RESEARCH ARTICLE

Assessing fish–fishery dynamics from a spatially explicit metapopulation perspective reveals winners and losers in fisheries management

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Abstract

1. Sustainable management of living resources must reconcile biodiversity conservation and socioeconomic viability of human activities. In the case of fisheries, sustainable management design is made challenging by the complex spatiotemporal interactions between fish and fisheries.

2. We develop a comprehensive metapopulation framework integrating data on species life-history traits, connectivity and habitat distribution to identify priority areas for fishing regulation and assess how management impacts are spatially distributed. We trial this approach on European hake fisheries in the north-western Mediterranean, where we assess area-based management scenarios in terms of stock status and fishery productivity to prioritize areas for protection.

3. Model simulations show that local fishery closures have the potential to enhance both spawning stock biomass and landings on a regional scale compared to a status quo scenario, but that improving protection is easier than increasing productivity. Moreover, the interaction between metapopulation dynamics and the redistribution of fishing effort following local closures implies that benefits and drawbacks are heterogeneously distributed in space, the former being concentrated in the proximity of the protected site.

4. A network analysis shows that priority areas for protection are those with the highest connectivity (as expressed by network metrics) if the objective is to improve the spawning stock, while no significant relationship emerges between connectivity and potential for increased landings.

5. *Synthesis and applications*. Our framework provides a tool for (1) assessing area-based management measures aimed at improving fisheries outcomes in terms of both conservation and socioeconomic viability and (2) describing the spatial distribution of costs and benefits, which can help guide effective management

and gain stakeholder support. Adult dispersal remains the main source of uncertainty that needs to be investigated to effectively apply our model to fisheries regulation.

KEYWORDS
connectivity, conservation planning, European hake, metapopulation dynamics, network analysis, site prioritization

1 | INTRODUCTION

Achieving ocean's sustainability is a grand challenge of our time (Claudet, 2021; Lubchenco et al., 2020; Melnychuk et al., 2021). Sustainable fisheries require reconciling biodiversity conservation and socioeconomic goals (Costello et al., 2016; Daw et al., 2015; Hilborn et al., 2012, 2020; Micheli et al., 2014). However, this remains difficult, because complex spatiotemporal interactions between fish and fisheries hinder effective management (Janßen et al., 2018; Russo et al., 2017). Marine protected areas (MPAs) and other area-based management tools are increasingly seen as effective means to protect marine ecosystems while reaching positive socioeconomic outcomes (Klein et al., 2013; Rassweiler et al., 2014).

Despite the increasing number of studies focusing on area-based management (Magris et al., 2018; Villegas-Ríos et al., 2021), few attempts have been made to integrate the spatiotemporal distribution of fish stocks and fishing effort into dynamical models quantifying distributed regional impacts of local management solutions (Peña et al., 2017). Quantitative tools describing the coupled dynamics of fish and fisheries and highlighting the spatial distribution of benefits and drawbacks are urgently needed to assess the actual implications of proposed management scenarios in a realistic way (Bastardie et al., 2017; Ovando et al., 2021).

Seascape connectivity, a fundamental ecological process supporting population persistence and resilience, is key to determining the effectiveness of protection measures, and hence to guiding marine spatial planning and fisheries management (Almany et al., 2017; Balbar & Metaxas, 2019; Botsford et al., 2009; Krueck, Ahmadia, Green, et al., 2017; Maina et al., 2020). Moreover, this process helps guaranteeing fishery viability, since fishing grounds connected to MPA benefit from recruitment subsidy (the passive export of eggs and larvae) and/or adult spillover (Di Lorenzo et al., 2016). A growing amount of research has been conducted to support the identification of areas that contribute most to keeping metapopulations and metacommunities connected across heterogeneous seascapes (Belharet et al., 2020; Dubois et al., 2016; Harrison et al., 2020; Melià et al., 2016).

Recently, network analysis has gained attention as a useful surrogate to support site prioritization and identify connectivity hotspots (Engelhard et al., 2017; Zamborain-Mason et al., 2017). While this approach can partially overcome the difficulties of developing complex metapopulations models, its ability to account for the interaction between fishing effort and fish demographic dynamics remains unexplored.

Here, we develop a metapopulation model to inform site prioritization for fisheries regulations and assess spatially distributed impacts and trade-offs in fisheries and conservation outcomes. We use European hake (*Merluccius merluccius*) fisheries in the north-western Mediterranean as a case study. In the last two decades, hake has been the most overfished species in the Mediterranean (Cardinale et al., 2017; FAO, 2022; STECF, 2022), prompting the adoption of multi-annual plans aimed to set fishing targets and introducing spatial closures to fisheries. We investigate larval connectivity between spawning grounds (where adult hakes lay their eggs) and nurseries (where juveniles settle at the end of the larval phase) at the basin scale and perform a network analysis to identify connectivity hotspots based on a set of network metrics. Then, we use the results of the connectivity analysis to build a spatially explicit, age-structured metapopulation model describing the coupled dynamics of hake and its fishery. We use the model to forecast the outcomes of area-based fishing restrictions on stock status and fishery productivity, highlight the spatial distribution of benefits and drawbacks and identify the best candidate areas for protection. Finally, we assess the consistency between those areas with connectivity hotspots identified via the network analysis.

2 | MATERIALS AND METHODS

This is a modelling study that did not involve direct interaction with fish. Therefore, it did not require ethical approval.

2.1 | Study area

The study area is the geographical subarea 9 (GSA 9), as defined by the General Fisheries Commission for the Mediterranean (GFCM), encompassing the Ligurian and Northern Tyrrhenian seas (Figure 1a). Hake nurseries along coasts of Tuscany and Lazio are particularly productive and persistent in time (Colloca et al., 2015; Milisenda et al., 2021). Since GSA 9 is strictly connected to GSA 10 (Southern Tyrrhenian Sea) by the basin-wide cyclonic circulation flowing northward along Italian coasts, we included both GSAs in the connectivity assessment.
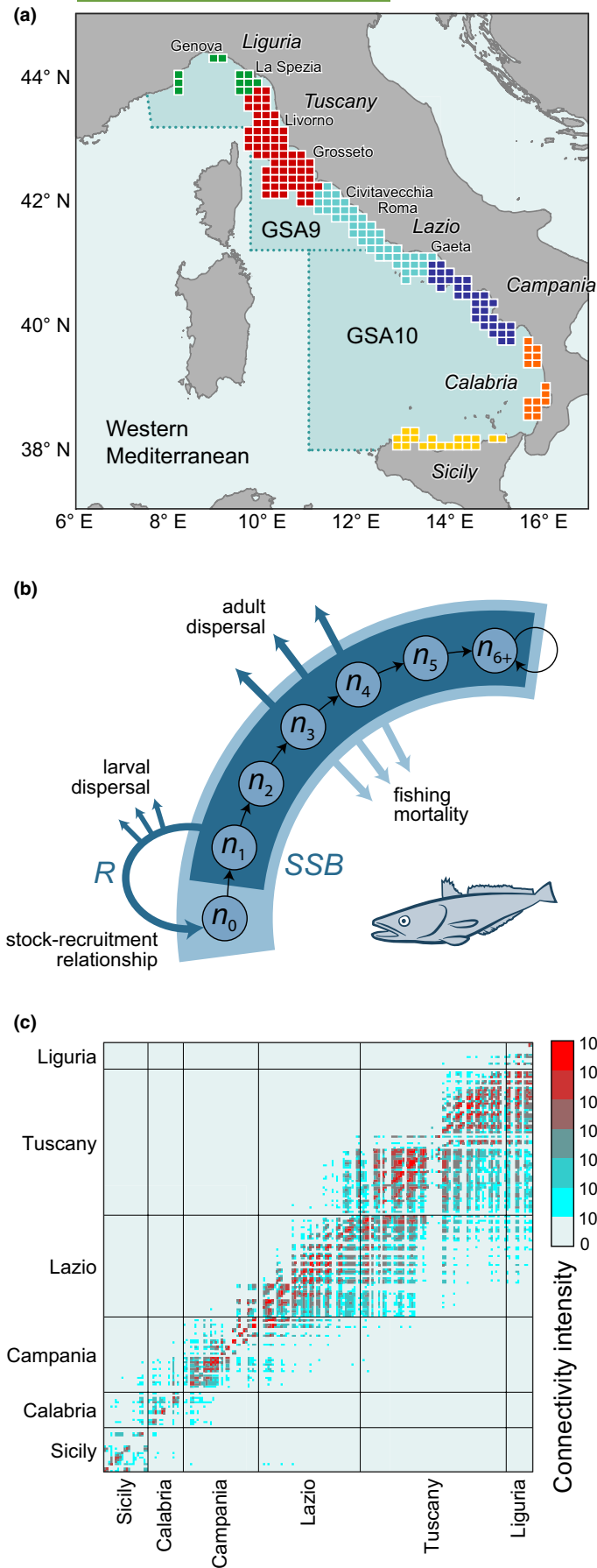
FIGURE 1 (a) Study area, encompassing geographical subareas (GSAs) 9 and 10, as defined by the General Fisheries Commission for the Mediterranean, and grid used for the connectivity analysis and the development of the metapopulation model. Cells are grouped into regions (labels in italics), indicated by different colours. The main cities mentioned in the text are also shown (roman font labels). (b) Structure of the metapopulation model. n_x ($x=1,\ldots,6+$) is the abundance of age class x in a cell of the model, while spawning stock biomass (SSB) indicates the abundance of the spawning stock. (c) Matrix of connectivity intensity (sensu Melià et al., 2016) across the study area. Matrix rows/columns indicate cells of origin/destination respectively (subdivided by region).

2.2 | Connectivity assessment

We assessed larval connectivity (intended here as the flow of propagules starting from a source cell and successfully arriving at the destination cell within the duration of the dispersal phase) with an individual-based biophysical model. We ran Lagrangian simulations over a discretized grid covering the simulation domain (Figure 1a), encompassing GSAs 9 and 10. The physical component of the model relies on daily water velocity fields produced by a physical reanalysis (Simoncelli et al., 2014) with a horizontal resolution of 1/16° and 72 unevenly spaced vertical levels (from 0 to about 5000m depth). The biological component accounts for available knowledge on life-history traits affecting the early life stage dispersal (reproduction and recruitment schedule, pelagic larval duration, nursery distribution; see Section S1.1 for details).

Assessing connectivity requires the knowledge of the location of spawning grounds and nurseries; the MEDISEH project (Colloca et al., 2015; Giannoulaki et al., 2013) provided a comprehensive picture of the latter in the western Mediterranean. To identify the most likely spawning grounds, we ran backward Lagrangian simulations by releasing 10^7 particles (over 10years, 2004–2013), from nurseries (Figure S1) at depths where hake juveniles are found in highest abundance during peak recruitment periods, and backtracked them for the duration of the larval phase. We reconstructed spawning grounds from the final locations of Lagrangian particles satisfying bathymetric and density-based suitability criteria (see Section S1.2 and Tables S1–S3 for details).

We then ran forward Lagrangian simulations to assess larval connectivity between reconstructed spawning grounds and nurseries across the region. Particles were released from spawning grounds according to the reproductive schedule and tracked for the duration of the larval phase, consistently with backward trajectories (see Section S1.3 for details). We generated a matrix of connectivity intensity (sensu Melià et al., 2016) over a grid of 194 cells measuring 0.125° in latitude×0.1875° in longitude (Figure 1a), representing fluxes (averaged over 10years) of hake larvae from spawning grounds to nurseries.

2.3 | Network analysis

To identify connectivity hotspots, we built a network in which each node represents a cell of the domain and each edge a non-empty element of the connectivity matrix, that is, an exchange of Lagrangian particles between two cells. The network is directed (each edge is oriented from the node of origin to that of destination) and weighted (connectivity intensity between two nodes is used to weight the related edge). We characterized each node with a set of six metrics: indegree and outdegree (i.e. the number of ingoing edges in node i, or outgoing from node i, respectively), in-strength and out-strength (the sum of the weights of ingoing edges in node i, or outgoing from node i), betweenness (the number of shortest paths between every couple of nodes j,k passing through node i) and information centrality (the loss of network efficiency caused by the removal of node i; see Section S1.4 for details).

2.4 | Metapopulation model

To describe the spatiotemporal dynamics of the stock, we set up a spatially explicit metapopulation model. The calibration of the model was only possible for GSA 9, for which data covering the period 2006–2014 were available from a local stock assessment (STECF, 2015; Table S4). The spatial domain encompasses 124 cells (out of 194); in each, we described demographics with a 7-age-class model (from 0 to 6+) that explicitly takes into account the most relevant life-history processes: juvenile recruitment, body growth, sexual maturation, natural and fishing mortality, larval and adult dispersal (Figure 1b). Recruitment in each cell was linked to spawning stock biomass via a Ricker stock-recruitment function (as in Hidalgo et al., 2019). The parameters of the function were calibrated for the whole GSA, but density dependence was assumed to act at the local scale (as suggested by Macchi et al., 2021 for the Argentine hake *Merluccius hubbsi*), so the function was expressed in terms of density and not absolute numbers. Larval dispersal was estimated through the previously built connectivity matrix. Unlike early life stages, adult hakes are excellent swimmers moving over great distances (Bartolino et al., 2008). In the absence of quantitative data allowing a realistic description of their motion, we described their redistribution across the study area with a Gaussian dispersal kernel with variance σ_D^2 to be estimated (Botsford et al., 2009). Body growth, sexual maturation and natural mortality curves were parameterized according to previous stock assessments (STECF, 2015).

The model accounts for the heterogeneous distribution of nurseries (Colloca et al., 2015) and spawning grounds, as well as of fishing effort (Fiorentino et al., 2014). Fishing mortality is the result of the action of otter bottom trawls and gillnets, each equipped with specific gears, operating in its own fishing grounds and targeting hake of different sizes. Therefore, we subdivided the model domain into sub-cells (by intersecting the metapopulation grid with the fishing footprint of the different fleet segments, Figure S2) and described the interaction between fish abundance and fishing effort in each sub-cell. Annual landings $L_i(t)$ in year t and cell i were estimated using the Baranov equation:

$$L_i(t) = \sum_{x=2}^{6+} w(x) n_i(x,t) \sum_{v \in i} \frac{A_v}{A_i} \frac{F_v(x,t)}{M(x)+F_v(x,t)} \left[1 - \exp\left(-\left(M(x) + F_v(x,t) \right) \right) \right],$$

(1)

where $w(x)$ is the average weight of a hake of age class x, $n_i(x,t)$ is the expected abundance of individuals of class x in cell i in year t, A_v is the area of sub-cell v, A_i is the area of cell i, $M(x)$ is the natural mortality rate of age class x and $F_v(x,t)$ is the fishing mortality rate, sum of the fishing mortalities determined by the different gears:

$$F_v(x,t) = \sum_m q_m \varphi_m(x) E_m(t) \psi_{v,m},$$

(2)

where q_m is an unknown catchability parameter associated with gear m, $\varphi_m(x)$ is the selectivity of gear m on age class x (Figure S3; Table S5), $E_m(t)$ is the normalized effort of the fleet segment equipped with gear m and $\psi_{v,m}$ is an effort multiplier proportional to the fishing

footprint of gear m in sub-cell v. Parameters q_{OTB33}, q_{OTB40}, $q_{GNS62.5}$, q_{GNS82} (OTB: otter bottom trawls; GNS: gill nets), expressing the catchability of the different gears, and σ_D^2, expressing the amplitude of the dispersal kernel of adult hake, were calibrated against a time series of abundance by age class covering the period 2006–2014 (STECF, 2015). To account for parameter uncertainty, we followed the bootstrap procedure described in Belharet et al. (2020) to derive an empirical probability distribution for each parameter. Landings estimated with the model for the same period were compared with data collected under the European Data Collection Framework for validation. Model structure and calibration procedure are described in detail in Section S2.

2.5 | Identifying priority areas for fishing regulation

To explore the ability of the model to effectively inform site prioritization, we assessed the effects of candidate area-based management scenarios by simulating the long-term impacts of local closures on the overall productivity of the hake fishery and the status of the stock. We chose landings (total fish biomass removed from each age class, excluding discards) and spawning stock biomass (total standing biomass of mature hake) as indicators of socioeconomic and environmental performance respectively (Rassweiler et al., 2014). In each cell, in turn, fishing effort was set to zero and relocated homogeneously across the remaining cells to keep the overall fishing effort unchanged. Stock dynamics were simulated over 50 years, and average values of landings and spawning stock biomass over the last 10 years of simulation were compared with those obtained simulating a status quo scenario, in which fishing effort was kept unchanged. A Monte Carlo approach was used to propagate uncertainty on model inputs (parameters, recruitment from GSA 10 to GSA 9 and fishing effort). For each closure scenario, the model was run 100 times, each time with a parameter set (q_{OTB33}, q_{OTB40}, $q_{GNS62.5}$, q_{GNS82} and σ_D^2) randomly drawn from the bootstrapped empirical distribution and using input time series of recruitment and fishing effort resampled from the original ones via a nearest neighbour bootstrap algorithm (Lall & Sharma, 1996). Eventually, a global sensitivity analysis (Saltelli et al., 2004) was performed to identify the parameters that most critically influence model output variance. Further details about the identification of priority protection areas are given in Section S3.

3 | RESULTS

3.1 | Connectivity and network analysis

The connectivity matrix (Figure 1c) linking spawning grounds (Figure S4) and nurseries has a strong diagonal structure, with ca. 16% of the particles retained within their cell of origin. The Tuscan Archipelago and the Gulf of Gaeta are important connectivity

hotspots in the area (Figure 2; Figure S5), encompassing the cells with the highest in-strength, out-strength and information centrality. Instead, the cells with the highest betweenness follow a backbone stretching from southern Campania up to the Tuscan Archipelago.

3.2 | Metapopulation model

The calibrated model (Table S6; Figure S6) correctly captures the order of magnitude of the different age classes (Figure S7) with the exception of the oldest, whose inter-annual fluctuations appear narrower than in the original time series. The model is also able to reproduce plausible values of landings over the study period, despite a slight systematic overestimation (further results in Section S6).

3.3 | Identifying priority areas for fishing regulation

Under current fishing pressure (status quo scenario), overall landings are projected to undergo an average 11% decrease over the next 50 years, while spawning stock biomass would remain essentially unchanged. Twenty-five per cent of the closure scenarios considered would on average improve both landings and spawning stock biomass at the regional scale compared with the status quo (Figure 3, first quadrant). Sixty-five per cent of the closure scenarios (mainly in cells along the Tuscan coasts, Figure 4) would benefit spawning stock biomass, with only a few scenarios (associated with closures in cells of central and northern Lazio) affecting it negatively. In contrast, cells whose closure would benefit landings represent only 29% of the total and are located in northern Tuscany (from La Spezia to Livorno), between Tuscany and Lazio (from Grosseto to Civitavecchia), and in the Gulf of Gaeta. The cell whose closure would ensure the highest improvement in spawning stock biomass compared to the status quo (+70% on average) is located off the Gulf of La Spezia (Figure 4a,c), while the largest benefit in terms of landings (+3% on average compared to the status quo, but lower than present levels) would be generated by closing one of two cells in the Gulf of Gaeta or one in northern Lazio (Figure 4b,d).

To investigate the spatial distribution of the impacts of a local closure, that is, to identify winners and losers in fisheries management, we calculated the change in landings and spawning stock biomass in each cell of the domain after the fishery closure that would contribute most to spawning stock protection (corresponding to the Gulf of La Spezia). The area between Liguria and Livorno (9% of the domain) would benefit from a strong improvement in spawning stock biomass (+183% on average and up to +990%, Figure 5a) and landings (+10% on average, and up to +179%, Figure 5b) compared to the status quo, while the relocation of fishing effort would cause a small decrease in spawning stock biomass and landings (−1% on average, up to −2%) in many cells south of Livorno. Although the overall impact on landings of closing the cell in the Gulf of La Spezia would be
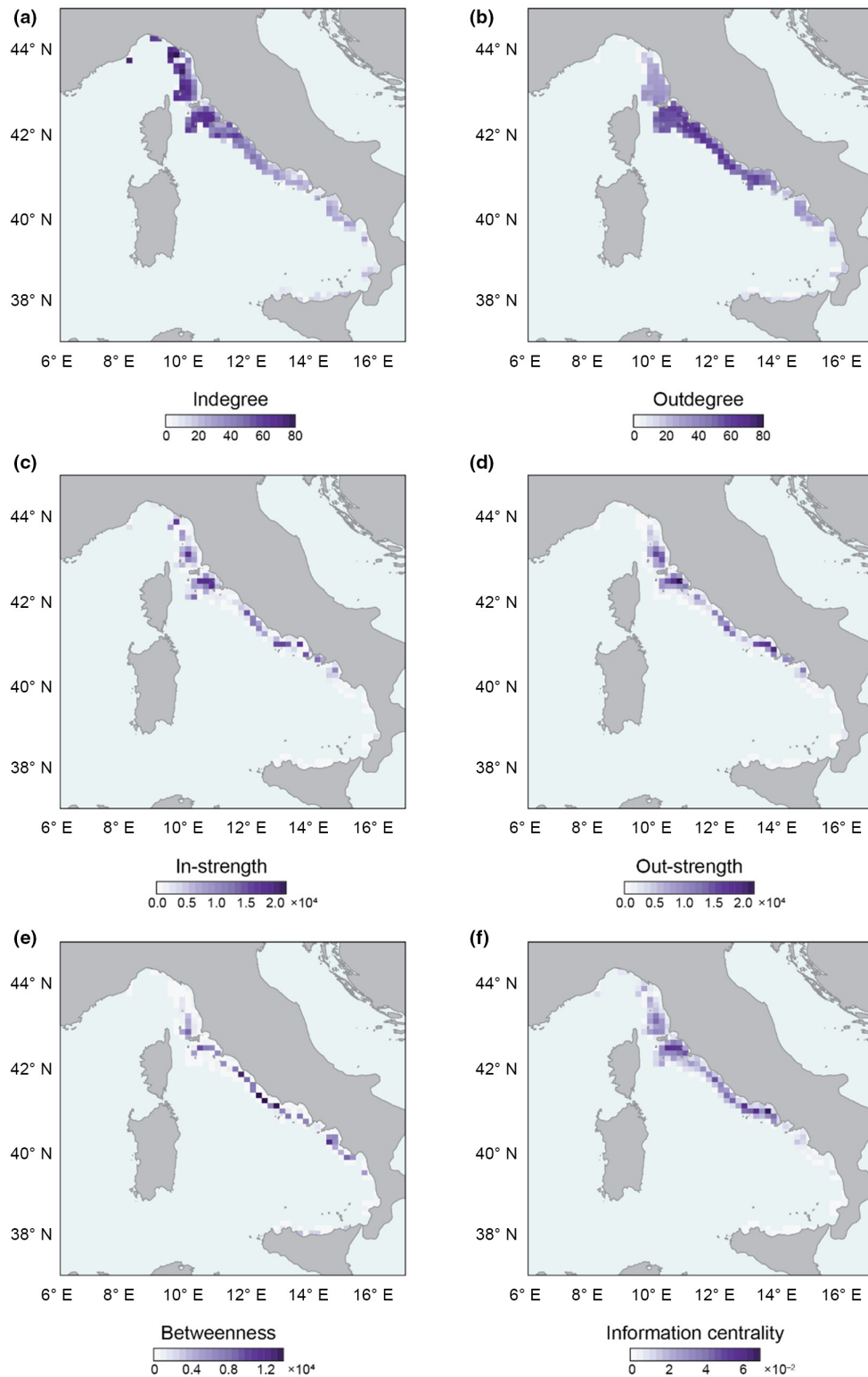
FIGURE 2 Results of the network analysis. (a) Indegree. (b) Outdegree. (c) In-strength. (d) Out-strength. (e) Betweenness. (f) Information centrality (see Section S1.4 for details on the metrics).

slightly negative (−2%), fleet segments would be affected in different directions, with an overall decrease of 3% in trawler landings and a 1% increase in gillnetter landings. The area over which the benefits would be distributed covers 27% of the domain up to southern Tuscany.

3.4 | Linking connectivity and protection performances

The performances of local fisheries closures are strictly related to the role of each cell in regional connectivity. In fact, most network
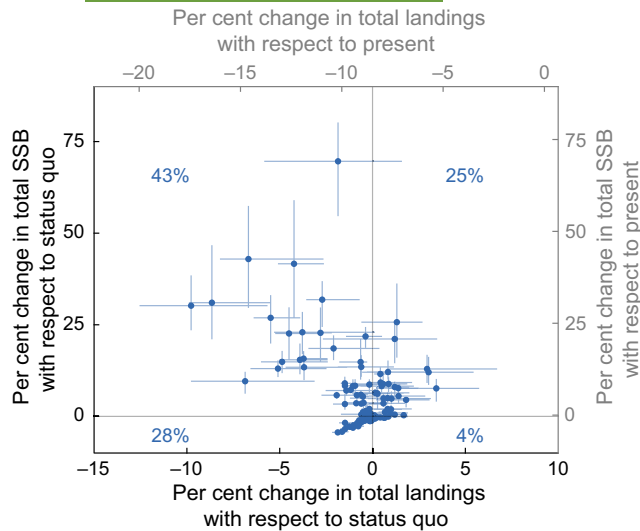
FIGURE 3 Median impacts of local closures of European hake fisheries in geographical subarea (GSA) 9. Each dot represents the per cent change, with respect to the status quo scenario, of regional landings and spawning stock biomass (SSB) over the whole GSA, 50 years after a complete closure of the fishery in one of the model cells (see Figure 1a). Dots indicate median values, while whiskers show interquartile ranges. Secondary axes (in grey) indicate per cent changes with respect to present. Percentages indicate the fraction of scenarios whose mean value falls in a given quadrant.

metrics are significantly correlated with the change in spawning stock biomass expected from the closure of each cell (Table S7). This means that the higher a cell is ranked with respect to a given metric, the more plausible it is that its closure to fishing would positively contribute to stock protection. The strongest correlations were found with in-strength, betweenness and information centrality, while no significant correlation was found between network metrics and the enhancement of fishery productivity at the regional scale.

3.5 | Sensitivity analysis

The global sensitivity analysis identified the variance of the adult dispersal kernel (σ_D^2) as the parameter that most critically affects model outputs (first-order index for average change in spawning stock biomass=0.60, for landings=0.92). A multiple linear regression between bootstrapped parameters (q_{OTB33}, q_{OTB40}, $q_{GNS62.5}$, q_{GNS82}, σ_D^2) and the corresponding model outputs (spawning biomass and landings) showed a positive correlation between σ_D^2 and landings and a negative correlation with spawning stock biomass (Table S8).

4 | DISCUSSION

We trialled a spatially explicit modelling approach to assess the expected impacts of area-based protection measures at the regional scale and their spatial distribution at the local scale. The outcomes of restricting fisheries in a given cell depend on its characteristics in terms of availability of nurseries and spawning grounds, fishing pressure and larval connectivity. About one quarter of the local closures would result in a win–win alternative (compared to the status quo scenario) in terms of both conservation and socioeconomic objectives. However, the areas to be closed as a priority depend strongly on the management goals (Melnychuk et al., 2021). If the primary objective is to ensure the viability of the stock, areas hosting larger extents of nurseries and spawning grounds and characterized by strong network centrality are prime candidates for protection. If maximizing productivity is the priority, it is more difficult to identify an effective rule of thumb to support site prioritization, as we found no correlation between network metrics and contribution to landings. Many of the cells whose protection would contribute most to improving productivity are located in the southern part of the study area (Gulf of Gaeta), most likely due to the current directing larval drift northward, thus supplying the whole domain with a constant flow of recruits.

Simulating fish–fishery dynamics with a spatially explicit model allowed us to highlight the consequences of local closures in different areas of the domain. Protecting the cells whose closure is expected to determine the best performance (in terms of spawning biomass) at the regional scale would sharply increase the spawning stock in its near surroundings, while the redistribution of fishing effort in the rest of the domain would cause small reductions of the local spawning stock. A wider area would benefit of an increase in landings, although landings at the regional scale are expected to decrease slightly. We assumed that the closure of fishing in a cell would induce a 'domino effect' in the spatial reorganization of fishing effort, leading to a homogeneous increase throughout the unprotected area, as in Krueck, Ahmadia, Green, et al. (2017). This is an alternative hypothesis to the 'fishing the line effect', that is the tendency of displaced fishing effort to concentrate along closure boundaries to exploit spillover (Kellner et al., 2007). We ran a few explorative simulations in which displaced fishing effort was allocated to the cells adjacent to the closure, resulting in a qualitatively similar pattern of regional impacts. Therefore, we decided to use the first reallocation rule, considering it as more neutral.

Overall, results suggest that there is room for alternatives able to potentially improve the status of the spawning stock while containing the decline in landings compared to the projected status quo scenario, consistently with other case studies (Chollett et al., 2017; Costello et al., 2016; Hilborn et al., 2020; Krueck, Ahmadia, Possingham, et al., 2017). However, we also show that no option is without side effects (Bastardie et al., 2017): the redistribution of fishing effort following the closure of an area to fishing would lead to an uneven distribution of positive and negative impacts, especially far from the protected area. Proper identification of potential winners and losers is therefore crucial to guide sustainable management design and gain stakeholder support (Rassweiler et al., 2014), as well as provide a scientific basis for compensation strategies.

Despite the scarcity of empirical studies addressing both connectivity and population dynamics, linking these aspects is crucial to design MPAs (Belharet et al., 2020; Bode et al., 2016;
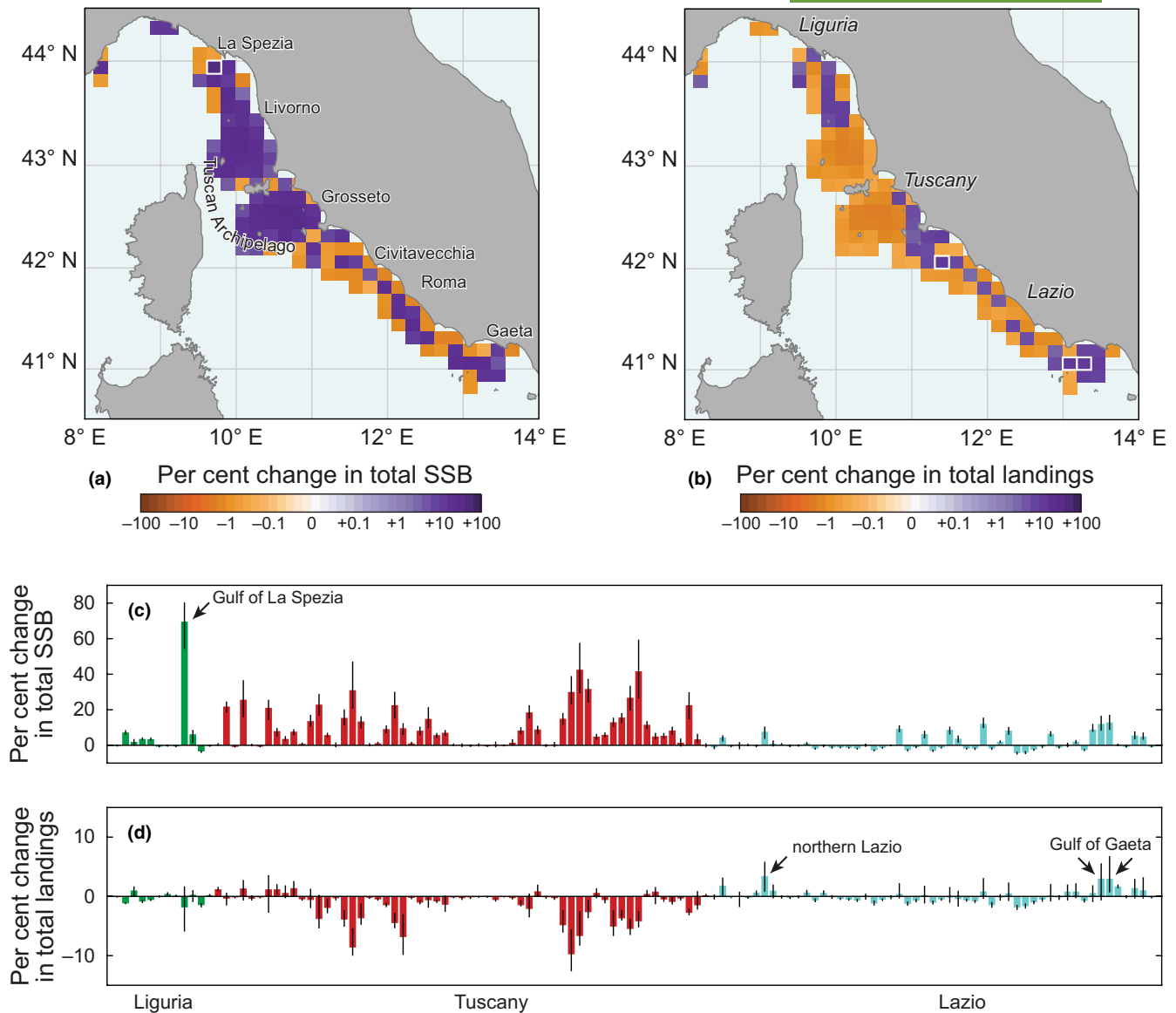
FIGURE 4 Impacts of local closures of European hake fisheries in geographical subarea (GSA) 9. In the two upper panels, the colour shade of each cell indicates the per cent change, with respect to the status quo scenario, of median (a) spawning stock biomass (SSB) and (b) landings calculated over the whole GSA 9, 50 years after a complete closure of the fishery in that cell. The histograms highlight the uncertainty of the estimates, showing the median (bars) and interquartile range (whiskers) of the per cent change in SSB (c) and landings (d). Colour codes in the histograms indicate the regions in which the study area is subdivided (see Figure 1a). Cells highlighted by a white border and bars indicated by an arrow are those whose closure would maximize SSB (a, c) and landings (b, d) respectively.

Johnson et al., 2018; Krueck, Ahmadia, Green, et al., 2017; Puckett & Eggleston, 2016). Integrating demographic and fishing effort dynamics into a consistent spatiotemporal modelling approach is also key to assess the effectiveness of area-based management tools (Janßen et al., 2018). The proposed modelling approach encompasses the key processes influencing marine metapopulation dynamics by incorporating current knowledge about biological traits, larval connectivity and spatially explicit information about fishing pressure exerted by different fleet segments into a unique framework. Although verifying that the stock under study actually behaves as a true metapopulation is beyond the scope of our work, we believe that habitat patchiness, spatial heterogeneity of fishing effort, spatial decoupling of life stages through flows of adults and larvae connecting otherwise

disjointed patches, and different contribution of each cell to the connectivity network make it conform to the conditions indicated by Kritzer and Sale (2006), that is, 'a system in which (1) local populations inhabit discrete habitat patches and (2) interpatch dispersal is neither so low as to negate significant demographic connectivity nor so high as to eliminate any independence of local population dynamics, including a degree of asynchrony with other local populations'. This is consistent with previous studies suggesting the existence of a metapopulation structure in Mediterranean and Atlantic European hake stocks (Hidalgo et al., 2019; Pita et al., 2016).

In the absence of information on the directional movement of adults, we assumed an isotropic Gaussian dispersion. Possible directional connectivity could play a crucial role in the redistribution of
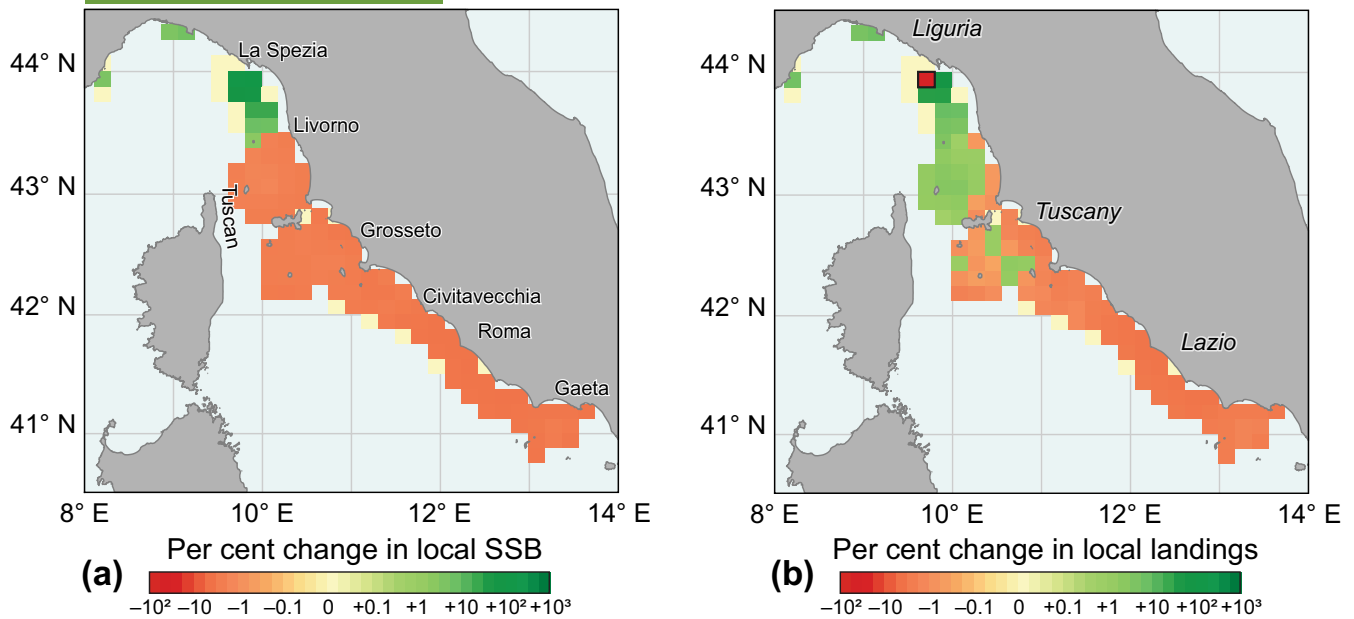
FIGURE 5 Spatial distribution of the impacts of closing European hake fisheries in a specific cell of geographical subarea 9 with respect to the status quo scenario, namely the median per cent change of local spawning stock biomass (c) and local landings (d) within each cell, 50 years after closing the fishery in the cell highlighted by a black border (corresponding to the Gulf of La Spezia).

adults within the metapopulation (e.g. in terms of its persistence). Neglecting this phenomenon could cause mismanagement, which we have tried to mitigate by formulating the most neutral hypothesis. However, this aspect should not be overlooked in policy decisions and should guide future research. The results of the sensitivity analysis show, in accordance with theoretical studies (e.g. Rinaldo et al., 2020), that the actual size of the area that would benefit from an increase in landings and/or spawning biomass depends critically on σ_D^2, the parameter expressing the dispersal capacity of adult hake. Changing this parameter has opposite effects on landings and spawning stock biomass: lower values of σ_D^2 imply higher retention, resulting in an increased spawning biomass that favours stock recovery within the protected cell and in its immediate proximity; conversely, higher values of σ_D^2 imply greater dispersal, lower density-dependent effects and a consequently wider area benefiting from higher landings.

This study corroborates the idea that network analysis can help explain the role of different areas in determining metapopulation connectivity and, consequently, in contributing to sustain stock viability. Recent literature has interpreted the ecological significance of network metrics: strength measures the magnitude of potential larval exchange from/to a node, while degree highlights the geographical diversity of connections from/to that node; in-(degree/strength) and out-(degree/strength) quantify the tendency of a node to act more as a larval sink or source respectively (Conklin et al., 2018; Dubois et al., 2016). Betweenness identifies key stepping stones for animal movement (Friesen et al., 2019), while information centrality quantifies how propagation on a network is affected by the deactivation of a node (Latora & Marchiori, 2007). Network metrics most correlated with the conservation performances of different cells take into consideration the connectivity network as a whole

(betweenness and information centrality) or reflect the availability of extended nursery habitats that act as effective receptors of juveniles (in-strength), another key ecological function.

Significant correlations between network metrics and metapopulation persistence had already been found in recent theoretical work (Zamborain-Mason et al., 2017), and recent studies have advocated the use of those metrics as effective tools to support site prioritization for biological conservation (Boschetti et al., 2020; Conklin et al., 2018; Watson et al., 2011). Given the increasing availability of relatively simple tools for assessing connectivity and estimating network metrics, approaches based on network analysis can be effective for a quick and cost-effective identification of candidate areas for protection, hence providing a potential surrogate to developing a full metapopulation model. In our case study, however, the lack of significant correlation between network metrics and the contribution of each cell to fishery productivity cautions against the actual potential of network analysis to completely replace a metapopulation approach. A comprehensive approach integrating available information on connectivity, habitat extent and suitability, species-specific life-history traits and the spatiotemporal dynamics of fishing effort, is hence essential to develop more realistic models that can support a robust site prioritization (Cabral et al., 2016).

The modelling approach proposed here could easily be extended to the scale of the entire Mediterranean or a larger portion of it, allowing for a Mediterranean-wide stock management as envisioned by the European Commission. Besides the limitations already highlighted here (such as inadequate knowledge of adult movement) that need to be urgently addressed, the lack of stock assessments in many regions is a major obstacle in this direction. Furthermore, this study addresses new issues beyond those commonly addressed

in Mediterranean fisheries management, which often prioritize the preservation of persistent nurseries over spawning grounds. While it is true that juveniles are particularly vulnerable to trawl fisheries when they assemble, too little attention has so far been paid to the protecting adult aggregations (Carbonara et al., 2019).

Despite some simplifications, essentially due to the lack of finer-scaled information on the stock under study, we believe that our approach provides a valuable tool for exploring alternative management policies from a truly spatially explicit perspective. Furthermore, our analysis identified the parameter (adult dispersal) on which future studies should focus to reduce uncertainty about the impacts of area-based measures and their geographical distribution, allowing for a more robust application of this framework to fisheries regulation. Our results provide a starting point for developing management rules aimed at a more equitable distribution in space and time of costs and benefits at the regional scale. Failing to properly take into account both the spatial and temporal dimensions of the problem may hinder stakeholders' support for management decisions.

AUTHOR CONTRIBUTIONS

Paco Melià and Andrea Radici conceived the research and designed the methodology. Andrea Radici developed the models and performed computations, with support from Paco Melià and Carlo Piccardi. Alessandro Ligas, Isabella Bitetto, Giuseppe Lembo, Maria Teresa Spedicato and Paolo Sartor contributed to acquisition and interpretation of data. Andrea Radici wrote the first draft with support from Paco Melià and Joachim Claudet. All the authors critically revised drafts, added intellectual content and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT
No conflict to declare.

DATA AVAILABILITY STATEMENT
Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.qz612jmn5 (Radici et al., 2023).

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REFERENCES

Almany, G. R., Planes, S., Thorrold, S. R., Berumen, M. L., Bode, M., Saenz-Agudelo, P., Bonin, M. C., Frisch, A. J., Harrison, H. B., Messmer, V., Nanninga, G. B., Priest, M. A., Srinivasan, M., Sinclair-Taylor, T., Williamson, D. H., & Jones, G. P. (2017). Larval fish dispersal in a coral-reef seascape. *Nature Ecology & Evolution*, 1(6), 1–7. https://doi.org/10.1038/s41559-017-0148

Balbar, A. C., & Metaxas, A. (2019). The current application of ecological connectivity in the design of marine protected areas. *Global Ecology and Conservation*, 17, e00569. https://doi.org/10.1016/j.gecco.2019.e00569

Bartolino, V., Ottavi, A., Colloca, F., Ardizzone, G. D., & Stefánsson, G. (2008). Bathymetric preferences of juvenile European hake (*Merluccius merluccius*). *ICES Journal of Marine Science*, 65(6), 963–969. https://doi.org/10.1093/icesjms/fsn079

Bastardie, F., Angelini, S., Bolognini, L., Fuga, F., Manfredi, C., Martinelli, M., Rasmus Nielsen, J., Santojanni, A., Scarcella, G., & Grati, F. (2017). Spatial planning for fisheries in the northern Adriatic: Working toward viable and sustainable fishing. *Ecosphere*, 8(2), e01696. https://doi.org/10.1002/ecs2.1696

Belharet, M., Di Franco, A., Calò, A., Mari, L., Claudet, J., Casagrandi, R., Gatto, M., Lloret, J., Sève, C., Guidetti, P., & Melià, P. (2020). Extending full protection inside existing marine protected areas, or reducing fishing effort outside, can reconcile conservation and fisheries goals. *Journal of Applied Ecology*, 57(10), 1948–1957. https://doi.org/10.1111/1365-2664.13688

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(5), 1–23. https://doi.org/10.1371/journal.pone.0154272

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), 1–13. https://doi.org/10.1002/eap.2011

Botsford, L. W., White, J. W., Coffroth, M. A., Paris, C. B., Planes, S., Shearer, T. L., Thorrold, S. R., & Jones, G. P. (2009). Connectivity and resilience of coral reef metapopulations in marine protected areas: Matching empirical efforts to predictive needs. *Coral Reefs*, 28(2), 327–337. https://doi.org/10.1007/s00338-009-0466-z

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(11). https://doi.org/10.1002/ecs2.1533

Carbonara, P., Porcu, C., Donnaloia, M., Pesci, P., Sion, L., Spedicato, M. T., Zupa, W., Vitale, F., & Follesa, M. C. (2019). The spawning strategy of European hake (*Merluccius merluccius*, L. 1758) across the Western and Central Mediterranean Sea. *Fisheries Research*, 219, 105333. https://doi.org/10.1016/j.fishres.2019.105333

Cardinale, M., Osio, G. C., & Scarcella, G. (2017). Mediterranean Sea: A failure of the European fisheries management system. *Frontiers in Marine Science*, 4, 72. https://doi.org/10.3389/fmars.2017.00072

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(5), 555–563. https://doi.org/10.1111/conl.12318

Claudet, J. (2021). The seven domains of action for a sustainable ocean. *Cell*, 184(6), 1426–1429. https://doi.org/10.1016/j.cell.2021.01.055

Colloca, F., Garofalo, G., Bitetto, I., Facchini, M. T., Grati, F., Martiradonna, A., Mastrantonio, G., Nikolioudakis, N., Ordinas, F., Scarcella, G., Tserpes, G., Tugores, M. P., Valavanis, V., Carlucci, R., Fiorentino, F., Follesa, M. C., Iglesias, M., Knittweis, L., Lefkaditou, E., … Spedicato, M. T. (2015). The seascape of demersal fish nursery areas in the North Mediterranean Sea, a first step towards the implementation of spatial planning for trawl fisheries. *PLoS ONE*, *10*(3), 1–25. https://doi.org/10.1371/journal.pone.0119590

Conklin, E. E., Neuheimer, A. B., & Toonen, R. J. (2018). Modeled larval connectivity of a multi-species reef fish and invertebrate assemblage off the coast of Moloka'i, Hawai'i. *PeerJ*, *2018*(9), 1–32. https://doi.org/10.7717/peerj.5688

Costello, C., Ovando, D., Clavelle, T., Strauss, C. K., Hilborn, R., Melnychuk, M. C., Branch, T. A., Gaines, S. D., Szuwalski, C. S., Cabral, R. B., Rader, D. N., & Leland, A. (2016). Global fishery prospects under contrasting management regimes. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(18), 5125–5129. https://doi.org/10.1073/PNAS.1520420113

Daw, T. M., Coulthard, S., Cheung, W. W. L., Brown, K., Abunge, C., Galafassi, D., Peterson, G. D., McClanahan, T., Omukoto, J. O., & Munyi, L. (2015). Evaluating taboo trade-offs in ecosystems services and human well-being. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(22), 6949–6954. https://doi.org/10.1073/pnas.1414900112

Di Lorenzo, M., Claudet, J., & Guidetti, P. (2016). Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. *Journal for Nature Conservation*, *32*, 62–66. https://doi.org/10.1016/J.JNC.2016.04.004

Dubois, M., Rossi, V., Ser-Giacomi, E., Arnaud-Haond, S., López, C., & Hernández-García, E. (2016). Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems. *Global Ecology and Biogeography*, *25*(5), 503–515. https://doi.org/10.1111/geb.12431

Engelhard, S. L., Huijbers, C. M., Stewart-Koster, B., Olds, A. D., Schlacher, T. A., & Connolly, R. M. (2017). Prioritising seascape connectivity in conservation using network analysis. *Journal of Applied Ecology*, *54*(4), 1130–1141. https://doi.org/10.1111/1365-2664.12824

FAO. (2022). *The state of Mediterranean and Black Sea fisheries 2022*. General Fisheries Commission for the Mediterranean. https://doi.org/10.4060/cc3370en

Fiorentino, F., Massutí, E., Tinti, F., Somarakis, S., Garofalo, G., Russo, T., Facchini, M. T., Carbonara, P., Kapiris, K., Tugores, P., & Spedicato, M. T. (2014). *Stock units: Identification of distinct biological units (stock units) for different fish and shellfish species and among different GFCM-GSA*. STOCKMED Deliverable 03: Final report.

Friesen, S. K., Martone, R., Rubidge, E., Baggio, J. A., & Ban, N. C. (2019). An approach to incorporating inferred connectivity of adult movement into marine protected area design with limited data. *Ecological Applications*, *29*(4), 1–14. https://doi.org/10.1002/eap.1890

Giannoulaki, M., Belluscio, A., Colloca, F., Fraschetti, S., Scardi, M., Smith, C., Panayotidis, P., Valavanis, V., & Spedicato, M. T. (2013). *Mediterranean sensitive habitats*. DG MARE Specific Contract SI2.600741, Final Report.

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*(41), 25595–25600. https://doi.org/10.1073/pnas.1920580117

Hidalgo, M., Rossi, V., Monroy, P., Ser-Giacomi, E., Hernández-García, E., Guijarro, B., Massutí, E., Alemany, F., Jadaud, A., Perez, J. L., & Reglero, P. (2019). Accounting for ocean connectivity and hydroclimate in fish recruitment fluctuations within transboundary metapopulations. *Ecological Applications*, *29*(5), 1–13. https://doi.org/10.1002/eap.1913

Hilborn, R., Akselrud, C. A., Peterson, H., & Whitehouse, G. A. (2020). The trade-off between biodiversity and sustainable fish harvest with area-based management. *ICES Journal of Marine Science*. https://doi.org/10.1093/icesjms/fsaa139

Hilborn, R., Stewart, I. J., Branch, T. A., & Jensen, O. P. (2012). Defining trade-offs among conservation, profitability, and food security in the California current bottom-trawl fishery. *Conservation Biology*, *26*(2), 257–268. https://doi.org/10.1111/j.1523-1739.2011.01800.x

Janßen, H., Bastardie, F., Eero, M., Hamon, K. G., Hinrichsen, H.-H., Marchal, P., Nielsen, J. R., Le Pape, O., Schulze, T., Simons, S., Teal, L. R., & Tidd, A. (2018). Integration of fisheries into marine spatial planning: Quo vadis? *Estuarine, Coastal and Shelf Science*, *201*, 105–113. https://doi.org/10.1016/J.ECSS.2017.01.003

Johnson, D. W., Christie, M. R., Pusack, T. J., Stallings, C. D., & Hixon, M. A. (2018). Integrating larval connectivity with local demography reveals regional dynamics of a marine metapopulation. *Ecology*, *99*(6), 1419–1429. https://doi.org/10.1002/ecy.2343

Kellner, J. B., Tetreault, I., Gaines, S. D., & Nisbet, R. M. (2007). Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications*, *17*(4), 1039–1054. https://doi.org/10.1890/05-1845

Klein, C. J., Tulloch, V. J., Halpern, B. S., Selkoe, K. A., Watts, M. E., Steinback, C., Scholz, A., & Possingham, H. P. (2013). Tradeoffs in marine reserve design: Habitat condition, representation, and socioeconomic costs. *Conservation Letters*, *6*(5), 324–332. https://doi.org/10.1111/conl.12005

Kritzer, J. P., & Sale, P. F. (2006). *Marine metapopulations*. Academic Press. https://doi.org/10.1016/B978-0-12-088781-1.X5000-6

Krueck, N. C., Ahmadia, G. N., Green, A., Jones, G. P., Possingham, H. P., Riginos, C., Treml, E. A., & Mumby, P. J. (2017). Incorporating larval dispersal into MPA design for both conservation and fisheries. *Ecological Applications*, *27*(3), 925–941. https://doi.org/10.1002/eap.1495

Krueck, N. C., Ahmadia, G. N., Possingham, H., Riginos, C., Treml, E., & Mumby, P. (2017). Marine reserve targets to sustain and rebuild unregulated fisheries. *PLoS Biology*, 1–20, e2000537. https://doi.org/10.1371/journal.pbio.2000537

Lall, U., & Sharma, A. (1996). A nearest neighbor bootstrap for resampling hydrologic time series. *Water Resources Research*, *32*(3), 679–693. https://doi.org/10.1029/95WR02966

Latora, V., & Marchiori, M. (2007). A measure of centrality based on network efficiency. *New Journal of Physics*, *9*. https://doi.org/10.1088/1367-2630/9/6/188

Lubchenco, J., Haugan, P., & Pangestu, M. E. (2020). Five priorities for a sustainable ocean economy. *Nature*, *588*, 30–32. https://doi.org/10.1038/d41586-020-03303-3

Macchi, G. J., Diaz, M. V., Leonarduzzi, E., Ehrlich, M., Machinandiarena, L., Cadaveira, M., & In, M. (2021). Temperature, maternal effects and density-dependent processes during early life stages of Argentine hake as relevant recruitment drivers. *Fisheries Research*, *238*, 105898. https://doi.org/10.1016/j.fishres.2021.105898

Magris, R. A., Andrello, M., Pressey, R. L., Mouillot, D., Dalongeville, A., Jacobi, M. N., & Manel, S. (2018). Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. *Conservation Letters*, *11*, e12439. https://doi.org/10.1111/conl.12439

Maina, J. M., Gamoyo, M., Adams, V. M., D'agata, S., Bosire, J., Francis, J., & Waruinge, D. (2020). Aligning marine spatial conservation priorities with functional connectivity across maritime jurisdictions. *Conservation Science and Practice*, *2*(2). https://doi.org/10.1111/csp2.156

Melià, P., Schiavina, M., Rossetto, M., Gatto, M., Fraschetti, S., & Casagrandi, R. (2016). Looking for hotspots of marine metacommunity connectivity: A methodological framework. *Scientific Reports*, *6*, 23705. https://doi.org/10.1038/srep23705

Melnychuk, M. C., Kurota, H., Mace, P. M., Pons, M., Minto, C., Osio, G. C., Jensen, O. P., de Moor, C. L., Parma, A. M., Little, L. R., Hively, D.,

Ashbrook, C. E., Baker, N., Amoroso, R. O., Branch, T. A., Anderson, C. M., Szuwalski, C. S., Baum, J. K., McClanahan, T. R., ... Hilborn, R. (2021). Identifying management actions that promote sustainable fisheries. *Nature Sustainability*, 4, 440–449. https://doi.org/10.1038/s41893-020-00668-1

Micheli, F., De Leo, G., Butner, C., Martone, R. G., & Shester, G. (2014). A risk-based framework for assessing the cumulative impact of multiple fisheries. *Biological Conservation*, 176, 224–235. https://doi.org/10.1016/j.biocon.2014.05.031

Milisenda, G., Garofalo, G., Fiorentino, F., Colloca, F., Maynou, F., Ligas, A., Musumeci, C., Bentes, L., Gonçalves, J. M. S., Erzini, K., Russo, T., D'Andrea, L., & Vitale, S. (2021). Identifying persistent hot spot areas of undersized fish and crustaceans in southern European waters: Implication for fishery management under the discard ban regulation. *Frontiers in Marine Science*, 8, 610241. https://doi.org/10.3389/fmars.2021.610241

Ovando, D., Liu, O., Molina, R., & Szuwalski, C. (2021). Models of marine protected areas must explicitly address spatial dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 118(23). https://doi.org/10.1073/PNAS.2025958118

Peña, T. S., Watson, J. R., González-Guzmán, L. I., & Keitt, T. H. (2017). Step-wise drops in modularity and the fragmentation of exploited marine metapopulations. *Landscape Ecology*, 32(8), 1643–1656. https://doi.org/10.1007/s10980-017-0532-9

Pita, A., Leal, A., Santafé-Muñoz, A., Piñeiro, C., & Presa, P. (2016). Genetic inference of demographic connectivity in the Atlantic European hake metapopulation (*Merluccius merluccius*) over a spatio-temporal framework. *Fisheries Research*, 179, 291–301. https://doi.org/10.1016/J.FISHRES.2016.03.017

Puckett, B. J., & Eggleston, D. B. (2016). Metapopulation dynamics guide marine reserve design: Importance of connectivity, demographics, and stock enhancement. *Ecosphere*, 7(6), e01322. https://doi.org/10.1002/ecs2.1322

Radici, A., Claudet, J., Ligas, A., Bitetto, I., Lembo, G., Spedicato, M. T., Sartor, P., Piccardi, C., & Melià, P. (2023). Data and code: Assessing fish-fishery dynamics from a spatially explicit metapopulation perspective reveals winners and losers in fisheries management [dataset]. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.qz612jmn5

Rassweiler, A., Costello, C., Hilborn, R., & Siegel, D. A. (2014). Integrating scientific guidance into marine spatial planning. *Proceedings of the Royal Society B: Biological Sciences*, 281(1781), 20132252. https://doi.org/10.1098/rspb.2013.2252

Rinaldo, A., Gatto, M., & Rodriguez-Iturbe, I. (2020). *River networks as ecological corridors: Species, populations, pathogens*. Cambridge University Press. https://doi.org/10.1017/9781108775014

Russo, T., Bitetto, I., Carbonara, P., Carlucci, R., D'Andrea, L., Facchini, M. T., Lembo, G., Maiorano, P., Sion, L., Spedicato, M. T., Tursi, A., & Cataudella, S. (2017). A holistic approach to fishery management:

Evidence and insights from a Central Mediterranean case study (Western Ionian Sea). *Frontiers in Marine Science*, 4(June), 1–18. https://doi.org/10.3389/fmars.2017.00193

Saltelli, A., Tarantola, S., Campolongo, F., & Ratto, M. (2004). *Sensitivity analysis in practice: A guide to assessing scientific models*. Wiley. https://doi.org/10.1002/0470870958

Simoncelli, S., Fratianni, C., Pinardi, N., Grandi, A., Drudi, M., Oddo, P., & Dobricic, S. (2014). *Mediterranean Sea physical reanalysis (MEDREA 1987-2015) (version 1)*. EU Copernicus Marine Service Information. https://doi.org/10.25423/Medsea_reanalysis_phys_006_004

STECF. (2015). *Mediterranean assessments part 1 (STECF-15-18)*. Publications Office of the European Union. https://doi.org/10.2788/406771

STECF. (2022). *71st Plenary report (STECF-PLEN-22-03)*. Publications Office of the European Union. https://doi.org/10.2760/016673

Villegas-Ríos, D., Claudet, J., Freitas, C., Moland, E., Thorbjørnsen, S. H., Alonso-Fernández, A., & Olsen, E. M. (2021). Time at risk: Individual spatial behaviour drives effectiveness of marine protected areas and fitness. *Biological Conservation*, 263, 109333. https://doi.org/10.1016/j.biocon.2021.109333

Watson, J. R., Siegel, D. A., Kendall, B. E., Mitarai, S., Rassweiler, A., & Gaines, S. D. (2011). Identifying critical regions in small-world marine metapopulations. *Proceedings of the National Academy of Sciences of the United States of America*, 108(43), 907–913. https://doi.org/10.1073/pnas.1111461108

Zamborain-Mason, J., Russ, G. R., Abesamis, R. A., Bucol, A. A., & Connolly, S. R. (2017). Network theory and metapopulation persistence: Incorporating node self-connections. *Ecology Letters*, 20(7), 815–831. https://doi.org/10.1111/ele.12784

SUPPORTING INFORMATION

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

Data S1: Supplementary materials and results.