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LETTER

Fisheries outcomes of marine protected area networks: Levels of protection, connectivity, and time matter

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Abstract

Establishing large networks of fully protected marine protected areas (MPAs) is challenging because of displacement costs for fisheries. The use of partially protected areas is often proposed as an alternative. However, how conservation and fisheries outcomes of MPA networks are mediated through time by the level of protection remains uncertain. Here we use a metapopulation model of a commercially exploited demersal coastal fish to assess conservation and fisheries outcomes of alternative management policies. We compare the temporal performances of nonspatial management, large MPAs, or networks of MPAs in an overfished case study. In addition, we assess how the magnitude of both outcomes is mediated by larval connectivity and level of protection. We distinguish the relative contribution to fisheries outcomes of unprotected areas in between MPAs, and unprotected areas further away, receiving less displaced fishing effort and potential biomass export. We show that spatial management outperforms nonspatial management, that conservation and fisheries outcomes increase with increasing levels of protection, that fisheries outcomes in areas in between MPAs are higher when connected through larval dispersal, and that increases in catch are preceded by a short-term decrease. Our results call for an increase in protection levels to meet both ecological and fisheries management goals.

KEYWORDS

catch regulation, fisheries management, full protection, larval dispersal, partially protected areas, resources management, spatial management, trade-off

1 | INTRODUCTION

Increasing human pressure on the ocean is causing unprecedented impacts on marine ecosystems (O'Hara et al., 2021). Overfishing is the main driver of change (IPBES, 2019) and threatens sustainable fisheries. Marine protected areas (MPAs) are an area-based management tool that is expected to deliver both conservation and fisheries benefits (Reimer et al., 2021). MPAs that are well-managed, well-enforced, and with strict enough protection levels accrue fish size, abundance, and biomass within their borders (Edgar et al., 2014; Zupan et al., 2018). These conservation benefits can increase with the time of protection (Claudet et al. 2008) and be exported outside protected areas via recruitment subsidy and spillover and hence support fisheries (Di Lorenzo et al., 2016, 2020; Harrison et al., 2012; Pelc et al., 2010).

Networks of MPAs are touted to balance conservation and fisheries benefits of MPAs by limiting the size of MPAs and/or offering a spatial configuration that can reduce fishers' displacement costs to unprotected areas of the network in between MPAs (Grorud-Colvert et al., 2014; Roberts, 2001). While fishable areas within MPA networks are expected to benefit the most from larval dispersal and spillover (two components of connectivity) from the networked MPAs (Barceló et al., 2021), they also receive most of the displaced fishing effort (Halpern et al., 2004). Fisheries benefits outside individual MPAs (Di Lorenzo et al., 2016; Harrison et al., 2012; Pelc et al., 2010) or outside MPA networks (Gaines et al., 2010; Harrison et al., 2020; Hastings & Botsford, 2003) have been extensively studied. However, less attention, if any, has been given to distinguishing the potential synergistic effects of networked MPAs *inside* a network and the overall effect *outside* the network. This implies comparing the relative ecological and fisheries outcomes of networks in unprotected areas between MPAs with those in unprotected areas further away from the area subject to protection.

Another component influencing conservation and fisheries outcomes of MPA networks, but often overlooked, is the level of protection (a classification based on the potential impacts on organism size and number, and on habitats, of allowed activities with an MPA; Horta e Costa et al., 2016). Full and high protection levels confer the largest conservation benefits (Grorud-Colvert et al., 2021; Zupan et al., 2018). Since the level of protection regulates the amount of fishing pressure that can remain within partially protected areas, it also drives the amount of displaced fishing pressure outside those protected areas. The highest levels of protection are mostly implemented in residual areas (Devillers et al., 2015). In areas under higher rates of fishing pressure, the majority of MPAs are of lower protection levels (sensu Horta e Costa et al., 2016), largely allowing fishing activities within their borders (Claudet et al., 2020; Dureuil et al. 2018). Globally, the majority of MPAs do not offer high protection (Pike et al., in press).

Here, using a metapopulation model of a demersal coastal species experiencing overharvesting (Belharet et al., 2020), we compare the potential conservation (standing biomass) and fisheries (catch) outcomes through time of a set of nonspatial and spatial management scenarios: (i) setting catch limits, (ii) implementing large MPAs, and (iii) implementing networks of MPAs of smaller size. For each scenario, we assess how the conservation and fisheries outcomes are mediated by the level of protection (or of catch limit) and connectivity (in this work represented by larval dispersal) in different locations.

2 | METHODS

2.1 | Metapopulation model

We use an age-structured, discrete-time, and spatially explicit metapopulation model of the white seabream, *Diplodus sargus* (Linnée 1758), developed by Belharet et al. (2020) to assess the effects of alternative configurations of management scenarios on conservation and fisheries outcomes. The metapopulation model describes the key biological traits and processes influencing the demographic dynamics of this demersal coastal species (i.e., reproduction, larval dispersal, recruitment, body growth, sexual maturation, natural, and fishing mortality). It explicitly considers connectivity among different subpopulations with larval dispersal. Due to the limited vagility of white seabream adults (Di Franco et al., 2018), adult displacement between cells is not represented in the model (see the Supporting Information for details on the model description).

The model is first calibrated (see Supporting Information) and run for 100 years to reach equilibrium before starting the simulations described below. Our study area covers the coastal area located between latitudes 41.8-42.6 and the longitude 3.10–3.77. The spatial resolution is about 2 × 2 km (i.e., one grid cell of the model, for a total of 86 cells).

We build $n = 3$ networks of six MPAs (each MPA is represented by one grid cell). The three networks are implemented at different locations to cover the whole study area and to better account for the spatial variability due mainly to larval connectivity. The MPAs composing each network are separated in space by unprotected cells (see the Supporting Information for details on modeled networks).

2.2 | Management scenarios

We create an overfishing context by increasing the fishing mortality rate that left 10% of the total unexploited biomass remaining (Worm et al., 2009; see the Supporting Information). We assess and compare potential conservation and fisheries outcomes by running several management scenarios in the overfished context (presented below) and in the nonoverfished context (fishing mortality rate set as in Belharet et al., 2020, results presented in the Supporting Information, Figures S4 and S5). Each management scenario is systematically compared with its associated

TABLE 1 Description of the simulations used to evaluate the effectiveness of nonspatial management scenarios (T0) and spatial management scenarios (T1, T2, T3) at delivering conservation and fisheries outcomes, compared to unmanaged control scenarios (C1, C2).

Simulations	Details about the simulations
Control, connected (C1)	No MPA Larval connectivity activated
Control, unconnected (C2)	No MPA Larval connectivity disactivated within the network
Catch limit (T0)	No MPA Reduction of the same proportion of fishing mortality for each cell in the model
Connected network (T1)	Activation of the MPA network in the fifth year Larval connectivity activated
Large MPA (T2)	Activation of the large MPA in the fifth year The large MPA has a surface equivalent to the total area covered by all the MPAs considered in scenario T1
Unconnected network (T3)	Activation of the MPA network in the fifth year Larval connectivity disactivated within the network

Abbreviation: MPA, marine protected area.

control scenario, that is, a scenario with the same parameters but where neither spatial nor nonspatial management is implemented. Management scenarios are the following (Figure 1, Table 1):

- nonspatial fishery management, in which catch limits are modeled through an evenly distributed reduction in fishing mortality (across all 86 cells);
- implementation of a large MPA (six cells in a spatially contiguous arrangement);
- implementation of a network of MPAs (six MPAs of one cell, nonadjacent to each other).

To assess how each management scenario can be mediated by levels of protection, we model the following configurations:

- *Full protection*: 100% reduction of fishing mortality in protected areas (large MPAs or networked MPAs). The equivalent fishing mortality is evenly redistributed in the adjacent unprotected cells;
- *Three levels of partial protection*: respectively, 75% (strong protection), 50% (intermediate protection), and 25% (low protection) reduction of fishing mortality in protected areas. The equivalent fishing mortality is redistributed in the adjacent unprotected cells; and
- *Nonspatial scenarios*: the three levels of reduced fishing mortality (strong, intermediate, and low) are not concentrated in six protected cells but evenly distributed across all 86 cells.

Each management scenario is tested with the previous levels of protection (four simulations per scenario). Simulations are run over a period of 40 years preceded by a period without protection of 4 years (before and after impact data). Control simulations are run over a period of 44 years (Figure 1 and Table 1).

As we are also interested in understanding if the ability of MPA networks to deliver both conservation and fisheries benefits is dependent on the network's connectivity, we test an additional group of simulations where the connectivity matrix is modified to exclude larval exchanges among network's cells in both managed and control scenarios (Figure 1 and Table 1, "unconnected network"). We assess the impact of each management scenario in different locations by defining focal areas (described in Figure 1).

2.3 | Statistical analysis

We use a meta-analytical approach (Hedges et al., 1999) to assess the effectiveness of each management measure. First, we calculate effect sizes to compare each test simulation T with the corresponding control simulation C. The effect size associated with scenario i is calculated as the log-response ratio R of biomass (or catch) in each area j and each year k with respect to the corresponding control scenario:

$$R_{i,j,k} = \frac{1}{n} \sum_{j}^{k} \ln\left(\frac{X_{T_{i,\ j,k,n}}}{X_{C_{i,\ j,\ k,n}}}\right),$$

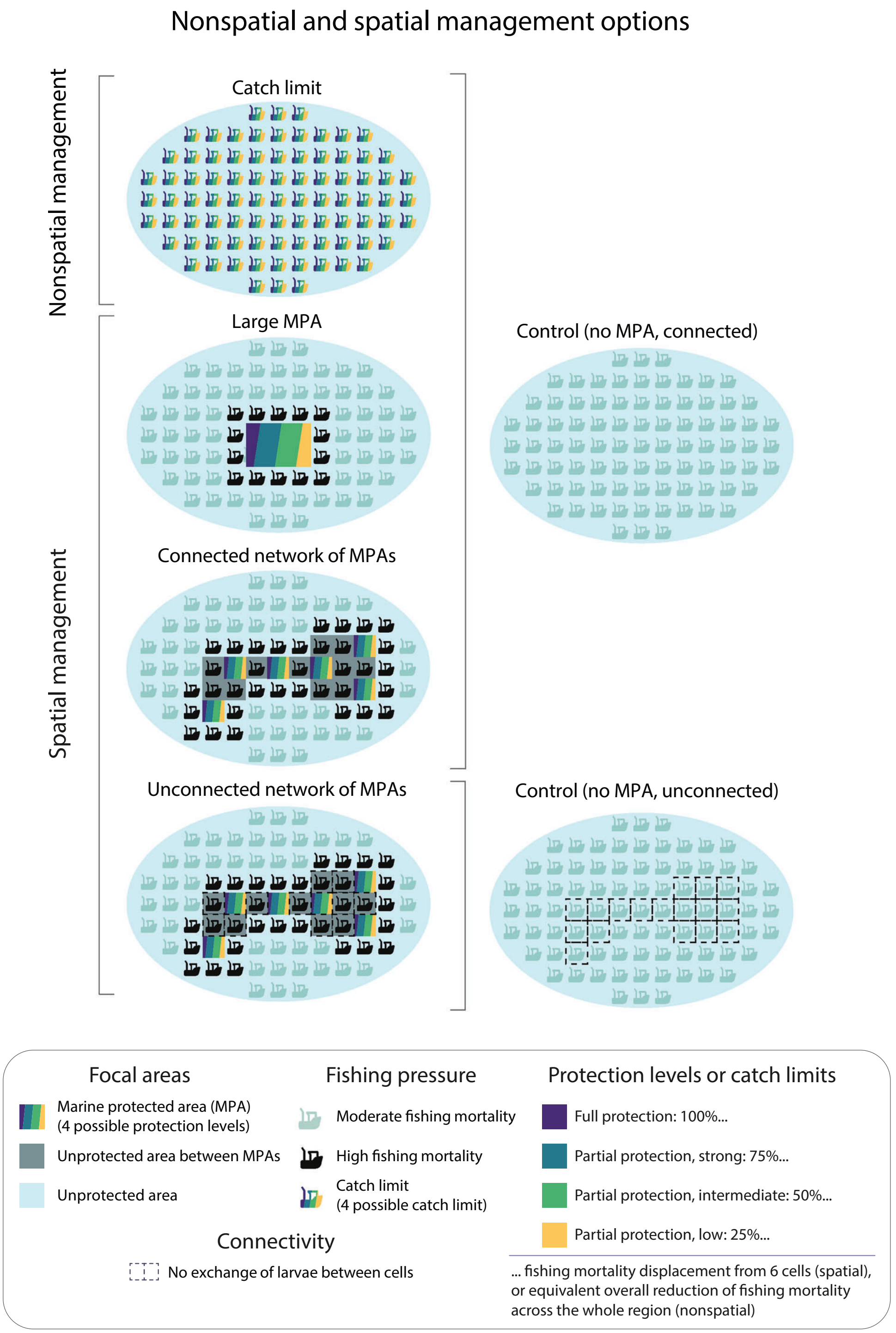

FIGURE 1 Schematic configurations of the nonspatial (catch limit) and spatial (large MPA and network of MPAs) management scenarios, and their associated control (without protection). Redistribution of fishing mortality, once an MPA is established, induces higher fishing mortality in cells adjacent to the MPA. Networks of MPAs have two focal areas: the marine protected areas, which can be fully or partially protected, and the unprotected areas in between the MPAs. In the spatial management options, MPAs of four protection levels are assessed: Full protection (100% of fishing mortality is removed from the protected cell and redistributed in adjacent cells); three levels of partial protection (75%, 50%, 25% of fishing mortality, respectively, redistributed in adjacent cells). In the nonspatial management scenarios, four levels of catch limit are assessed by applying the same reduction of overall fishing mortality as in the spatial management options across all cells.

where n is the number of spatial replicates for scenario i; $X_{T_{i,\ j,\ k,n}}$ and $X_{C_{i,\ j,\ k,n}}$ are the total biomass or catch in all cells of area j and year k, in test T and control C simulations, respectively.

For each effect size $R_{i,j,k}$, 95% confidence intervals (CI) were calculated as

$$CI_{R_{i,j,k}} = R_{T_{i,j,k}} \pm u_{\alpha/2} * \sqrt{\frac{S^2_{T_{i,j,k}}}{n}},$$

where u is the two-tailed critical value of the standard normal distribution at the significance level α and $S^2_{T_{i,j,k}}$ is the variance associated with the effect size in area j and year k.

All the analyses are carried out using the statistical software R (R Core Team, 2020).

3 | RESULTS

Implementation of nonspatial fishery management scenarios (scenario T0, Figure 1), with reductions in fishing mortality evenly distributed throughout the region rather than concentrated in protected cells, leads to negligible differences in total biomass or total catch compared to the control scenario (Figures 2 and 3).

Implementation of large fully protected MPAs (scenario T1, Figure 1) results in overall average increases of about 90% in biomass ($R = 0.64 \pm 0.11$; Figure 2) and 60% in catch ($R = 0.47 \pm 0.10$; Figure 3) across the whole region, after 40 years of protection (see Figures S4 and S5 in the Supporting Information for specific values of effect size). This is due to an 877% increase in biomass inside the fully protected area ($R = 2.28 \pm 0.16$), a 65% increase in biomass ($R = 0.52 \pm 0.12$), and about the same increase in catch ($R = 0.51 \pm 0.12$) outside the fully protected area (Figures 2 and 3). Overall gains in biomass and catch decrease as levels of protection decrease (Figure 2), with only full protection and the two most restrictive levels of partial protection providing long-term increases in biomass and catch across the region (Figures 2 and 3). Inside the partially protected areas, catches first decline, with the largest catch losses associated with the strongest levels of protection (Figure 3). Then, catches recover between 5 and 15 years of protection, for low and high levels of protection, respectively, reaching higher values than those without protection (Figure 3).

Implementation of connected networks of fully protected MPAs leads to similar increases, in biomass (both inside the protected areas and outside the networks), and catch (outside the networks) as in the large fully protected MPAs scenarios (Figures 2 and 3). In the unprotected areas in between networked MPAs, there is first a slight decrease in biomass, compared to the absence of protection, but biomass then starts to be larger, resulting in a 30% increase after 40 years of protection ($R = 0.25 \pm 0.04$; Figure 2). Catch also increases over the same period, compared to the case without the implementation of a network of fully protected areas, to almost a 50% increase ($R = 0.40 \pm 0.06$; Figure 3) after 40 years of protection. These gains in biomass and catch in fishable areas in between the fully protected networked MPAs are higher than those observed outside the large fully protected areas. Biomass and fisheries benefits in all three areas decrease with decreasing levels of protection. Benefits in catch are only observed for full and the two most restrictive (strong and intermediate) levels of partial protection (Figures 2 and 3).

In the absence of connectivity (scenario T3; Figure 1), no biomass or catch benefits are observed in unprotected areas between the MPAs of the network (Figures 2 and 3). Within MPAs, biomass gains are similar to those of connected networks.

In a nonoverfished situation, biomass increases inside connected MPAs follow the same dynamics as in the overfished situation but with a smaller magnitude of increase ($R = 1.17 \pm 0.01$ after 40 years of full protection; see Figure S4 and S5 in the Supporting Information).

4 | DISCUSSION

Here, we assessed for the first time the relative contribution of different levels of protection in MPA networks to conservation and fisheries outcomes for a commercially exploited demersal coastal fish. Although our results are species-specific, the general patterns that emerge are also potentially valid for other coastal species characterized by low mobility of adult life stages. We showed that networks of partially protected areas can effectively support both fisheries and conservation, with benefits increasing with the level of protection and with time. We also confirm the role of connectivity for the fisheries effectiveness of networks of MPAs, emphasizing the importance of distinguishing unprotected areas in between MPAs from those further away.

Our most compelling result is that protection level and time matter not only for conservation outcomes but also for fisheries outcomes. For conservation, stronger protection levels generate higher biomass, as observed in recent empirical studies (Turnbull et al., 2021; Zupan et al., 2018). Gains in catch are not only linked to biomass gains but also to the spatial dynamics of fisheries. For all levels of protection, the initial decrease in catch is short and quickly offset by the increase in biomass. Thus, after a few years, even with lower fishing pressure in the MPAs, catches are

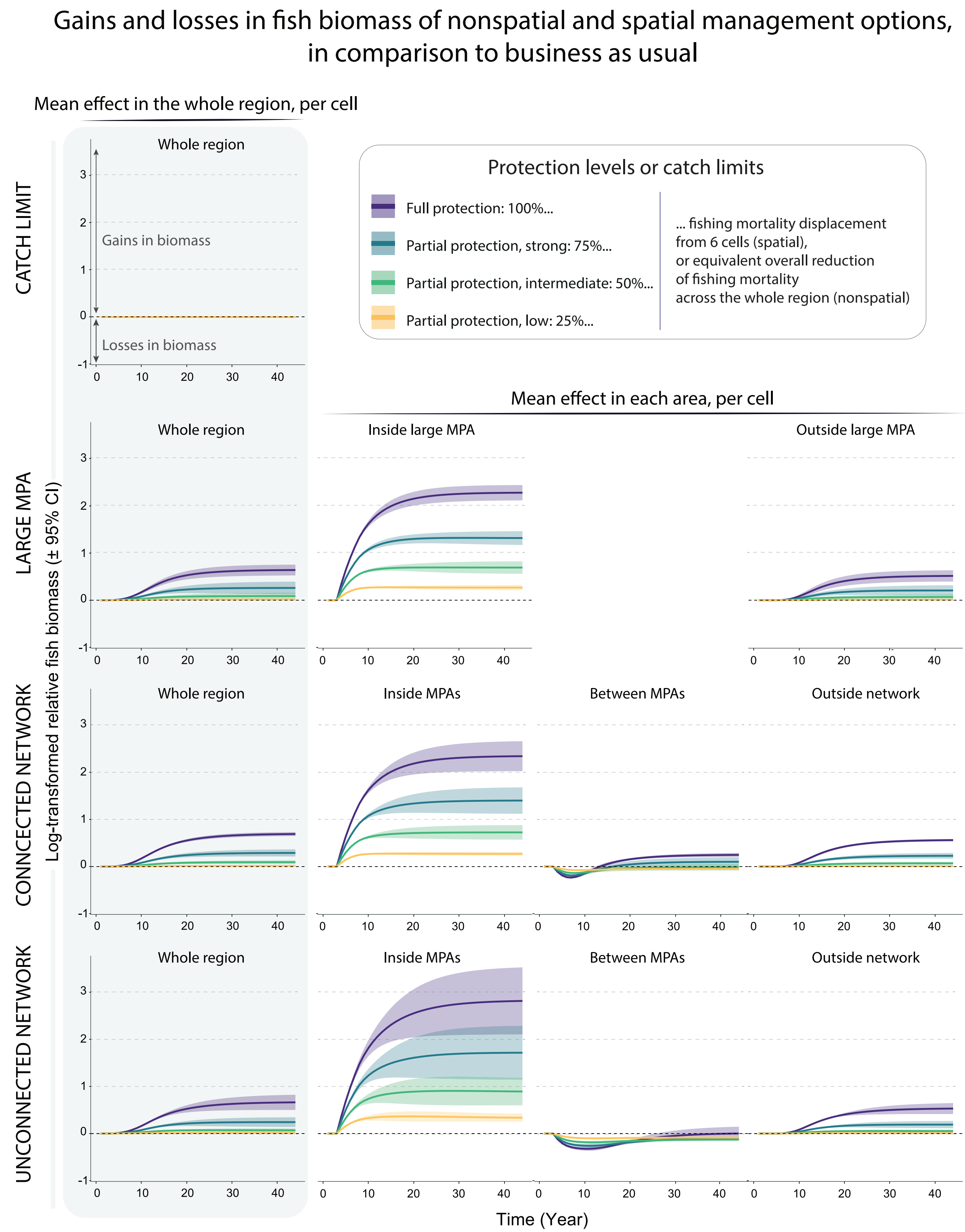

FIGURE 2 Simulated dynamics of effect sizes (log ratio of the biomass in test simulation compared to their respective control simulation) in the whole region (first column), in each focal area (inside large MPA or inside networked MPAs, between networked MPAs, and outside large MPA or MPA network; second to fourth column, respectively), for each set of simulations (nonspatial management, large MPA, connected MPA network, unconnected MPA network; first to fourth line, respectively).

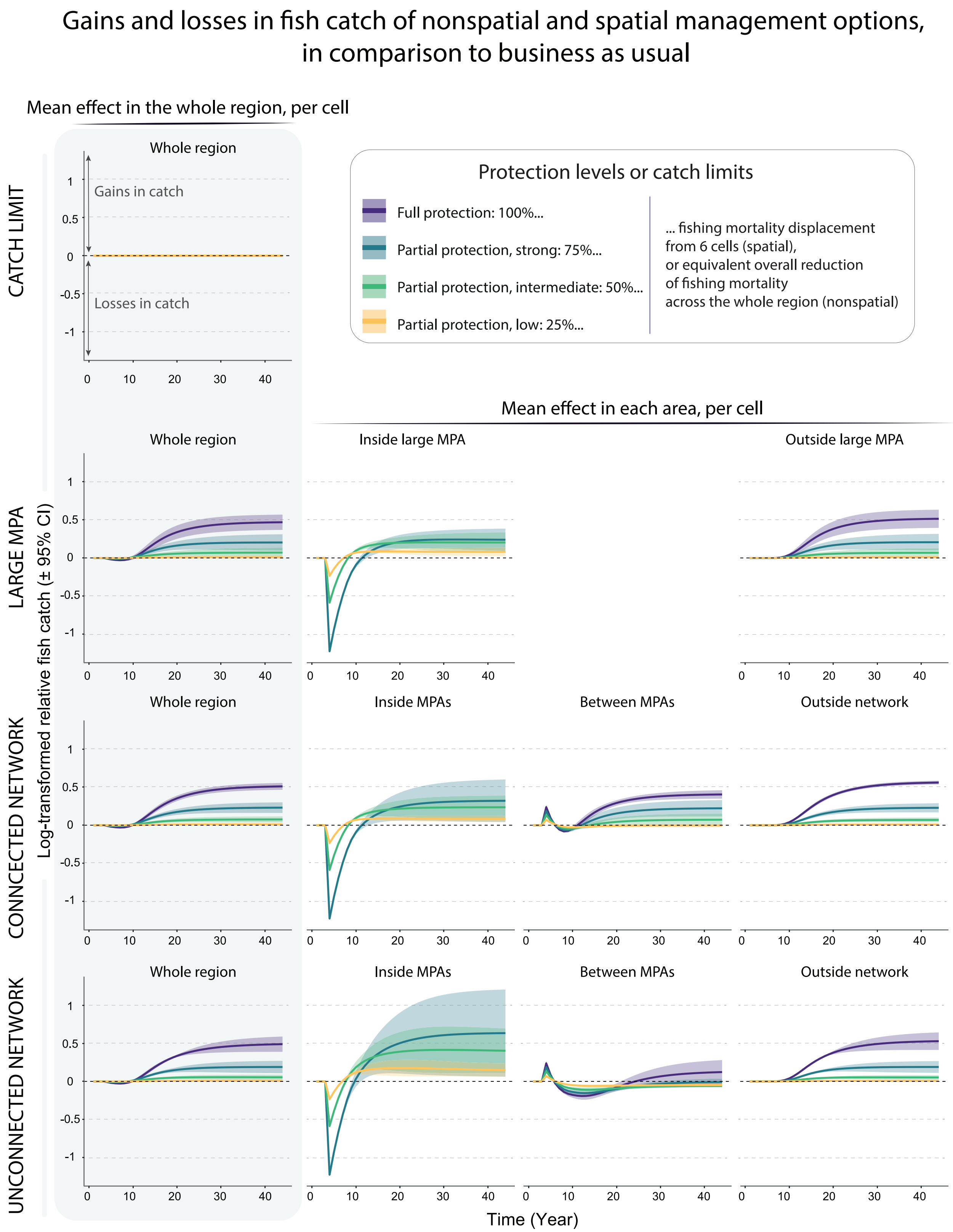

FIGURE 3 Simulated dynamics of effect sizes (log ratio of the catch in test simulation compared to their respective control simulation) in the whole region (first column), in each focal area (inside large MPA or inside networked MPAs, between networked MPAs, and outside large MPA or MPA network; second to fourth column, respectively), for each set of simulations (nonspatial management, large MPA, connected MPA network, unconnected MPA network; first to fourth line, respectively).

at least equivalent to what they would have been without protection.

Inside MPAs, patterns of response to protection are very similar for the three spatial management scenarios. After a rapid increase in biomass—about 10 years for fully protected MPAs and 15 years for partially protected MPAs—gains tend to stabilize after 20 years of protection, as also evidenced by empirical studies on other demersal species (Ferreira et al., 2022; MacNeil et al., 2015; Magris, 2021). In the nonoverfished situation, the increase in biomass for full and partial protection (from 20% to 240%) is comparable to that reported in the literature on similar reef-associated demersal species in the Mediterranean (Giakoumi et al., 2017) or globally (Zupan et al., 2018). In the overfished situation, biomass increases for full (+800%) and partial protection (from 30% to 300%) are larger because the rate of change in fish biomass is higher when reducing fishing mortality inside MPAs by a large proportion. These results are consistent with those of Ziegler et al. (2022), who showed that the MPAs response ratio increases in heavily fished situations, simply because of high deterioration of stocks outside MPAs.

Outside MPAs, full and high protection levels lead to a notable increase in biomass (+25% to +75%), slightly higher with an MPA network than with a large MPA. In our study, MPAs can become saturated by adults due to their limited displacement. Single large MPAs generate large numbers of larvae that are mainly retained within the protected area but do not all become adults due to density dependence (Melià et al., 2020). In a network, MPAs are interspersed with fished areas that can benefit from contributions from several surrounding MPAs, and where larvae can survive to become adult fish that can then be caught (Hastings & Botsford, 2003).

Between MPAs of a connected network, positive conservation, and fisheries outcomes appear after 10 years of protection for full and strong protection levels. First, MPAs generate larval subsidies that can offset the loss of biomass caused by fishing effort displacement and, subsequently, sustain fisheries (Cowen, 2006), representing the ecological and fisheries benefits of spillover, respectively (Di Lorenzo et al., 2016). Fisheries benefits from MPA networks have been demonstrated before for full protection (Le Port et al., 2017). Barceló et al. (2021) estimated that benefits would appear 8–18 years after ecological benefits inside MPAs. Here, we show for the first time that those benefits can occur, over a similar period, also with a strong protection level. In the unconnected network, however, the overall gains in catch and biomass are lower than in a connected network. Larval exchanges within the network can compensate for biomass offset between MPAs and benefit fisheries in those areas. While previous empirical and modeling studies have shown how spillover of adults and export of larvae from single MPAs can contribute to fisheries (Di Lorenzo et al., 2016, 2020; Gell & Roberts, 2003; Le Port et al., 2017), fisheries benefits within fishable areas of networks have never been studied specifically. When such areas have been included in models (Hastings & Botsford, 2003) or when studies have evaluated the magnitude of networks' fisheries benefits (Fovargue et al., 2018), the impact of fishing displacement has been overlooked and thus the export benefits might also have been overestimated. While Pelc et al. (2010) showed that larval export from networked MPAs can be large enough to offset mortality due to displaced fishing efforts, they did not specifically focus on the dynamics of fish biomass in unprotected areas between networked MPAs. Here, we show that alternating unprotected fished areas with MPAs could be a key solution to optimize the export of benefits from MPAs for the most restrictive protection levels.

We have shown that, in the case of overfishing, spatial management outperforms nonspatial management when comparing cases of a similar overall reduction in fishing mortality, as also evidenced elsewhere (Carvalho et al., 2019; Rassweiler et al., 2012). In the case of spatial management, the reduction in fishing mortality is concentrated inside MPAs and thus locally higher than in the nonspatial management scenario with the same overall reduction of fishing pressure but distributed throughout the modeled area. Inside MPAs, even when partially protected, fish increase in size and produce more larvae as propagule production increases disproportionately to the size of spawners (Marshall et al., 2019). These larval subsidies can thus support fisheries outcomes by being exported from the protected areas towards the unprotected areas (Harrison et al., 2020; Rassweiler et al., 2012), and contributing to the persistence of metapopulations (Almany et al., 2007; Saenz-Agudelo et al., 2011). In contrast, in nonspatial management scenarios, reducing fishing mortality in each cell might not be sufficient to provide population-wide benefits in an overfished situation. Comparing the overall effectiveness of different spatial management scenarios, it appears that large MPAs and networks of MPAs can deliver similar conservation and fisheries benefits when networks are connected through larval dispersal. MPAs that are not connected by larval dispersal result in suboptimal, underperforming MPA networks (Rassweiler et al., 2012).

Our inferences are based on a number of assumptions. First, as detailed in the Supporting Information, we developed our model using the characteristics of a typical temperate demersal coastal species. However, our results should remain valid for a broad range of overfished species (Carvalho et al., 2019; Costello et al., 2012). Coastal areas are often places where fishing pressure is high and where space is a limiting factor, so connected networks of fully protected areas such as those developed here could prove most useful. Further developments of our model could aim to better capture the behavior of pelagic species with large movements or to account for the population implications of time at risk when species cross MPA boundaries (Villegas-Ríos et al., 2021). Second, we did not consider density-dependent spillover. Thus, our model might underestimate fisheries benefits and overestimate conservation benefits. Third, we used an average larval connectivity matrix to represent larval export. Several studies have shown that larval behavior produces spatial and temporal variability in connectivity patterns (Bode et al., 2019; Cowen & Sponaugle, 2009). Nevertheless, the connectivity portfolio effect (Harrison et al., 2020) suggests that MPA networks' emergent properties may provide overall stability in larval supply. Finally, to reduce complexity, we only use one single size for each of the six MPAs that are part of a network, and one single size (six times larger) for the large MPA. Including size as a continuous variable could help better inform MPA network planning (Fovargue et al., 2018). Future developments of our model could include, among other aspects, multi-species interactions, the influence of habitat heterogeneity, or fishing effort increase within MPA boundaries (Magris, 2021).

In a world of increasing tension between conservation and resource use, there is a need to identify and improve sustainable management scenarios with multiple social and ecological outcomes. Currently, the two main global strategies for implementing marine conservation consist of establishing few very large (often remote) fully or partially protected areas (Lubchenco & Grorud-Colvert, 2015) or many smaller partially protected areas with often insufficient protection levels to deliver conservation benefits (Claudet et al., 2020). Our results show that a nonmutually exclusive third path is possible in areas where fisheries displacement costs are high. Networks of connected fully protected areas can reduce displacement costs while still delivering positive conservation and fisheries outcomes. Increases in catch are preceded by a short-term decrease that calls for the identification of mechanisms to compensate for those short-term losses (Garraud et al., 2023). Our findings provide novel evidence that can support decision-making in designing a network of MPAs that reconcile conservation and fisheries goals.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Supporting information and the published paper of Belharet et al. (2020).

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