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► **To cite this version:**

Charlotte Sève, Mokrane Belharet, Paco Melià, Antonio Di Franco, Antonio Calò, et al.. Fisheries outcomes of marine protected area networks: Levels of protection, connectivity, and time matter. Conservation Letters, In press, 10.1111/conl.12983 . hal-04284148

HAL Id: hal-04284148

<https://hal.science/hal-04284148v1>

Submitted on 17 Nov 2023

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1 Fisheries outcomes of marine protected area networks: levels of
2 protection, connectivity and time matter

3 Short running title: Networks of protected areas benefit fisheries

4

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25 **Keywords:** catch regulation, fisheries management, full protection, larval dispersal, partially
26 protected areas, resources management, spatial management, trade-off

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30 **Abstract**

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

46

47 **Main Text**

48

49 **Introduction**

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

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

72 Another component influencing conservation and fisheries outcomes of MPA networks is the level
73 of protection (a classification based on the potential impacts on species size and number, and on
74 habitats, of allowed activities with an MPA; Horta e Costa et al. 2016). Full and high protection
75 levels confer the largest conservation benefits (Zupan et al. 2018; Grorud-Colvert et al. 2021).
76 Since the level of protection regulates the amount of fishing pressure that can remain within partially
77 protected areas, it also drives the amount of displaced fishing pressure outside those protected
78 areas. The highest levels of protection are mostly implemented in residual areas (Devillers et al.
79 2015). In areas under higher rates of fishing pressure, the majority of MPAs are of lower protection
80 levels (*sensu* Horta e Costa et al. 2016), largely allowing fishing activities within their borders

81 (Dureuil et al. 2018; Claudet et al. 2020). Globally, the majority of MPAs do not offer high protection
82 (Pelc et al., in press).

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

90

91 **Methods**

92 1. Metapopulation model

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

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

106 We build n=3 networks of six MPAs (each MPA is represented by one grid cell). The three networks
107 are implemented at different locations to cover the whole study area and to better account for the
108 spatial variability due mainly to larval connectivity. The MPAs composing each network are

109 separated in space by unprotected cells (see Supporting Information for details on modeled
110 networks).

111 2. Management scenarios

112 We create an overfishing context by increasing the fishing mortality rate that left 10% of the total
113 unexploited biomass remaining (Worm et al. 2009, see Supplementary Information). We assess
114 and compare potential conservation and fisheries outcomes by running several management
115 scenarios in the overfished context (presented below) and in the non-overfished context (fishing
116 mortality rate set as in Belharet et al., 2020, results presented in Supporting Information). Each
117 management scenario is systematically compared with its associated control scenario, i.e., a
118 scenario with the same parameters but where neither spatial nor non-spatial management is
119 implemented. Management scenarios are the following (Figure 1, Table 1):

- 120 ● non-spatial fishery management, in which catch limits are modelled through an
121 evenly distributed reduction in fishing mortality (across all 86 cells);
- 122 ● implementation of a large MPA (6 cells in a spatially contiguous arrangement);
- 123 ● implementation of a network of MPAs (6 MPAs of one cell, non-adjacent to each
124 other).

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

- 127 ● full protection: 100% reduction of fishing mortality in protected areas (large MPAs
128 or networked MPAs). The equivalent fishing mortality is evenly redistributed in the
129 adjacent unprotected cells;
- 130 ● three levels of partial protection: respectively 75% (strong protection), 50%
131 (intermediate protection) and 25% (low protection) reduction of fishing mortality in
132 protected areas. The equivalent fishing mortality is redistributed in the adjacent
133 unprotected cells;
- 134 ● non-spatial scenarios: the three levels of reduced fishing mortality (strong,
135 intermediate and low) are not concentrated in 6 protected cells but evenly
136 distributed across all 86 cells.

137 Each management scenario is tested with the previous levels of protection (4 simulations per
138 scenario). Simulations are run over a period of 40 years preceded by a period without protection of

139 4 years (before and after impact data). Control simulations are run over a period of 44 years (Figure
140 1, Table 1).

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

147 3. Statistical analysis

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

$$153 R_{i,j,k} = \frac{1}{n} \sum_j^k \ln \left(\frac{X_{T_{i,j,k,n}}}{X_{C_{i,j,k,n}}} \right).$$

154 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
155 or catch in all cells of area j and year k , in test T and control C simulations, respectively.

156

157 For each effect size $R_{i,j,k}$, 95% confidence intervals were calculated as:

$$158 CI_{R_{i,j,k}} = R_{T_{i,j,k}} \pm u_{\alpha/2} * \sqrt{\frac{S_{T_{i,j,k}}^2}{n}},$$

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

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

162

163 **Results**

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

168 Implementation of large fully protected MPAs (scenario T1, Figure 1) results in overall average
169 increases of about 90% in biomass ($R = 0.64 \pm 0.11$, Table S4) and 60% in catch ($R = 0.47 \pm 0.10$,
170 Table S5) across the whole region, after 40 years of protection. This is due to a 877% increase in
171 biomass inside the fully protected area ($R = 2.28 \pm 0.16$, Table S4), and a 65% increase in biomass
172 ($R = 0.52 \pm 0.12$, Table S4) and about the same increase in catch ($R = 0.51 \pm 0.12$, Table S5)
173 outside the fully protected area (Figure 2 and 3). Overall gains in biomass and catch decrease as
174 levels of protection decrease (Figure 2), with only full protection and the two most restrictive levels
175 of partial protection providing long-term increases in biomass and catch across the region (Figure
176 2 and 3). Inside the partially protected areas, catches first decline, with the largest catch losses
177 associated with the strongest levels of protection (Figure 3). Then, catches recover between 5 and
178 15 years of protection, for low and high levels of protection, respectively, reaching higher values
179 than those without protection (Figure 3).

180 Implementation of connected networks of fully protected MPAs leads to similar increases, in
181 biomass (both inside the protected areas and outside the networks), and catch (outside the
182 networks) as in the large fully protected MPAs scenarios (Figure 2 and 3). In the unprotected areas
183 in between networked MPAs, there is first a slight decrease in biomass, compared to the absence
184 of protection, but biomass then starts to be larger, resulting in a 30% increase after 40 year of
185 protection ($R = 0.25 \pm 0.04$, Table S4). Catch also increases over the same period, compared to
186 the case without the implementation of a network of fully protected areas, to almost a 50% increase
187 ($R = 0.40 \pm 0.06$, Table S5) after 40 years of protection. These gains in biomass and catch in
188 fishable areas in between the fully protected networked MPAs are higher than those observed
189 outside the large fully protected areas. Biomass and fisheries benefits in all three areas decrease

190 with decreasing levels of protection. Benefits in catch are only observed for full and the two most
191 restrictive (strong and intermediate) levels of partial protection (Figures 2 and 3).

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

195 In a non-overfished situation, biomass increases inside connected MPAs follow the same dynamics
196 as in the overfished situation but with a smaller magnitude of increase ($R = 1.17 \pm 0.01$ after 40
197 years of full protection, Table S4).

198

199 **Discussion**

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

208 Our most compelling result is that protection level matters not only for conservation outcomes but
209 also for fisheries outcomes. For conservation, stronger protection levels generate higher biomass,
210 as observed in recent empirical studies (Zupan et al. 2018; Turnbull et al. 2021). For fisheries
211 outcomes, time matters. Gains in catch are not only linked to biomass gains, but also to the spatial
212 dynamics of fisheries. For all levels of protection, the initial decrease in catch is short and quickly
213 offset by the increase in biomass. Thus, after a few years, even with lower fishing pressure in the
214 MPAs, catches are at least equivalent to what they would have been without protection.

215 Inside MPAs, patterns of response to protection are very similar for the three spatial management
216 scenarios. After a rapid increase in biomass –about 10 years for fully protected MPAs and 15 years
217 for partially protected MPAs – gains tend to stabilize after 20 years of protection, as also evidenced
218 by empirical studies on other demersal species (MacNeil et al. 2015; Magris 2021; Ferreira et al.
219 2022). In the non-overfished situation, the increase in biomass for full and partial protection (from
220 20% to 240%) is comparable to that reported in the literature on similar reef-associated demersal
221 species in the Mediterranean (Giakoumi et al. 2017) or globally (Zupan et al. 2018). In the
222 overfished situation, biomass increases for full (+800%) and partial protection (from 30 to 300%)

223 are larger, because the rate of change in fish biomass is higher when reducing fishing mortality
224 inside MPAs by a large proportion. These results are consistent with those of Ziegler et al. (2022),
225 who showed that MPAs response ratio increase
226 in heavily fished situations, simply because of high deterioration of stocks outside MPAs.

227 Outside MPAs, full and high protection levels lead to a notable increase in biomass (+25% to
228 +75%), slightly higher with an MPA network than with a large MPA. In our study, MPAs can become
229 saturated by adults due to their limited displacement. Single large MPAs generate large numbers
230 of larvae that are mainly retained within the protected area, but do not all become adults due to
231 density dependence (Melià et al. 2020). In a network, MPAs are interspersed with fished areas that
232 can benefit from contributions from several surrounding MPAs, and where larvae can survive to
233 become adult fish that can then be caught (Hastings & Botsford 2003).

234 Between MPAs of a connected network, positive conservation and fisheries outcomes appear after
235 10 years of protection for full and strong protection levels. First, MPAs generate larval subsidies
236 that can offset the loss of biomass caused by fishing effort displacement and, subsequently, sustain
237 fisheries (Cowen 2006), representing the ecological and fisheries benefits of spillover, respectively
238 (Di Lorenzo et al. 2016). Fisheries benefits from MPA networks have been demonstrated before
239 for full protection (Le Port et al. 2017). Barceló et al. (2021) estimated that benefits would appear
240 8-18 years after ecological benefits inside MPAs. Here, we show for the first time that those benefits
241 can occur, over a similar period, also with a strong protection level. In the unconnected network,
242 however, the overall gains in catch and biomass are lower than in a connected network. Larval
243 exchanges within the network can compensate for biomass offset between MPAs and benefit
244 fisheries in those areas. While previous empirical and modelling studies have shown how spillover
245 of adults and export of larvae from single MPAs can contribute to fisheries (Gell & Roberts 2003;
246 Di Lorenzo et al. 2016, 2020; Le Port et al. 2017), fisheries benefits within fishable areas of networks
247 have never been studied specifically. When such areas have been included in models (Hastings &
248 Botsford 2003) or when studies have evaluated the magnitude of networks' fisheries benefits
249 (Fovargue et al. 2018), the impact of fishing displacement has been overlooked and thus the export
250 benefits might also have been overestimated. While Pelc et al. (2010) showed that larval export
251 from networked MPAs can be large enough to offset mortality due to displaced fishing effort, they
252 did not specifically focus on the dynamics of fish biomass in unprotected areas between networked
253 MPAs. Here, we show that alternating unprotected fished areas with MPAs could be a key solution
254 to optimize the export of benefits from MPAs for the most restrictive protection levels.

255 We have shown that, in the case of overfishing, spatial management outperforms non-spatial
256 management when comparing cases of similar overall reduction in fishing mortality, as also

257 evidenced elsewhere (Rassweiler et al. 2012; Carvalho et al. 2019). In the case of spatial
258 management, the reduction in fishing mortality is concentrated inside MPAs and thus locally higher
259 than in the non-spatial management scenario with the same overall reduction of fishing pressure
260 but distributed throughout the modelled area. Inside MPAs, even when partially protected, fish
261 increase in size and produce more larvae as propagule production increases disproportionately to
262 the size of spawners (Marshall et al. 2019). These larval subsidies can thus support fisheries
263 outcomes by being exported from the protected areas towards the unprotected areas (Rassweiler
264 et al. 2012; Harrison et al. 2020), and contributing to the persistence of meta populations (Almany
265 et al. 2007; Saenz-Agudelo et al. 2011). In contrast, in non-spatial management scenarios,
266 reducing fishing mortality in each cell might not be sufficient to provide population-wide benefits in
267 an overfished situation. Comparing the overall effectiveness of different spatial management
268 scenarios, it appears that large MPAs and networks of MPAs can deliver similar conservation and
269 fisheries benefits when networks are connected through larval dispersal. MPAs that are not
270 connected by larval dispersal result in suboptimal, underperforming MPA networks (Rassweiler et
271 al. 2012).

272 Our inferences are based on a number of assumptions. First, as detailed in Supporting Information,
273 we developed our model using the characteristics of a typical temperate demersal coastal species.
274 However, our results should remain valid to a broad range of overfished species (Costello et al.
275 2012; Carvalho et al. 2019). Coastal areas are often places where fishing pressure is high and
276 where space is a limiting factor, so where connected networks of fully protected areas such as
277 those developed here could prove most useful. Further developments of our model could aim to
278 better capture the behavior of pelagic species with large movements or to account for the
279 population implications of time-at-risk when species cross MPA boundaries (Villegas-Ríos et al.
280 2021). Second, we did not consider density-dependent spillover. Thus, our model might
281 underestimate fisheries benefits and overestimate conservation benefits. Third, we used an
282 average larval connectivity matrix to represent larval export. Several studies have shown that larval
283 behavior produces spatial and temporal variability in connectivity patterns (Cowen & Sponaugle
284 2009; Bode et al. 2019). Nevertheless, the connectivity portfolio effect (Harrison et al. 2020)
285 suggests that MPA networks' emergent properties may provide overall stability in larval supply.
286 Finally, to reduce complexity, we only use one single size for each of the six MPAs that are part of
287 a network, and one single size (six times larger) for the large MPA. Including size as a continuous
288 variable could help better inform MPA network planning (Fovargue et al. 2018). Future

289 developments of our model could include, among other aspects, multi-species interactions,
290 influence of habitat heterogeneity, or fishing effort increase within MPAs boundaries (Magris 2021).

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

303

304 **Acknowledgements and Data**

305 We thank two anonymous reviewers for useful comments on an earlier version of this manuscript.
306 This work was supported by Biodiversa (MOVE and METRODIVER), Fondation de France
307 (MultiNet), and by the European Commission (SafeNet; MARE/2014/41). The opinions expressed
308 in this article are those of the authors only and do not represent the European Commission's official
309 position.

310

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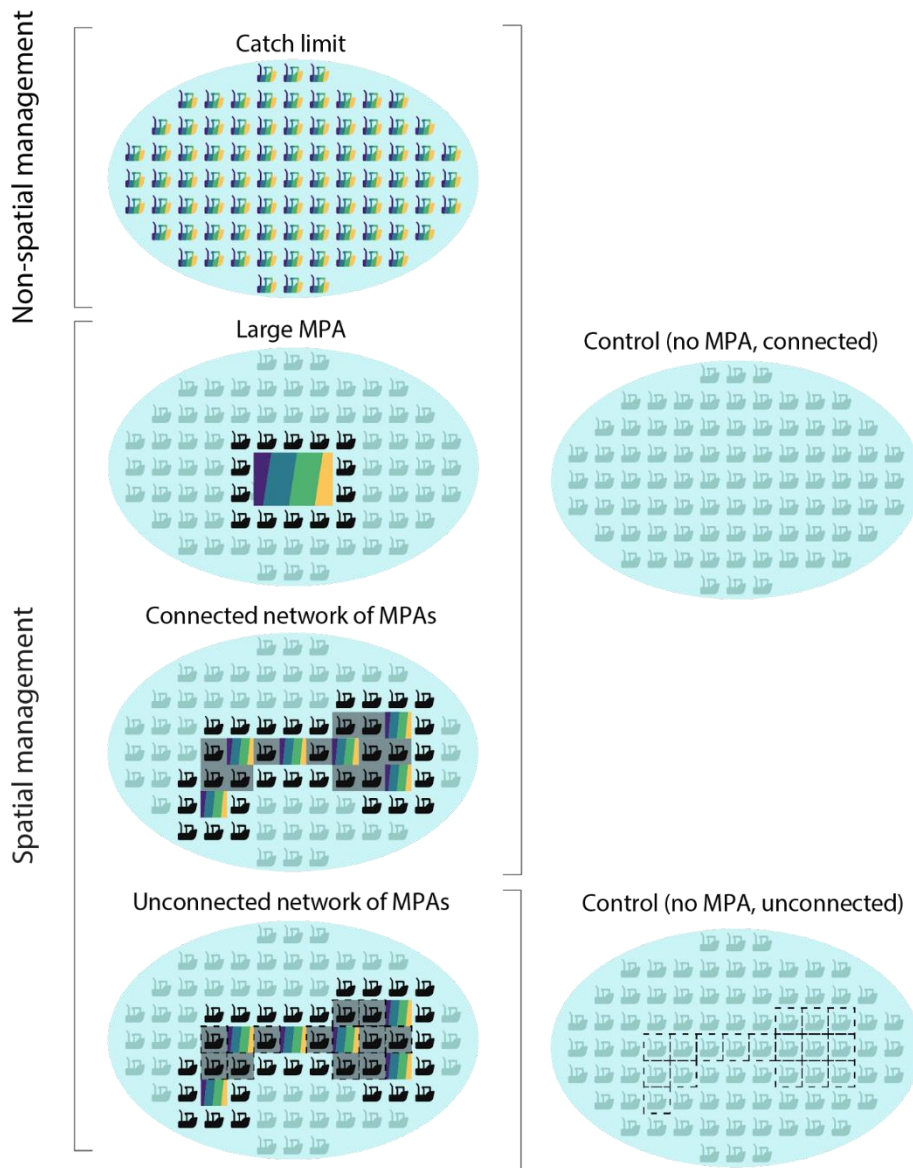
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Figures and Tables

Non-spatial and spatial management options



Focal areas	Fishing pressure	Protection levels or catch limits
Marine protected area (MPA) (4 possible protection level)	Moderate fishing mortality	Full protection: 100%...
Unprotected area between MPAs	High fishing mortality	Partial protection, strong: 75%...
Unprotected area	Catch limit (4 possible catch limit)	Partial protection, intermediate: 50%...
		Partial protection, low: 25%...
Connectivity		
No exchange of larvae between cells		
... fishing mortality displacement from 6 cells (spatial), or equivalent overall reduction of fishing mortality across the whole region (non-spatial)		

Figure 1. Schematic configurations of the non-spatial (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 4 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 non-spatial 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.

Gains and losses in fish biomass of non-spatial and spatial management options, in comparison to business as usual

Mean effect in the whole region, per cell

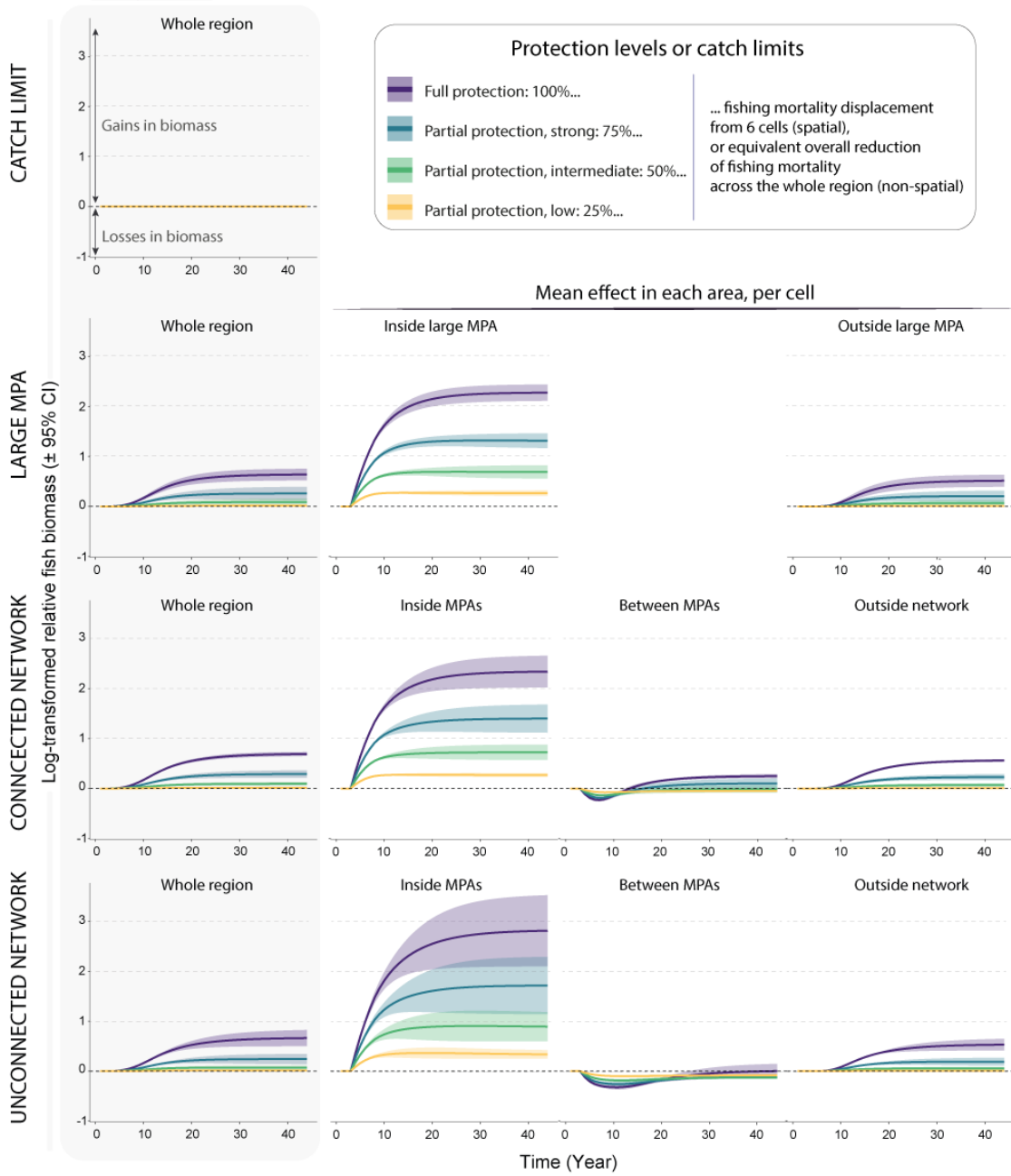


Figure 2. Simulated dynamics of effect sizes (log-ratio of the biomass in test simulation compared to their respective control simulation) in the whole region (first column), in each focal area (inside large MPA or inside networked MPAs, between networked MPAs, and outside large MPA or MPA network),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

Gains and losses in fish catch of non-spatial and spatial management options, in comparison to business as usual

Mean effect in the whole region, per cell

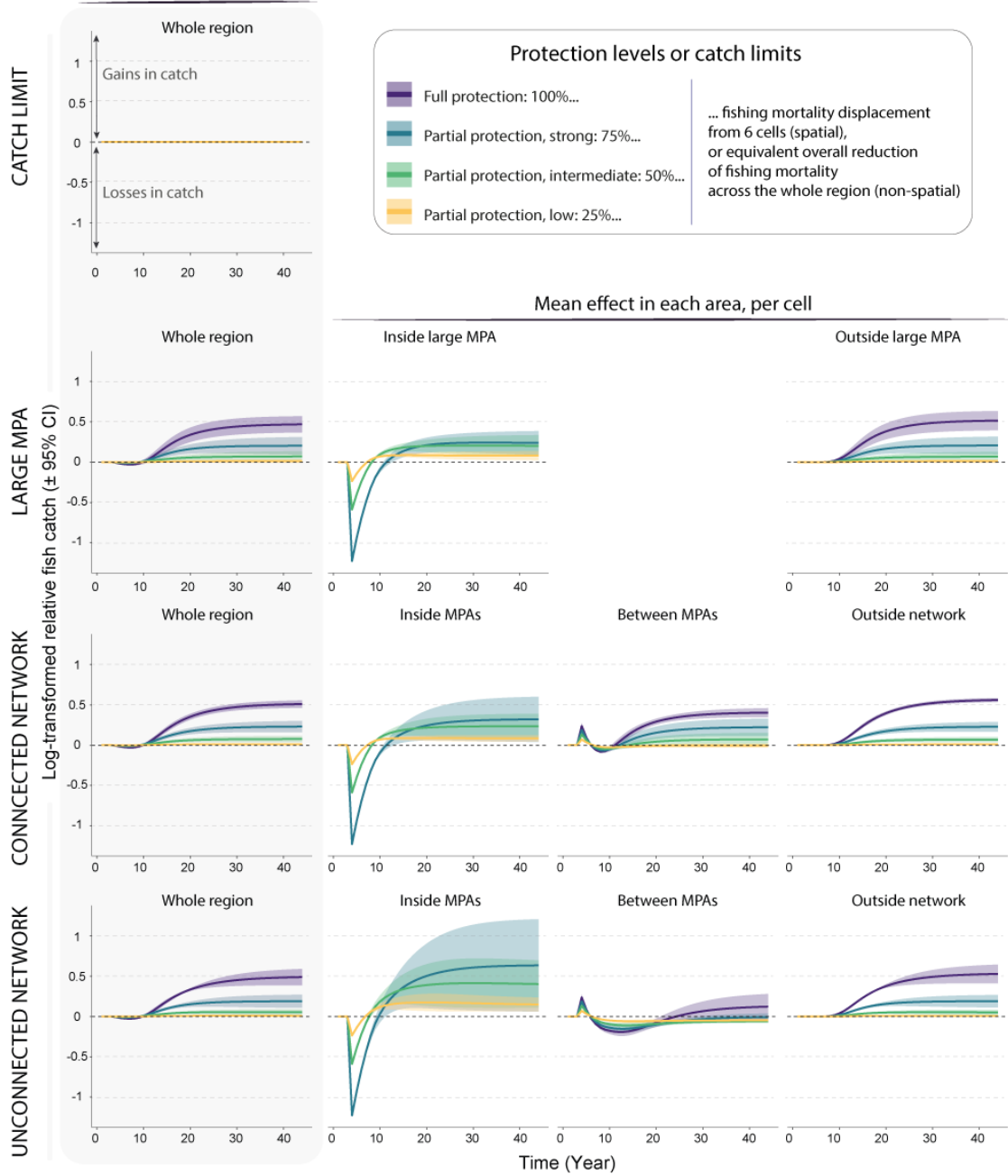


Figure 3. Simulated dynamics of effect sizes (log-ratio of the catch in test simulation compared to their respective control simulation) in the whole region (first column), in each focal area (inside large MPA or inside networked MPAs, between networked MPAs, and outside large MPA or MPA network), for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

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456 **Table 1.** Description of the simulations used to evaluate the effectiveness of non-spatial
457 management scenarios (T0) and spatial management scenarios (T1, T2, T3) at delivering
458 conservation and fisheries outcomes, compared to unmanaged control scenarios (C1, C2).
459

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 the 5th year Larval connectivity activated
Large MPA (T2)	Activation of the large MPA the 5th 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 the 5th year Larval connectivity disactivated within the network

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