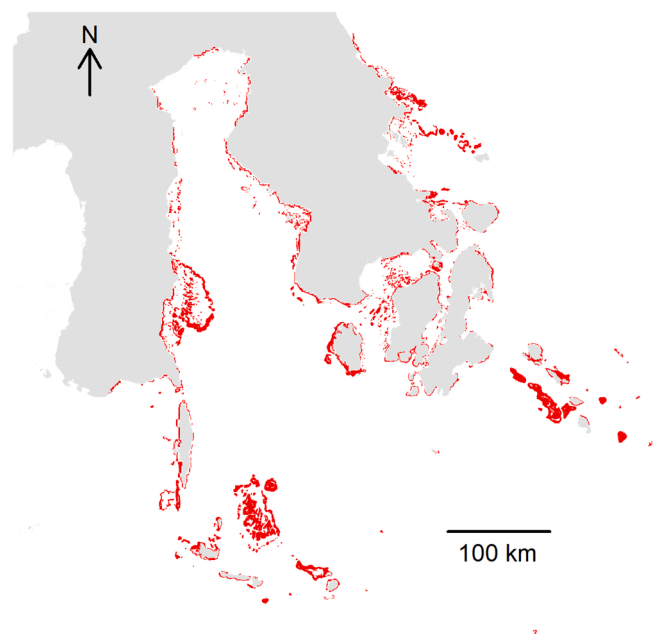


Fig. 1. Map of the study area in Southeast Sulawesi, Indonesia, highlighting the distribution of coral reef habitat (red) used for dispersal modelling and spatial prioritization.

## 2.2. Metrics of population connectivity

To use dispersal simulation outcomes to parameterize algorithms for MPA placement prioritization we built on an existing approach [33], which has been advanced over recent years following additional practical experience with MPA design applications and associated communication with practitioners, decision makers and stakeholders. The three principal connectivity metrics considered were (1) larval retention (R: representing larvae that were released from and then settled at the same candidate location), (2) larval export (E: representing larvae that were released from the candidate location but settled at other locations), and (3) larval import (I: representing larvae that settled at the candidate location following their release from other locations). These principal connectivity metrics represent three fundamental ecological management objectives: (1) to maintain or enhance self-replenishment of fish populations at candidate locations, (2) to maintain or enhance larval subsidies from candidate locations that rescue or boost the productivity of populations at other locations, and (3) to provide an insurance policy of external larval subsidies that rescue or boost the productivity of populations at the candidate location.

The first consideration for using the metrics Retention, Import and Export meaningfully for MPA placement prioritization was that they are not generally positively related [33]. Thus, we applied a weight of importance to each of them that could be used to balance any potential trade-offs in conservation and fisheries performance indicators.

Our second consideration for connectivity parameterization was that all three principal metrics can be calculated based on one or more of the alternative dispersal matrices **P**, **F** and **M** [65]. If probability matrix **P** was used, connectivity was prioritized based on probabilities of larval dispersal, which considers only the extent and location of a patch and does not incorporate heterogeneity in current or potential fish population biomass at different locations. Thus, matrix **P** has limited utility for practical MPA design application unless the focus is exclusively on considering larval retention at the candidate site (the diagonal of **P**, which is commonly referred to as local retention) [66]. Flow matrix **F** is likely to be more broadly useful for practical MPA design application than **P**, because **F** represented numbers of larvae exchanged between locations, which was achieved by multiplying **P** with a vector of assumed local larval output (approximated here based on the area of local coral reef habitat) [33]. Finally, migration matrix **M** represented a column- (or destination-) normalized version of **F**, which quantified the relative contributions of settlers from all source populations to total larval settlement at each destination. Intuitively, **M** provides a meaningful estimate of metapopulation organization that can be useful for conservation planning. However, the authors are not aware of any tests of the extent to which using **M** for spatial prioritization helps achieve commonly stated marine management objectives.

Our third consideration to parameterize connectivity referred to the weight of connection strengths vs the diversity of connections. In some cases, we experienced that decision makers choose to prioritize a high diversity of connections to and from MPAs, in addition to, or instead of how strong these connections are [33]. The underlying rationale can be that MPAs are then likely to function as a rescue insurance for disturbed downstream locations, or that MPAs themselves are least likely to turn into a failed investment because their populations receive larval import from diverse (and protected) sources [33]. Similar to relationships among the three principal metrics Retention, Export and Import, connection strength is not necessarily closely related to a high diversity of connections to and from candidate sites, which is why our parameterizations included an exponent  $z$ , which allowed for down weighting connection strength ( $z = 1$ ) in favor of connection diversity ( $z \approx 0$ ) [33, 67].

Finally, we tested how weighted metrics of Retention, Export and Import across managed areas (MPAs) and unmanaged locations are summarized to calculate performance scores during the MPA placement prioritization process. The first option (SS: sum of sums) used the

summed sum of dispersal matrix values across locations to calculate a total dispersal connectivity score for a given MPA network. The second option (MS: mean of sums) used the mean of sums across tested MPA locations. The third option (MM: mean of means) used the mean of mean dispersal matrix values.

In combination, these considerations allowed for testing tens of thousands of potential connectivity metrics for marine spatial planning (summarized in Supplementary Table S2). Some of these metrics have been used for practical MPA design applications by the authors in the past, but the performance of all has not yet been measured against the same commonly stated management objectives. Additionally, we aimed at highlighting MPA network design performance associated with nine relatively simple metrics of connectivity (Table 1), some of which can be measured empirically, would be ecologically defensible, easy to justify and communicate, and less computationally demanding than many of the more complex calculations captured by the complete suite of balanced and individually weighted metrics of connectivity outlined in Supplementary Table S2.

## 2.3. Spatial prioritization

Priority sites for MPA placement were identified based on connectivity scores calculated according to a combination of four objective functions:

$$R_{MPA} = \sum_{i=1}^m x_i L_{i,i}^{zR}(M_R), \quad (1)$$

$$E_{MPA} = \sum_{i=1}^m \sum_{\substack{j=1 \\ j \neq i}}^m x_i (1 - x_j) L_{i,j}^{zE}(M_E), \quad (2)$$

$$I_{MPA} = \sum_{i=1}^m \sum_{\substack{j=1 \\ j \neq i}}^m x_i x_j L_{j,i}^{zI}(M_I), \quad (3)$$

$$C_{MPA} = w_R R_{MPA} + w_I I_{MPA} + w_E E_{MPA}, \quad (4)$$

where  $R_{MPA}$ ,  $E_{MPA}$ , and  $I_{MPA}$  represent connectivity scores for Retention, Export and Import, respectively, associated with a given MPA network configuration,  $m$  is the total number of locations or planning units to be considered for MPA designation,  $x_i$  is the status of location  $i$  as either protected ( $x_i = 1$ ) or fished ( $x_i = 0$ ), and  $L$  is larval dispersal between pairs of locations  $i$  and  $j$ , which is a function of the type of dispersal matrix  $M$  used to calculate  $L$  (**P**, **F**, or **M**). As defined according to Eq. (1), scores for R represent the sum of local larval retention at protected locations. In contrast, according to Eqs. (2) and (3), scores for I and E represent the sum of the sum of larval export from protected locations  $i$  to unprotected destinations  $j$ , and the sum of the sum of larval import from protected sources  $j$  to protected destinations  $i$ , respectively. A total dispersal connectivity score  $C_{MPA}$  can then be calculated according to Eq. (4) as the sum of normalized scores for R, I and M (divided by maxima across  $i$ ) balanced by their corresponding weights of importance ( $w$ ). If any of the weights in (4) is unspecified or equal to zero,  $C_{MPA}$  neglects the corresponding component of the equation. However, placing no weight on a metric does not mean that high scoring MPA locations do not have any value with respect to this metric, but that the resulting MPA network was not optimized for it. We further note that while the set of equations above represents the sum of the sum across locations to derive  $C_{MPA}$ , Eqs. 1–3 can easily be adapted to represent the two alternative summary statistics (the mean of the sum and the mean of the mean). A heuristic optimization procedure was used to identify high-performing MPA network designs according to objective functions 1–4 (see Supplementary Material Text for details). Results from the optimization procedure included an overall best MPA network design as well as MPA site selection frequencies associated with each connectivity parameterization strategy outlined in Table 1 and Supplementary Table S2. In all scenarios, MPA networks were designed to cover 20% of coral reef habitat in the study area, which represents (1) the anticipated

**Table 1**  
Nine simple population connectivity metrics for spatial prioritization tested in this study.

Scenario names (Abbreviation, Symbol)	Definition	Value	Empirically measurable	Parameterization	Synonyms
Retention Strength (RS, ◆)	Number of native settlers	Absolute	No	Weight ( $w_R$ ): 1; Exponent ( $z_R$ ): 1; Matrix ( $M_R$ ): F; Summary: Mean	–
Self-Recruitment (SR, ▲)	Native settlers relative to total settlement	Proportion (0–1)	Yes	Weight ( $w_R$ ): 1; Exponent ( $z_R$ ): 1; Matrix ( $M_R$ ): M; Summary: Mean	–
Local Retention (LR, ✱)	Native settlers relative to output	Proportion (0–1)	No	Weight ( $w_R$ ): 1; Exponent ( $z_R$ ): 1; Matrix ( $M_R$ ): P; Summary: Mean	–
Import Strength (IS, ◆)	Non-native settlers	Absolute	No	Weight ( $w_I$ ): 1; Exponent ( $z_I$ ): 1; Matrix ( $M_I$ ): F; Summary: Mean	In-degree / Sink Strength
Import Influence (II, ▲)	Non-native settlers relative to total settlement	Proportion (0–1)	Yes	Weight ( $w_I$ ): 1; Exponent ( $z_I$ ): 1; Matrix ( $M_I$ ): M; Summary: Mean	In-degree / Source Dependence
Import Diversity (ID, ■)	Non-native settlers relative to total settlement	Absolute	Yes	Weight ( $w_I$ ): 1; Exponent ( $z_I$ ): $10^{-10}$ ; Matrix ( $M_I$ ): F; Summary = Mean	Weighted In-degree ( $0 < z_I < 1$ )
Export Strength (ES, ◆)	Number of settlers at external destinations	Absolute	No	Weight ( $w_E$ ): 1; Exponent ( $z_E$ ): 1; Matrix ( $M_E$ ): F; Summary: Mean	Out-degree / Source Strength
Export Influence (EI, ▲)	Contribution of settlers to settlement at external destination	Proportion (0–1)	Yes	Weight ( $w_E$ ): 1; Exponent ( $z_E$ ): 1; Matrix ( $M_E$ ): M; Summary: Mean	Out-degree / Source Influence
Export Diversity (ED, ■)	Number of settlement destinations	Absolute	Yes	Weight ( $w_E$ ): 1; Exponent ( $z_E$ ): $10^{-10}$ ; Matrix ( $M_E$ ): F; Summary: Mean	Weighted Out-degree ( $0 < z_E < 1$ )

minimum long-term target for the region [6,11], and (2) ongoing MPA design collaborations with local communities supported by the authors.

### 2.4. Fishery simulations

To test how well alternative MPA designs performed, we ran fishery simulations representing all four selected families. Fishery simulations were based on a Deriso-Schnute delay-difference model, which mimicked the dynamics of age-structured populations under data-poor conditions (for details see [68]). Simulations were based on an annual time step, capturing changes in fish biomass and catch according to natural adult mortality (survival), growth, larval dispersal, density-dependent recruitment, and fishing pressure in each area of the planning grid. Simulations started with a spawning event based upon which eggs were released from all areas and in proportion to the local biomass of mature fish in those areas at a given time. Eggs were assumed to develop into larvae and distributed according to simulated family-specific dispersal probability matrices (P). A Beverton-Holt stock-recruitment relationship was assumed to expose settled juveniles to density dependent mortality before they entered adult populations [69]. Further detail on the modelling procedure is available in multiple previous studies [50,70].

To parameterize simulations for the four different families we used the same strategy as for larval dispersal simulations by choosing either broad family-wide estimates of natural mortality, growth, and density-dependent recruitment, or data for individual species which we considered representative of the family and associated larval dispersal simulations. The grouper fishery scenario was parameterized based on previous studies of the coral trout *P. leopardus* by assuming annual adult survival ( $s$ ) of 0.63, a growth coefficient ( $p$ ) of 0.34, and steepness of the Beverton-Holt recruitment function ( $h$ ) of 0.5 [71]. As detailed above, *P. leopardus* is a key target species in the study area which also served to parameterize the larval dispersal model representing groupers. The associated parameterization of productivity through recruitment via  $h$  (0.5) reflects a moderately resilient species, which will be maximally productive when population biomass is depleted to 33% of unfished levels (for a meta-analysis of  $h$  estimated for commercial fish stocks see [72]). The same resilience and density-dependent maximum productivity through recruitment was assumed also for snappers and emperors. However, natural adult survival and growth for emperors was set to values of  $s = 0.79$  and  $p = 0.17$ , respectively, reflecting empirical estimates available for the spangled emperor (*Lethrinus lentjan*) from similar latitudes [73]. For snapper, we used values of  $s = 66\%$  and  $p = 0.3$  representing empirical measurements for the Malabar blood snapper

(*Lutjanus malabaricus*) from Vanuatu [73]. In contrast, rabbitfishes were represented based on a broad family-wide estimate of comparatively high mortality and growth using values of  $s = 60\%$  and  $p = 1$ , respectively (see e.g. *Signaus guttatus* and *S. sutor* [73]). The greater assumed resilience of rabbitfishes was further reflected by a steepness parameter  $h$  set to 0.7, which means that populations will be maximally productive when population biomass is depleted to 25% of unfished levels. A summary of all parameter values is given in Supplementary Table S1. We note that these parameter values were intended to capture a diversity of dispersal and life history characteristics that are broadly representative of key target species within some of the most important fish families across Southeast Sulawesi.

Key outcomes from fishery simulations were predictions of fish biomass and catch (relative to unfished biomass) under equilibrium conditions (assumed to be achieved after 100 years). By default, metapopulations were assumed to be depleted to 10% of unfished levels before networks of fully protected MPAs (no fishing) were introduced to test associated impacts on fish population biomass and catch. The depletion assumption might be pessimistic for some areas, but is realistic for most key target species in heavily overfished systems of the study area [50,51], helping to identify priority areas that are most likely to support recovery under heavy fishing pressure. However, multiple alternative depletion and protection scenarios were run to analyze implications for high performing connectivity prioritization strategies. These scenarios included baseline depletions down to just 25% and 50% of unfished levels coupled with MPA protection that varied from recovery to unfished levels (no fishing in MPAs) to sustainable fisheries management (50% of unfished biomass in MPAs) to full exploitation (25% of unfished biomass in MPAs).

Finally, in all scenarios, simulation results for connectivity optimized MPA systems were contrasted against those for 1000 random MPA designs, which were generated based on a haphazard selection of MPA locations until 20% of all coral reef habitat was covered.

### 3. Results

Dispersal simulations revealed clear differences among the four fish families represented in our model, reflecting differences in spawning period, settlement competency and maximum Pelagic Larval Duration (PLD). The most widely connected metapopulation was evident for snappers. Metapopulations for groupers and rabbitfishes were less widely connected, but with higher dispersal probabilities within regional connectivity hubs. The most vulnerable metapopulation was evident for emperors, as revealed by the lowest dominant eigenvalue of

P and the highest number of isolated patches. Based on these results we assigned the following rough classifications of metapopulation vulnerability for subsequent consideration in the interpretation of effective connectivity parameterization strategies: “Low” (snappers), “Medium” (groupers and rabbitfishes) and “High” (emperors) (Table 2).

### 3.1. MPA design performance

Fishery simulations based on alternative MPA design strategies revealed that even randomly selected MPA locations were likely to increase protected area biomass for all four families, but that declines in both fished area biomass and catch could be substantial, with potentially severe implications for coastal communities (Supplementary Figs. S1–S4). Systematic MPA placement based on connectivity substantially improved predicted MPA network performance, achieving increases in biomass and catch that either exceeded or at least resembled those of the best randomly designed MPA networks. Importantly, even most of the nine simple and measurable connectivity metrics achieved outcomes very similar to those for much more complex calculations which balanced multiple weighted metrics (see Fig. 2 and Supplementary Figs. S5–S7). Overall, maximizing larval export from the MPA network to fished areas appeared to be an effective strategy to recover metapopulation biomass while simultaneously increasing or maintaining catch. Across all four simulated fish families, which represented diverse life histories and variable levels of metapopulation vulnerability, simply maximizing export influence, as the mean proportion of settlers from MPAs, resulted in MPA designs which achieved improvements relative to business-as-usual conditions before MPAs of  $1.3 \pm 0.3$  (mean  $\pm$  SD) in catch and  $3.2 \pm 0.3$  in total fish biomass ( $9.7 \pm 1.2$  in MPAs, which covered 20 % of coral reef habitat, and  $1.4 \pm 0.3$  in fished areas, which covered the remaining 80% of coral reef habitat) (see Fig. 3). Only the catch of rabbitfishes, which were of comparatively lowest importance to fishing communities, was slightly lower than prior to MPA establishment (see Supplementary Fig. S7).

Maximizing export strength, which represented absolute numbers of larvae exported from MPAs to fished locations regardless of their contribution to local settlement, was widely beneficial too, specifically for the most widely connected metapopulation represented by snappers (Supplementary Fig. S6). In contrast, maximizing export diversity, which represented the number of export connections from MPAs to fished locations, performed poorly, resulting in notable decreases in both fished area biomass and catch for all species. As expected, a similarly poor performance was evident for the single-metric import diversity scenario. Prioritizations of import influence and strength among MPAs performed better but resulted in considerable performance trade-offs for the least vulnerable metapopulations of groupers and snappers

**Table 2**  
Characteristics of metapopulation connectivity and vulnerability of the four fish families.

	Groupers	Emperors	Snappers	Rabbitfishes
Dominant eigenvalue of P	0.38	$9.24 \times 10^{-5}$	0.2	0.54
Mean retention probability	0.06	$1.12 \times 10^{-5}$	0.02	0.09
Mean self-recruitment	0.36	0.47	0.28	0.39
Mean number of destinations	25	4	35	28
Mean contribution to destinations	0.04	0.16	0.04	0.04
Maximum number of destinations	73	20	124	89
Number of isolated patches	5	48	8	1
Total number of connections	8157	1206	11241	8925
Metapopulation vulnerability	Medium	High	Low	Medium

(Fig. 2 and Supplementary Fig. S6).

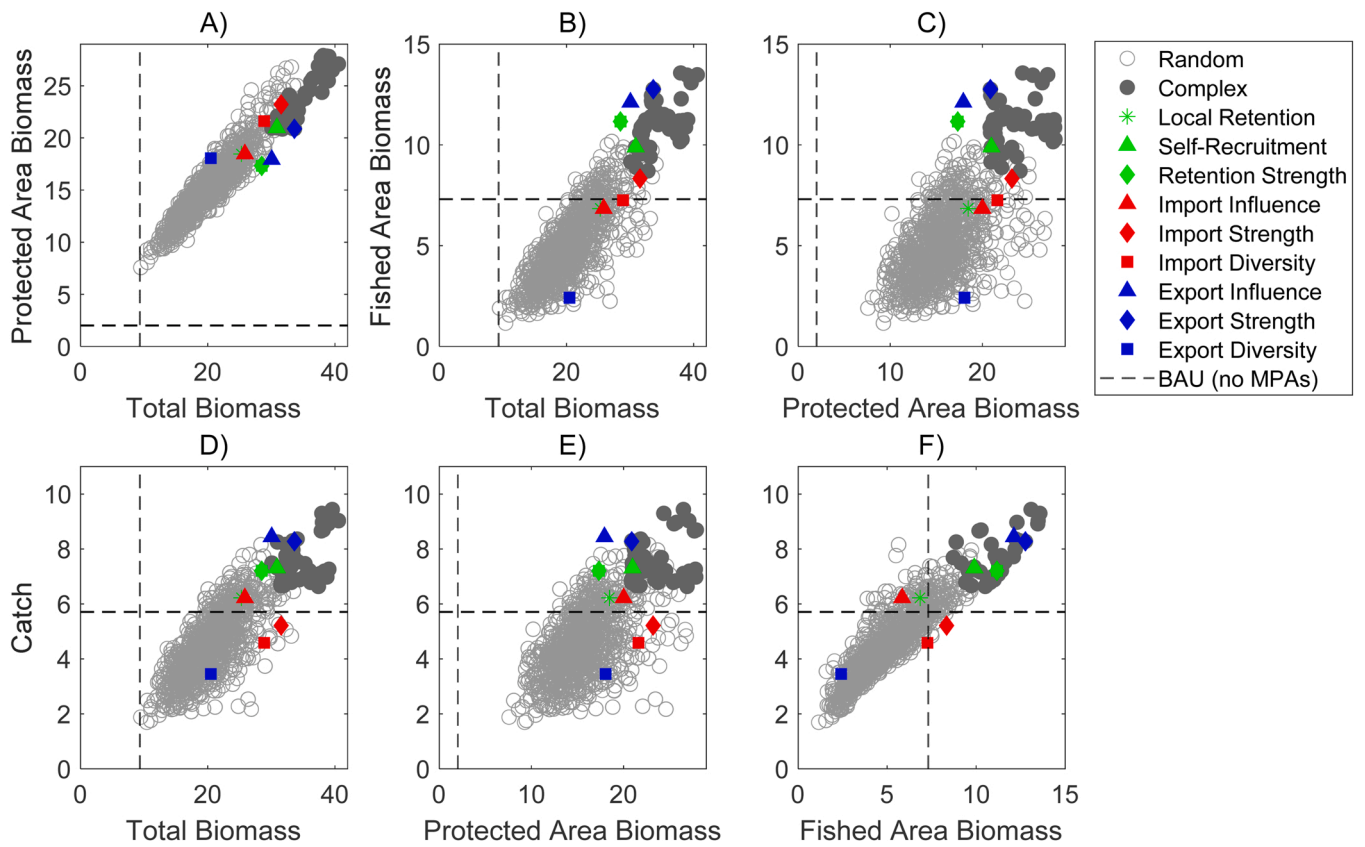
Thus, in agreement with workshop hypotheses, maximizing export contributions at destinations (the export influence scenario) appeared to be the most desirable strategy across indicators and species. The only notable trade-off was that this strategy did not achieve near-optimal protected area biomass recovery when population connectivity was limited as represented by emperors (Supplementary Fig. S5). In that case, performance of MPA placement prioritizations based on maximum self-recruitment in MPAs might be preferable (Fig. 3). Maximizing local retention in MPAs as well as larval import among MPAs also achieved high levels of protected area biomass recovery for emperors, but with a notable trade-off in fished area biomass, which accounted for 80% of the habitat, and thus biomass recovery potential. Moreover, prioritizations of maximum larval import between MPAs tended to produce the most spatially clustered MPA systems which might be difficult to implement. In contrast, MPA placement prioritizations based on self-recruitment and other retention-based connectivity metrics tended to produce the most spatially scattered MPA configurations. MPA configurations based on the generally high performing export influence scenario were neither highly scattered nor clustered (Fig. 4).

While both biomass and fishery outcomes depended on assumed levels of depletion and recovery in MPAs, the relative performance of alternative connectivity metrics for spatial prioritization was consistent. Thus, our findings should hold regardless of system states and management effectiveness. However, decisions on management and protected area coverage may need to be adjusted to balance desirable levels of recovery and fisheries production.

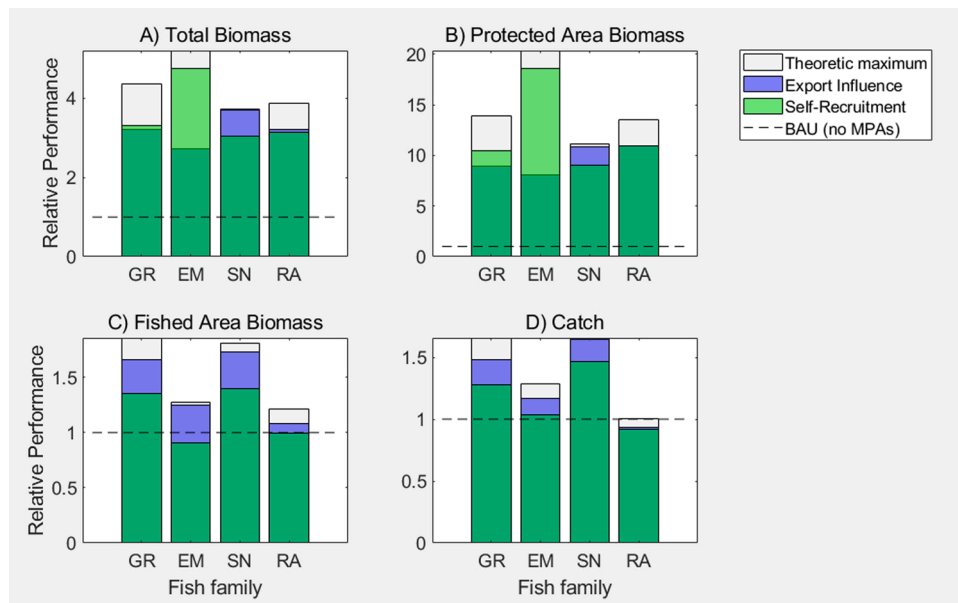
## 4. Discussion

Our study confirms the likely importance to consider population connectivity through larval dispersal for area-based marine management. It further quantifies how alternative site prioritization strategies impact the likely trade-offs between biodiversity conservation and sustainable fisheries production on coral reefs. A simple but effective approach to achieve both goals was to select candidate locations for management or protection that maximize the influence of larval export, defined as the relative contribution to settlement in surrounding areas. In other words, this strategy can prioritize the export of larvae to locations where fish populations are most likely to benefit from an associated boost in larval replenishment. Recovery in both fish biomass and catch associated with this comparatively simple larval export strategy were close to theoretical maxima based on various more complex, multi-metric prioritization strategies that have previously been applied for area-based management decision support across Southeast Asia [33]. Clearly, maximizing export influence will not always suffice to achieve near-optimal outcomes for potentially conflicting management objectives. Whenever metapopulations are highly fragmented, as represented by emperors, for example, a focus on metrics of larval retention within and among managed areas is likely to be important to ensure the sustainability of individual or regionally isolated populations [74,75]. We demonstrated here that this conservation-focused objective can be effectively achieved by maximizing self-recruitment (locations characterized by a high proportion of native settlers) or strong managed area connectivity (managed or protected populations that exchange many larvae). Notably, however, these alternative single-metric prioritization strategies resulted in more scattered (self-recruitment) or clustered (managed area connectivity) configurations of priority locations, with potentially important implications for practical implementation in terms of both economic costs and social equity.

More in-depth analyses covering more species, locations and alternative dispersal models are clearly desirable to support these findings. Moreover, more complex area prioritization strategies based on multiple weighted and balanced metrics of population connectivity can help better navigate potential trade-offs between conservation and fishery outcomes. However, as demonstrated based on our case study, benefits



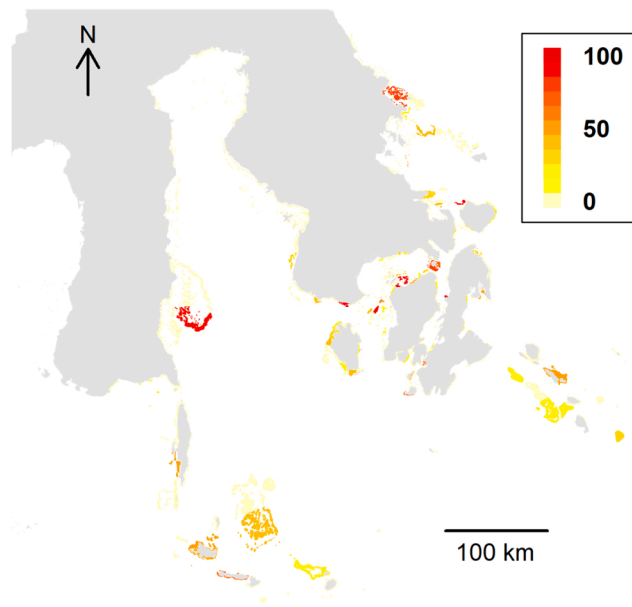
**Fig. 2.** MPA network design performance for groupers relative a business-as-usual (BAU) scenario without MPAs. Colored symbols highlight outcomes based on the nine “simple” connectivity metrics. Filled circles highlight outcomes for high-performing complex scenarios, including 1–3 balanced and/or weighted connectivity metrics. Biomass and catch are expressed as percentages of unfished biomass.



**Fig. 3.** MPA performance based on prioritizations of export influence and self-recruitment relative to a business-as-usual (BAU) scenario without MPAs. The theoretic maximum performance was based on the best complex connectivity prioritization strategy (top 5% across all indicators). Dark green areas indicate overlap of the two tested scenarios. GR: Groupers; EM: Emperors; SN: Snappers; RA: Rabbitfishes.

in performance against commonly stated objectives (biodiversity conservation through fish population recovery and the sustainability of productive fisheries) might be minimal. One critical assumption underlying the findings from this study was that all larvae were equally

likely to be demographically relevant, regardless of dispersal distance. This might be defensible over scales of tens to hundreds of kilometers [24,25], but should be carefully considered once spatial planning projects extend across countries and continents. Over such larger



**Fig. 4.** Map of the planning region in Southeast Sulawesi (light grey) highlighting combined selection frequencies of MPA locations based on the high-performing export influence prioritization strategy. Locations highlighted in orange and red were selected in most runs for most species.

international or global scales, objectives for area-based management networks might switch in focus from ecological to evolutionary time-scales, including a higher weighting of connection diversity over connection strength.

An important consideration for the choice of future connectivity prioritization strategies is that all three simple but high-performing metrics tested in our study (export influence, self-recruitment, and import influence) can be measured empirically using established methods [22–25]. Such empirical measurements provide the critical opportunity to build an evidence base of real-world impact behind the widely advocated use of larval dispersal data for area-based management decision support. Recent evidence suggests broad agreements between simulated and measured patterns of larval dispersal [76]. However, an ensemble of larval dispersal models and a time series of measured patterns of larval dispersal are likely to be useful for successful validations [76,77], which is not currently feasible in by far most situations, including our own study. Moreover, an empirical evidence base of positive spatial management outcomes requires rigorous impact evaluation [78]. These are key reasons to ensure that any quantitative approach for area-based management decision support (e.g. MPA placement as in this study) based on simulated larval dispersal data is (1) clearly justified and explained, including associated uncertainties, and (2) simple enough to communicate the rationale behind placement recommendations to those impacted by management implementation. Spatial prioritization based on intuitive, theoretically tested, and empirically measurable metrics of population connectivity provide several advantages over more complex strategies in this context. MPA placement recommendations, for example, can then be visualized and communicated more easily to engage both decision makers and stakeholders into the MPA design process, which is likely to be critical for MPA effectiveness [44–47, 50]. MPA placement recommendations based on larval dispersal data can then also be separated from those based on potentially more critical and easily validated information, such as environmental threats, habitat quality, economic costs, and various social factors that are likely to determine community support and compliance [50].

Spatial prioritizations based on all population connectivity metrics tested here can be implemented using straightforward optimization

procedures as described in the [Supplementary Material Methods](#). Alternatively, more established procedures and spatial planning software, such as Marxan, can be used. Marxan, for example, is a software that many conservation practitioners are already familiar, with and which can be useful to integrate connectivity metrics with various other planning considerations, such as the representation of multiple biodiversity features [33,40,42,75]. In either case, independent spatial prioritization based on larval dispersal is recommendable and should now be computationally feasible to cover multiple species and protection targets, which is an important practical consideration. Although not explicitly addressed in this study, both the number and habitat coverage of multi-species candidate locations for management or protection were considerable and could easily be increased by using a higher coral reef coverage target. Management decision support could then be based primarily on site selection frequencies rather than any single putatively best network of areas. Decision making based on site selection frequencies would also be more appropriate to account for the high level of temporal variation in larval dispersal data. Overall, the underlying assumption is that multiple managed or protected areas cannot necessarily be expected to function as a coherent network, but that an ecologically informed selection of priority locations enhances the prospects of a portfolio effect [22].

Any selection of candidate sites for effective management or protection should further include locations that are most likely to be resilient to future climate change [11]. Spatial prioritization that accounts directly for the effect of future climate change on larval dispersal is important but extremely challenging [42]. While ocean-atmosphere interactions under continued warming over the next century are expected to alter coastal and oceanic hydrodynamics [79], predicting such interactions is highly complex. Thus, explicit simulations of larval dispersal under future climate change are not generally feasible [80]. Nevertheless, some changes can be anticipated without a need for explicit dispersal modelling, including, for example, that the physiology of marine larvae is likely to favor shorter dispersal durations and higher rates of local retention under increasing temperatures [81,82]. Where these expected changes intensify the fragmentation of metapopulations [83], a focus on retention-based characteristics of larval dispersal (e.g. self-recruitment) would meaningfully complement considerations of larval export to ensure that area-based marine management contributes effectively to population recovery and species persistence.

## 5. Conclusions

In tropical biodiversity hotspots, such as Indonesia, where the availability of environmental data is often limited [84], the fisheries management capacity is often poor [7–9], and marine populations are under intense pressure from human impacts [31,32], area-based management in the form of zoned MPAs is a simple and potentially effective option to increase the prospects of marine population recovery and sustainable fisheries production [5,15,85,86]. The ongoing degradation and widespread recent decline of coral reefs [28,30,85] gives reason to assume that recruitment limitation and its relationship to larval dispersal should be considered for associated MPA placement decisions [29]. MPA placement based on larval dispersal characteristics requires clear justification against stated management objectives and an empirical evidence base of positive outcomes. Maximum larval export influence and self-recruitment appear to be suitable metrics for this purpose because they provide a rationale for decision making and communication, are empirically measurable, and are likely to help balance key biodiversity and fisheries objectives for conservation policy implementation. More complex spatial prioritization approaches that balance multiple dispersal metrics [33], or which integrate larval dispersal data with multiple other data layers, such as economic costs [40], are conceptually appealing but risk confusion about the selection and impact of individual priority locations. As long as simulated data on larval dispersal remains highly uncertain, it might best be considered as



a stand-alone additional, albeit potentially critical, consideration for area-based management decision support [77].

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## CRediT authorship contribution statement

**Nils C. Krueck:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Colm Tong:** Conceptualization, Writing – review & editing. **Courtney Cox:** Conceptualization, Funding acquisition, Project administration, Resources, Writing – review & editing. **Eric A. Trembl:** Conceptualization, Writing – review & editing. **Kay Critchell:** Conceptualization, Writing – review & editing. **Illiana Chollett:** Conceptualization, Writing – review & editing. **Dedi S. Adhuri:** Conceptualization, Writing – review & editing. **Maria Beger:** Conceptualization, Writing – review & editing. **Dominic Muenzel:** Conceptualization, Writing – review & editing. **Daniel Holstein:** Conceptualization, Writing – review & editing. **Stuart Campbell:** Conceptualization, Writing – review & editing. **Raymond Jakob:** Conceptualization, Writing – review & editing.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.marpol.2022.105210](https://doi.org/10.1016/j.marpol.2022.105210).

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