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# Assessing spillover from Marine Protected Areas and its drivers: a meta-analytical approach

Running title: Spillover from marine protected areas

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Keywords: Coastal, coral reefs, temperate reef, fully protected areas, no-take zone, marine reserve, fish, small-scale fisheries

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## Abstract

The ocean offers vital ecosystem services to mankind. However, human activities, especially overfishing, may seriously impact fish populations and ecosystems. Fully protected areas (FPAs) are an effective tool for biodiversity conservation and can sustain local fisheries via spillover, i.e. the export of juvenile and adult individuals from FPAs outwards. Yet, whether or not spillover is a general phenomenon following the establishment and effective management of an FPA is still controversial. Here, we developed a meta-analysis of a unique global database covering 23 FPAs in

37 12 countries, including both published literature and specifically collected field data, to assess the  
38 capacity of FPAs to export biomass and whether this response was mediated by specific FPA  
39 features (e.g. size, age) or species characteristics (e.g. mobility, economic value). Results, on  
40 average, show that fish biomass and abundance outside FPAs are higher: i) in locations close to  
41 FPA borders (<200m) than in locations further away (>200m); ii) for species with a high  
42 commercial value; iii) in the presence of a partially protected area (PPA) surrounding the FPA.  
43 Spillover slightly increased as FPAs are larger and older and as species are more mobile. Our work  
44 grounds on the broadest dataset compiled to date on marine species ecological spillover beyond  
45 FPAs' borders and highlights elements that could enhance local fishery management.

46

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48

## 49 1. INTRODUCTION

50 Human activities are leading to dramatic modifications of the ocean (McCauley et al., 2015)  
51 and overfishing is among the most damaging stressors on marine biodiversity (IPBES, 2019).  
52 However, fisheries, especially small scale fisheries, are valuable economic activities, often vital for  
53 food security and poverty alleviation, and sources of livelihood with strong socio-cultural  
54 implications in coastal areas worldwide (Cisneros-Montemayor, Pauly, & Weatherdon, 2016).  
55 There is, therefore, an urgent need to identify management strategies able to reconcile  
56 conservation and fisheries goals by both protecting marine biodiversity and enhancing fishing  
57 yields/revenues (Gaines, Lester, Grorud-Colvert, Costello, & Pollnac, 2010; Jupiter et al., 2017).

58 Although marine protected areas (MPAs) are widely recognized as an important tool for  
59 biodiversity conservation (Claudet et al., 2008; Edgar et al., 2014; Giakoumi et al., 2017) and  
60 fisheries management (Abesamis, Russ, & Alcala, 2006; Goñi et al., 2008; Russ & Alcala, 2011),  
61 how ubiquitous are fishery benefits delivered by MPAs is still largely debated (Hilborn, 2016;  
62 Kerwath, Winker, Götz, & Attwood, 2013; Sale et al., 2005). There is a body of evidence suggesting

63 that FPAs can play an important role for fisheries management, especially for SSF (Di Franco et al.,  
64 2016; Januchowski-Hartley, Graham, Cinner, & Russ, 2013; Russ & Alcala, 2011). Two ecological  
65 processes can drive fishery benefits of FPAs: population replenishment through larval subsidies  
66 (Manel et al., 2019; Marshall, Gaines, Warner, Barneche, & Bode, 2019) and the spillover of fish  
67 biomass from protected areas to surrounding fishing grounds (Rowley 1994). While both  
68 processes require populations to firstly recover within the boundaries of the FPAs, generally the  
69 former is key to the long-term persistence of exploited populations also at relatively large distance  
70 from the MPA (i.e. hundreds of kms, Manel *et al.* 2019), while the latter produces faster benefits  
71 to fisheries mainly across shorter distances (Halpern, Lester, & Kellner, 2010). The spatio-temporal  
72 scale of these two processes is species-specific (Green et al., 2015; McCauley et al., 2015).

73 The occurrence and magnitude of spillover is variable and context-dependent (Di Lorenzo,  
74 Claudet, & Guidetti, 2016). The maximum distance from FPA borders at which spillover effects are  
75 still detectable is a crucial issue to better understand the spatial extent of FPA benefits to local  
76 fisheries. Most studies found that spillover occur on average at distances of about 200 m from  
77 FPAs' borders, and all agree that it does not exceed 1 km (Abesamis et al., 2006; Abesamis & Russ,  
78 2005; Guidetti, 2007; Halpern et al., 2010; Marques, Hill, Shimadzu, Soares, & Dornelas, 2015; Russ  
79 & Alcala, 2011). According to Di Lorenzo et al. (2016), two types of spillover should be considered  
80 on the basis of their assessment: "ecological spillover" encompassing all forms of net emigration  
81 of juveniles, subadults and/or adults from the MPA outwards; "fishery spillover", i.e. the fraction  
82 of ecological spillover that can directly benefit fishery yields and revenues through the marine  
83 species biomass that can be fished (Di Lorenzo et al 2016).

84 Spillover is not only important for local SSFs, but also for tourism-based blue economy.  
85 More abundant and larger fish exported from FPAs (where scuba-diving is often forbidden) attract  
86 more divers, thus supporting the local economy (Micheli & Niccolini, 2013; Roncin et al., 2008).

87 The overall relative contribution of potential drivers of spillover is poorly known. Two main  
88 categories of drivers may affect spillover: (i) MPA features: age, design (e.g. size, shape, location),  
89 presence of PPAs, the level of enforcement, habitat continuity/discontinuity across FPA borders  
90 (Goñi et al., 2008; Harmelin-Vivien et al., 2008; Kaunda-Arara & Rose, 2004; Kay et al., 2012); (ii)  
91 species characteristics: the species-specific ability to move across the FPA borders, related, e.g., to  
92 the intraspecific behaviour of individuals, habitat preferences and species mobility, fishing  
93 pressure (Kaunda-Arara & Rose, 2004). Some studies reported that spillover may require several  
94 years (>10 years) to take place after a FPA is established (Abesamis et al., 2006; Harmelin-Vivien et

95 al., 2008; Russ & Alcala 1996; Russ, Alcala, & Maypa, 2003), while others detected spillover after  
96 only a few years from FPA creation (< 5 years; (Francini-Filho & Moura, 2008; Guidetti, 2007).  
97 Spillover has been observed from FPAs surrounded or not by a PPA (Abesamis et al., 2006;  
98 Francini-Filho & Moura, 2008; Harmelin-Vivien et al., 2008; Zeller, Stoute, & Russ, 2003) and  
99 detected both from small (< 1km<sup>2</sup>; (Abesamis et al., 2006; Harmelin-Vvivien et al., 2008; Russ &  
100 Alcala 1996; Russ et al., 2003) and large FPAs (Ashworth & Ormond, 2005; Fisher & Frank, 2002;  
101 Stobart et al., 2009). Habitat continuity inside and outside the FPA is thought to facilitate spillover  
102 (Abesamis & Russ, 2005; Kaunda-Arara & Rose, 2004), but several studies detected spillover also  
103 where the habitat was discontinuous across FPA borders (Goñi, Quetglas, & Reñones, 2006;  
104 Guidetti, 2007; Harmelin-Vivien et al., 2008; Kay et al., 2012). Spillover is expected to occur mostly  
105 for relatively mobile species (Buxton, Hartmann, Kearney, & Gardner, 2014; Halpern et al., 2010),  
106 but some studies showed that sedentary, (Chapman & Kramer, 1999; Eggleston, & Parsons, 2008;  
107 Forcada et al., 2009; Goñi et al., 2008; Goñi et al., 2006; Zeller et al., 2003), vagile, (Abesamis et al.,  
108 2006; Forcada, Bayle-Sempere, Valle, & Sánchez-Jerez, 2008; Guidetti, 2007), and highly vagile  
109 species, (Chapman & Kramer, 1999; Kaunda-Arara & Rose, 2004; Stobart et al., 2009) may spillover  
110 beyond FPA borders.

111 Here, we performed a meta-analysis to 1) investigate the extent of spillover occurrence  
112 from FPAs globally and 2) assess which FPA features and species characteristics mainly drive  
113 spillover. To do so, we compiled the most complete global database on spillover, covering 23 FPAs  
114 in 12 countries, combining information from reviewed literature and data gathered through  
115 specific underwater visual census samplings on the field.

116  
117

## 118 **2. METHODS**

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### 120 **2.1. Data collection**

121 We assembled our dataset using two different approaches: extracting data from literature  
122 and performing *ad hoc* field activities to collect new data.

123 Articles on spillover from published peer-reviewed literature were collected through Web  
124 of Science back to 1994, when the term spillover was used for the first time (Rowley 1994). The  
125 following search string was used: ("spillover" OR "spill-over" OR "spill over") AND ("marine  
126 protected area\*" OR "marine reserve\*" OR "no-take zone\*" OR "fisher\* closure\*" OR "fully  
127 protected area\*"). It was decided to focus strictly on FPAs as this protection level is the more likely  
128 to produce spillover effects (Di Lorenzo et al., 2016 and references therein). Sixty-three studies of

129 empirical assessments of spillover were found. They were either based on underwater visual  
130 census (UVC), catch or tagging abundance and/or biomass data. Spillover has been modelled in  
131 various ways in the literature, such as using linear gradients of abundance/biomass decline from  
132 FPA borders (e.g. (Goñi et al., 2006; Harmelin-Vivien et al., 2008) or tracking individual movements  
133 across FPA borders (Afonso, Morato, & Santos, 2008; Barrett, Buxton, & Gardner, 2009; Follesa et  
134 al., 2011; Kay et al., 2012; Kerwath et al., 2013). In order to keep the maximum number of studies,  
135 we built a model of spillover that would be as inclusive as possible in terms of different  
136 measurements and ways to report the data. Data from papers were extracted either from tables  
137 or from graphs using ImageJ (<http://imagej.nih.gov/ij>). Contextual information about the FPAs was  
138 recorded from the articles and/or by contacting their authors: FPA age and size, whether the FPA  
139 was situated on an island or along a coastline, presence of PPA surrounding the FPA, and habitat  
140 continuity/discontinuity along FPA borders (Table 1). Information on species mobility (sedentary  
141 or vagile) and economic value (commercial, low commercial or not commercial) was also collected  
142 from the papers or FishBase (<http://www.fishbase.org>). It is worth noting that juveniles of target  
143 species were also included in the low commercial category as during that life stage they are not  
144 fishery targets.

145 To enhance the dataset, we conducted additional fieldwork in 13 FPAs in 6 countries. Data  
146 were gathered using underwater visual census (UVC). SCUBA diving was carried out on rocky  
147 substrates between 5 and 15 m deep, using 25x5 m strip transects parallel to the coast. Along  
148 each transect, the divers swam one way at constant speed, identifying all fishes encountered to  
149 the lowest taxonomic level possible and recording their number and size. Fish sizes were  
150 estimated visually in 2 cm increments of total length (TL) for most of the species, and within 5 cm  
151 size classes for large-sized species (i.e. with maximum size >50 cm). Fish biomass was estimated  
152 from size data by means of length-weight relationships from the available literature and existing  
153 databases. UVC replicates (from 6 to 12 transects) were carried out close and far from FPAs  
154 borders, according to the rationale we used to detect spillover (see section 2.2).

155 Only one study used fisheries yield to assess spillover. Due to the absence of replication we  
156 could not account for fisheries spillover and had to restrict our analysis on ecological spillover  
157 (REF). A total of 334 assessments from 23 [well enforced?] MPAs and 31 taxonomic groups  
158 (including species, genus or family) worldwide were finally used in the meta-analysis (Fig. 1; Table  
159 1; Supplementary material Table S1).

160

161

## 162 2.2. Data analysis

163 A meta-analytical approach was used to investigate spillover occurrence and drivers in our  
164 database. We used as effect size the log-relative difference in mean fish abundance and biomass  
165 between locations close (<200 m) and far (>200 m) from the FPA borders. We set the threshold at  
166 200 m according to the distance up to which spillover is generally observed in the literature  
167 (Abesamis et al., 2006; Guidetti, 2007; Harmelin-Vivien et al., 2008; Russ et al., 2003; Russ &  
168 Alcalá, 2011). This approach is conservative in the sense that it favours false negative (absence of  
169 detection of spillover if it occurs over larger spatial extents) over false positive (detection of  
170 spillover when it does not occur, or over spatial extents with no significance for [small scale]  
171 fisheries management).

172 We used a weighted mixed-effects meta-analysis (Gurevitch & Hedges, 1999) to quantify  
173 the magnitude of spillover and assess its drivers. Two different meta-analyses were done on  
174 abundance and biomass. For each study  $i$ , the spillover effect size  $R_i$  of the studied species across  
175 the studied FPA was modelled as the natural logarithm response ratio (Gurevitch & Hedges, 1999;  
176 Osenberg, Sarnelle, & Cooper, 1997) of the mean abundance or biomass measured within 200  
177 meters ( $\bar{X}_{close,i}$ ) and over 200 meters ( $\bar{X}_{far,i}$ ) from the FPA boundary:

$$R_i = \ln\left(\frac{\bar{X}_{close,i}}{\bar{X}_{far,i}}\right)$$

178

179

180 The within-study variance  $v_i$  associated to the effect sizes was calculated as follows:

$$v_i = \frac{sd_{close,i}^2}{n_{close,i} * \bar{X}_{close,i}} + \frac{sd_{far,i}^2}{n_{far,i} * \bar{X}_{far,i}}$$

181

182

183 where  $sd_{close,i}^2$  and  $sd_{far,i}^2$  are the standard deviations of  $\bar{X}_{close,i}$  and  $\bar{X}_{far,i}$ , respectively, and  
184 where  $n_{close,i}$  and  $n_{far,i}$  are the associated sample sizes.

185 All effect sizes were weighted, accounting for both the within- and among-study variance  
186 components (Hedges & Vevea 1998). Models were fitted and heterogeneity tests were run to  
187 assess how MPA-level (FPA age and size, island or coastline FPA, presence of a PPA, habitat  
188 continuity/discontinuity along FPA borders) and species-level (mobility and economic) drivers  
189 could mediate spillover from FPAs (Table 1). All analyses were done in R (R Core Team 2016) and

190 weighted mixed-effects model fitting and heterogeneity tests were carried out using the metaphor  
191 package (Viechtbauer, 2015).

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194

### 3. RESULTS

195 Overall, we found 33% higher fish abundance and 54% higher biomass close to the FPA  
196 borders (<200m) compared to further away ( $\bar{R} = 0.29 \pm 0.15$  95% CI and  $\bar{R} = 0.43 \pm 0.21$  95% CI,  
197 respectively), indicating the general occurrence of spillover. However, effect sizes were  
198 heterogeneous across assessments ( $Q_T = 7314$ ,  $df = 167$ ,  $p < 0.001$ ;  $Q_T = 7777$ ,  $df = 164$ ,  $p < 0.001$ ;  
199 respectively) (Supplementary material Table S2).

200 The presence of a PPA around FPAs played an important role. Spillover was observed more  
201 often from those FPAs surrounded by or next to a PPA (Figure 1). Abundance and biomass were  
202 respectively 37% and 84% higher closer to rather than further away from the FPA boundaries  
203 (Supplementary Materials Table S3).

204 For abundance data, spillover was mostly observed in FPAs established along coastlines  
205 rather than in FPAs surrounding a whole island (Figure 1). This difference was not observed when  
206 considering biomass data (Figure 1; Supplementary material: Table S2).

207 The occurrence and magnitude of spillover was only slightly affected by the age or the size  
208 of the FPA. Although statistically significant, the effect of age was marginal both for abundance  
209 ( $\bar{R} = 0.008 \pm 0.007$  95% CI) and biomass ( $\bar{R} = 0.014 \pm 0.010$  95% CI). The effect of the size of the FPA  
210 played a limited but detectable role only in the case of abundance ( $\bar{R} = 0.04 \pm 0.03$  95% CI for  
211 abundance;  $\bar{R} = 0.02 \pm 0.03$  95% CI for biomass).

212 Habitat continuity/discontinuity across FPA borders did not seem to affect the occurrence  
213 of spillover, both for abundance ( $Q_E = 6767.35$ ;  $df = 165$ ;  $p = 0.0001$ ) and biomass ( $Q_E = 7299.05$ ;  
214  $df = 163$ ;  $p = 0.0001$ ) (Figure 1).

215 Spillover density and biomass was detected either for sedentary or vagile species (Figure 1;  
216 Supplementary Material: Table S1). Only species with high commercial value showed a spillover  
217 effect from FPA both in terms of abundance and biomass (Figure 1; Supplementary Material: Table  
218 S1).

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220

### 4. DISCUSSION

221  
222

223 Our results showed that spillover of marine species, both in terms of abundance and  
224 biomass, can be expected as a general response of FPAs. Based on the data that we have been  
225 able to gather, the present study focused on ecological spillover (*sensu* Di Lorenzo et al. 2016). We  
226 found only one study that assessed fisheries spillover (using yield as response variable), which  
227 precluded us to account for this component of spillover in our meta-analysis. More efforts should  
228 be directed towards assessing spillover through fish catches along gradients across MPA borders.  
229 We showed that fish biomass and abundance outside FPAs are higher in locations close to FPA  
230 borders (<200m) than in locations further away (>200m), for species with a high commercial value,  
231 and that it is occurring more in the presence of a partially protected area (PPA) surrounding the  
232 FPA. Spillover slightly increased as FPAs are larger and older and as species are more mobile.

233 To the best of our knowledge this is the first study considering the presence of PPA as  
234 potential driver of spillover, as well as benthic habitat continuity. Our findings suggest that the  
235 presence of a PPA might help the net export of biomass through spillover (and consequently the  
236 detection of fish abundance and/or biomass in the water) from the FPA. However, it is crucial to  
237 highlight that these patterns can be affected/alterd by the magnitude of fishing effort around  
238 FPAs (in PPAs or in unprotected areas, depending on MPA zonation scheme). Fishing the line, i.e.  
239 fishers' tendency to fish close to the boundaries of FPAs (Kellner, Tetreault, Gaines, & Nisbet,  
240 2007), is a recognized activity occurring around FPAs. In the absence of a PPA, fishery activities  
241 around FPAs' borders are not subject to strict spatially-explicit regulations beside the ones  
242 imposed by national and international laws, generally resulting in a higher concentration of the  
243 fishing effort close to the FPA borders (Abesamis & Russ, 2005; Chapman & Kramer, 1999;  
244 Davidson, Villouta, Cole, & Barrier, 2002; Follesa et al., 2011; Russ & Alcala, 2011; Stamoulis &  
245 Friedlander, 2013). The detection of ecological spillover could be negatively impacted by fishing  
246 pressure in the fished areas, but high fishing effort can also concentrate within PPAs leading to  
247 negative consequences of fishing the line in terms of fisheries spillover (Figure 2) (Kleiven et al.,  
248 2019; Zupan, Fragkopoulou, et al., 2018).

249 Our findings can shed light on the results observed in a recent global meta-analysis  
250 assessing the ecological effectiveness of different levels of protection in partially protected areas  
251 (Zupan, Bulleri, et al., 2018). While the authors observed that fully and highly protected MPAs  
252 (*sensu* Horta e Cosat et al. 2016) harbour higher fish abundance and biomass than surrounding  
253 unprotected areas, they found that moderately protected areas are effective only when adjacent  
254 to a fully protected area. A possible explanation can thus be that in the absence of a fully

255 protected area providing spillover, such moderately protected areas allow too much fishing  
256 activities to be effective. Spillover can thus be an important component driving the effectiveness  
257 of multi-zoned MPAs, allowing combinations of protection levels favouring both conservation and  
258 fishing access in partially protected area concentrating fishing (Zupan, Bulleri, et al., 2018).

259 We observed a slightly influence of time since protection (i.e. MPA age) on ecological  
260 spillover, in agreement with what has been observed for the response to protection within the  
261 FPA boundaries (Claudet et al., 2008; Edgar et al., 2014; Molloy, McLean, & Côté, 2009). This can  
262 be due to the fact that our synthesis included FPAs with a large variation in age (min=6 years,  
263 median=19 years, max=32 years).

264 The fact that only species with a high commercial value display spillover is not surprising as  
265 they are the ones responding more favorably to protection (Kerwath et al., 2013) hence the ones  
266 most likely exporting adults from the FPA boundaries. According to Halpern et al (2010), highly  
267 valued species are often the ones mostly targeted by extractive activities. For this reason, these  
268 are also the species responding most favourably and most rapidly to MPA establishment (Claudet,  
269 Pelletier, Jouvenel, Bachet, & Galzin, 2006; Babcock et al., 2010; Kerwath et al., 2013). An  
270 important difference between our synthesis and that by Halpern et al. (2010) is that while their  
271 study focussed on highly valued fish species only, our analysis, for the first time, integrated data of  
272 three commercial value categories of species (i.e. no value, low and high).

273 Differently to Halpern et al 2010, a slightly effect of FPA size on spillover was also found; it  
274 suggests that the set of MPAs included in our study cover a range of sizes representing a trade-off  
275 between the inclusion of the home ranges of most species and the optimal size for spillover to  
276 neighbouring areas (Di Franco et al., 2018; Weeks, Green, Joseph, Peterson, & Terk, 2017). In fact,  
277 the size of a FPA should include the full home ranges of the protected species to obtain high  
278 conservation benefits (Di Franco et al., 2018; Weeks et al., 2017).

279 While several experimental studies have shown that habitat continuity between inside and  
280 outside FPAs may play a role in facilitating spillover (Forcada et al., 2008; Goñi et al., 2008; Halpern  
281 et al., 2010; Kaunda-Arara & Rose, 2004), our meta-analysis showed that spillover could occur  
282 where the habitat across FPA borders is either homogeneous or heterogeneous. Such studies refer  
283 to the landscape connectivity theory (“the degree to which the landscape facilitates or impedes  
284 movement among resource patches”; Taylor *et al.* 1993), suggesting that similar habitat types  
285 across FPAs and fished areas may enhance the borders permeability (Bartholomew et al., 2008).  
286 However, our results suggest that the likelihood that fish cross a different habitat rather than the

287 preferred one also depends on how fish can perceive and respond behaviourally to integrate the  
288 patched habitat to minimize overall costs (Bélisle, 2005; Wiens, 2008). Therefore, although  
289 different habitats outside FPAs could be a barrier to fish movements (due e.g. to the increased risk  
290 of predation), individuals may be able to move beyond FPA borders most likely when a threshold  
291 level of population density/biomass (i.e. competition for local resources such as preys and refuges)  
292 is exceeded.

293 Here, we observed evidence of spillover for species regardless of their mobility. In  
294 agreement with previous findings (Halpern et al., 2010), we observed that species, regardless of  
295 their mobility, are able to perform spillover. Contrary to Halpern et al. (2010) we decided to use  
296 only sedentary and vagile species in our analysis and removed the highly vagile species. The fact  
297 that any species with different mobility levels can display spillover may support the use of FPAs for  
298 coastal, SSF management, as these fisheries are multi-specific and usually target both sedentary  
299 and mobile species (Claudet, Guidetti, Mouillot, & Shears, 2011).

300 As in any qualitative review or quantitative synthesis or meta-analysis our study can  
301 harbour a publication bias. As studies evidencing spillover could be more likely published than  
302 those where no spillover is observed this would translate in some overestimation of spillover.  
303 However, our sample covers a large array of species, MPA types, and biogeographic regions and is  
304 well representative of spillover assessment in marine protection worldwide. Besides, the way we  
305 modelled spillover can in fact have led to underestimations. We are thus quite confident that  
306 MPAs, through spillover and larval subsidies (Marshall et al., 2019), can play a significant role in  
307 replenishing surrounding areas, therefore enhancing fisheries and non-extractive activities that  
308 may benefit from increased fish density and biomass (e.g. scuba diving and tourism more in  
309 general).

310 In terms of socio-economic implications, therefore, the potential benefits induced by  
311 spillover could raise expectations in stakeholders (e.g. fishers, divers, tourists) that if shattered  
312 could induce a negative attitude and finally reduce support toward conservation initiatives and  
313 potentially foster non-compliant behaviours (e.g. poaching) (Bergseth, Russ, & Cinner, 2015). In  
314 our study we use a conservative approach to assess spillover occurrence (i.e. spillover might have  
315 been underestimated in some cases), and in addition we point out the circumstances under which  
316 spillover could occur, which is more appropriate from a management point of view as deception  
317 can be dramatic when a management tool is oversold (Chaigneau & Brown, 2016; Hogg, Gray,  
318 Noguera-Méndez, Semitiel-García, & Young, 2019). This can allow to deliver a clear message to

319 stakeholders and avoid overselling the occurrence of spillover, preventing unrealistic expectations,  
320 and contributing to foster support to conservation initiatives (Bennett et al. 2019).

321

322 Our findings highlight under which conditions spillover may be expected, allowing MPA  
323 managers and policy-makers to develop sound management strategies to eventually maximise the  
324 exploitation of fishable biomass exported by FPAs. In fact, contrary to FPAs for which well-  
325 established regulations of human activities have been identified to reach conservation goals  
326 (essentially no extractive activities allowed), proven conditions for PPAs effectiveness are still  
327 scarce (in terms of which activities to allow and to which limits) (Zupan et al., 2018). Globally PPAs  
328 include a variety of management measures that range from almost unprotected areas (with no  
329 regulations implemented) to virtually FPA (Zupan et al. 2018). From this perspective, an effort  
330 should be made to assess under which conditions PPAs can benefit local communities within a  
331 multiple-use MPA. As PPAs currently lack a consistent and well-designed set of regulations  
332 worldwide (Horta e Costa et al., 2016), MPAs, mainly aimed to maximize fishery benefits, should  
333 assess the fisheries yield within PPAs and fished areas integrated with integrated with fishing  
334 effort data in order to optimise spillover (Figure 2).

335

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351

352 **REFERENCES AND NOTES**

353

354 Abesamis, R. A., Russ, G. R., & Alcala, A. C. (2006). Gradients of abundance of fish across no-take  
355 marine reserve boundaries: evidence from Philippine coral reefs. *Aquatic Conservation:  
356 Marine and Freshwater Ecosystems*, 16(4), 349–371. <https://doi.org/10.1002/aqc.730>

357 Abesamis Renee and Russ. (2005). Density-dependent spillover from a marine reserve : long-term  
358 evidence. *Marine Ecology Progress Series*, 15(5), 1798–1812.

359 Afonso, P., Morato, T., & Santos, R. S. (2008). Spatial patterns in reproductive traits of the  
360 temperate parrotfish *Sparisoma cretense*. *Fisheries Research*, 90(1–3), 92–99.

361 <https://doi.org/10.1016/j.fishres.2007.09.029>

362 Alcala, A. C., Russ, G. R., Maypa, A. P., & Calumpong, H. P. (2005). A long-term , spatially replicated  
363 experimental test of the effect of marine reserves on local fish yields, 108, 98–108.

364 <https://doi.org/10.1139/F04-176>

365 Ashworth, J. S., & Ormond, R. F. G. (2005). Effects of fishing pressure and trophic group on  
366 abundance and spillover across boundaries of a no-take zone. *Biological Conservation*, 121(3),  
367 333–344. <https://doi.org/10.1016/j.biocon.2004.05.006>

368 Babcock, R. C., Shears, N. T., Alcala, a C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., ... Russ, G. R.  
369 (2010). Decadal trends in marine reserves reveal differential rates of change in direct and  
370 indirect effects. *Proceedings of the National Academy of Sciences of the United States of  
371 America*, 107(43), 18256–61. <https://doi.org/10.1073/pnas.0908012107>

372 Barrett, N., Buxton, C., & Gardner, C. (2009). Rock lobster movement patterns and population  
373 structure within a Tasmanian Marine Protected Area inform fishery and conservation  
374 management. *Marine and Freshwater Research*, 60(5), 417.

375 <https://doi.org/10.1071/MF07154>

376 Bartholomew, A., Bohnsack, J. A., Smith, S. G., Ault, J. S., Harper, D. E., & McClellan, D. B. (2008).  
377 Influence of marine reserve size and boundary length on the initial response of exploited reef  
378 fishes in the Florida Keys National Marine Sanctuary, USA. *Landscape Ecology*, 23(SUPPL. 1),  
379 55–65. <https://doi.org/10.1007/s10980-007-9136-0>

380 Bélisle, M. (2005). Measuring landscape connectivity: The challenge of behavioral landscape  
381 ecology. *Ecology*, 86(8), 1988–1995. <https://doi.org/10.1890/04-0923>

382 Bennett, N. J., Di Franco, A., Calò, A., Nethery, E., Niccolini, F., Milazzo, M., & Guidetti, P. (2019).  
383 Local support for conservation is associated with perceptions of good governance, social  
384 impacts, and ecological effectiveness. *Conservation Letters*, (December 2018), 1–10.  
385 <https://doi.org/10.1111/conl.12640>

386 Bergseth, B. J., Russ, G. R., & Cinner, J. E. (2015). Measuring and monitoring compliance in no-take  
387 marine reserves. *Fish and Fisheries*, 16(2), 240–258. <https://doi.org/10.1111/faf.12051>

388 Buxton, C. D., Hartmann, K., Kearney, R., & Gardner, C. (2014). When is spillover from marine  
389 reserves likely to benefit fisheries? *PLoS ONE*, 9(9), 1–7.  
390 <https://doi.org/10.1371/journal.pone.0107032>

391 Chaigneau, T., & Brown, K. (2016). Challenging the win-win discourse on conservation and  
392 development: Analyzing support for marine protected areas. *Ecology and Society*, 21(1).  
393 <https://doi.org/10.5751/ES-08204-210136>

394 Chapman, M., & Kramer, D. (1999). Gradients in coral reef fish density and size across the  
395 Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics.  
396 *Marine Ecology Progress Series*, 181, 81–96. <https://doi.org/10.3354/meps181081>

397 Cisneros-montemayor, M., Pauly, D., & Weatherdon, L. V. (2016). A Global Estimate of Seafood  
398 Consumption by Coastal Indigenous Peoples, 1–16.  
399 <https://doi.org/10.1371/journal.pone.0166681>

400 Claudet, J., Pelletier, D., Jouvenel, J.-Y., Bachet, F., & Galzin, R. (2006). Assessing the effects of  
401 marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean  
402 marine reserve: Identifying community-based indicators. *Biological Conservation*, *130*(3),  
403 349–369. <https://doi.org/10.1016/j.biocon.2005.12.030>

404 Claudet, J., Guidetti, P., Mouillot, D., & Shears, N. T. (2011). ECOLOGY – Ecological effects of  
405 marine protected areas: functioning.

406 Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-Ruzafa,  
407 A., ... Planes, S. (2008). Marine reserves: size and age do matter. *Ecology Letters*, *11*(5), 481–  
408 9. <https://doi.org/10.1111/j.1461-0248.2008.01166.x>

409 Davidson, R. J., Villouta, E., Cole, R. G., & Barrier, R. G. F. (2002). Effects of marine reserve  
410 protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine  
411 Reserve, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *12*(2), 213–  
412 227. <https://doi.org/10.1002/aqc.505>

413 Di Franco, A., Plass-Johnson, J. G., Di Lorenzo, M., Meola, B., Claudet, J., Gaines, S. D., ... Guidetti,  
414 P. (2018). Linking home ranges to protected area size: The case study of the Mediterranean  
415 Sea. *Biological Conservation*, *221*, 175-181 <https://doi.org/10.1016/j.biocon.2018.03.012>

416 Di Franco, A., Thiriet, P., Di Carlo, G., Dimitriadis, C., Francour, P., Gutiérrez, N. L., ... Guidetti, P.  
417 (2016). Five key attributes can increase marine protected areas performance for small-scale  
418 fisheries management. *Scientific Reports*, *6*(November), 38135.  
419 <https://doi.org/10.1038/srep38135>

420 Di Lorenzo, M., Claudet, J., & Guidetti, P. (2016). Spillover from marine protected areas to adjacent  
421 fisheries has an ecological and a fishery component. *Journal for Nature Conservation*, *32*.  
422 <https://doi.org/10.1016/j.jnc.2016.04.004>

423 Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., ... Thomson, R. J.

424 (2014). Global conservation outcomes depend on marine protected areas with five key  
425 features. *Nature*, 506(7487), 216–220. Retrieved from  
426 <http://dx.doi.org/10.1038/nature13022>

427 Eggleston, D., & Parsons, aDM. (2008). Disturbance-induced “spill-in” of Caribbean spiny lobster  
428 to marine reserves. *Marine Ecology Progress Series*, 371, 213–220.  
429 <https://doi.org/10.3354/meps07699>

430 Fisher, J., & Frank, K. (2002). Changes in finfish community structure associated with an offshore  
431 fishery closed area on the Scotian Shelf. *Marine Ecology Progress Series*, 240, 249–265.  
432 <https://doi.org/10.3354/meps240249>

433 Follesa, M. C., Cannas, R., Cau, A., Cuccu, D., Gastoni, A., Ortu, A., ... Cau, A. (2011). Spillover  
434 effects of a Mediterranean marine protected area on the European spiny lobster *Palinurus*  
435 *elephas* (Fabricius, 1787) resource. *Aquatic Conservation: Marine and Freshwater Ecosystems*,  
436 21(6), 564–572. <https://doi.org/10.1002/aqc.1213>

437 Forcada, A., Bayle-Sempere, J. T., Valle, C., & Sánchez-Jerez, P. (2008). Habitat continuity effects on  
438 gradients of fish biomass across marine protected area boundaries. *Marine Environmental*  
439 *Research*, 66(5), 536–47. <https://doi.org/10.1016/j.marenvres.2008.08.003>

440 Forcada, a, Valle, C., Bonhomme, P., Criquet, G., Cadiou, G., Lenfant, P., & Sánchez-Lizaso, J.  
441 (2009). Effects of habitat on spillover from marine protected areas to artisanal fisheries.  
442 *Marine Ecology Progress Series*, 379, 197–211. <https://doi.org/10.3354/meps07892>

443 Francini-Filho, R. B., & Moura, R. L. (2008). Evidence for spillover of reef fishes from a no-take  
444 marine reserve: An evaluation using the before-after control-impact (BACI) approach.  
445 *Fisheries Research*, 93(3), 346–356. <https://doi.org/10.1016/j.fishres.2008.06.011>

446 Gaines, S. D., Lester, S. E., Grorud-Colvert, K., Costello, C., & Pollnac, R. (2010). Evolving science of  
447 marine reserves: new developments and emerging research frontiers. *Proceedings of the*

448 *National Academy of Sciences of the United States of America*, 107(43), 18251–5.  
449 <https://doi.org/10.1073/pnas.1002098107>

450 Giakoumi, S., Scianna, C., Plass-Johnson, J., Micheli, F., Grorud-Colvert, K., Thiriet, P., ... Guidetti, P.  
451 (2017). Ecological effects of full and partial protection in the crowded Mediterranean Sea: A  
452 regional meta-analysis. *Scientific Reports*, 7(1), 1–12. [https://doi.org/10.1038/s41598-017-](https://doi.org/10.1038/s41598-017-08850-w)  
453 08850-w

454 Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, a, Reñones, O., Criquet, G., ... Planes, S.  
455 (2008). Spillover from six western Mediterranean marine protected areas: evidence from  
456 artisanal fisheries. *Marine Ecology Progress Series*, 366, 159–174.  
457 <https://doi.org/10.3354/meps07532>

458 Goñi, R., Quetglas, A., & Reñones, O. (2006). Spillover of spiny lobsters *Palinurus elephas* from a  
459 marine reserve to an adjoining fishery, 308, 207–219.

460 Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., ... White, A. T.  
461 (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for  
462 marine reserve network design. *Biological Reviews*, 90(4), 1215–1247.  
463 <https://doi.org/10.1111/brv.12155>

464 Guidetti, P. (2007). Potential of marine reserves to cause community-wide changes beyond their  
465 boundaries. *Conservation Biology : The Journal of the Society for Conservation Biology*, 21(2),  
466 540–5. <https://doi.org/10.1111/j.1523-1739.2007.00657.x>

467 Gurevitch, J., & Hedges, L. V. (1999). Statistical issues in ecological meta-analysis. *Ecology*, 80(4),  
468 1142–1149. [https://doi.org/10.1890/0012-9658\(1999\)080\[1142:SIEMA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1142:SIEMA]2.0.CO;2)

469 Halpern, B. S., Lester, S. E., & Kellner, J. B. (2010). Spillover from marine reserves and the  
470 replenishment of fished stocks. *Environmental Conservation*, 36(4), 268–276.  
471 <https://doi.org/10.1017/S0376892910000032>

472 Harmelin-Vivien, M., Ledireach, L., Baylesempere, J., Charbonnel, E., Garciacharton, J., Ody, D., ...  
473 Valle, C. (2008). Gradients of abundance and biomass across reserve boundaries in six  
474 Mediterranean marine protected areas: Evidence of fish spillover? *Biological Conservation*,  
475 141(7), 1829–1839. <https://doi.org/10.1016/j.biocon.2008.04.029>

476 Hedges, L. V., Vevea, J.L., 1998. Fixed- and Random-Effects Models in Meta-Analysis. *Psychological*  
477 *Methods*, 3, 486–504. <https://doi.org/10.1037/1082-989X.3.4.486>

478 Hilborn, R. (2016). Marine biodiversity needs more than protection. *Nature*, 535, 224–226.  
479 <https://doi.org/10.1038/535224a>

480 Hogg, K., Gray, T., Noguera-Méndez, P., Semitiel-García, M., & Young, S. (2019). Interpretations of  
481 MPA winners and losers: a case study of the Cabo De Palos- Islas Hormigas Fisheries Reserve.  
482 *Maritime Studies*, 18(2), 159–171. <https://doi.org/10.1007/s40152-019-00134-5>

483 Horta e Costa, B., Claudet, J., Franco, G., Erzini, K., Caro, A., & Gonçalves, E. J. (2016). A  
484 regulation-based classification system for Marine Protected Areas (MPAs). *Marine Policy*, 72,  
485 192–198. <https://doi.org/10.1016/j.marpol.2016.06.021>

486 IPBES, (2019). Summary for policymakers of the global assessment report on biodiversity and  
487 ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and  
488 Ecosystem Services. S. Díaz, J. Settele, E. S. Brondizio E.S., H. T. Ngo, M. Guèze, J. Agard, A.  
489 Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J.  
490 Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky,  
491 A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J.  
492 Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany.

493 Januchowski-Hartley, F.A., Graham, N. a J., Cinner, J. E., & Russ, G. R. (2013). Spillover of fish  
494 naïveté from marine reserves. *Ecology Letters*, 16(2), 191–7.  
495 <https://doi.org/10.1111/ele.12028>

496 Jupiter, S. D., Epstein, G., Ban, N. C., Mangubhai, S., Fox, M., & Cox, M. (2017). A Social–Ecological  
497 Systems Approach to Assessing Conservation and Fisheries Outcomes in Fijian Locally  
498 Managed Marine Areas. *Society and Natural Resources*, 30(9), 1096–1111.  
499 <https://doi.org/10.1080/08941920.2017.1315654>

500 Kaunda-Arara, B., & Rose, G. A. (2004). Out-migration of Tagged Fishes from Marine Reef National  
501 Parks to Fisheries in Coastal Kenya. *Environmental Biology of Fishes*, 70(4), 363–372.  
502 <https://doi.org/10.1023/B:EBFI.0000035428.59802.af>

503 Kay, M., Lenihan, H., Kotchen, M., & Miller, C. (2012). Effects of marine reserves on California spiny  
504 lobster are robust and modified by fine-scale habitat features and distance from reserve  
505 borders. *Marine Ecology Progress Series*, 451, 137–150. <https://doi.org/10.3354/meps09592>

506 Kellner, J. B., Tetreault, I., Gaines, S. D., & Nisbet, R. M. (2007). Fishing the line near marine  
507 reserves in single and multispecies fisheries. *Ecological Applications : A Publication of the*  
508 *Ecological Society of America*, 17(4), 1039–54. Retrieved from  
509 <http://www.ncbi.nlm.nih.gov/pubmed/17555217>

510 Kerwath, S. E., Winker, H., Götz, A., & Attwood, C. G. (2013). Marine protected area improves yield  
511 without disadvantaging fishers. *Nature Communications*, 4, 1–6.  
512 <https://doi.org/10.1038/ncomms3347>

513 Kleiven, P. J. N., Espeland, S. H., Olsen, E. M., Abesamis, R. A., Moland, E., & Kleiven, A. R. (2019).  
514 Fishing pressure impacts the abundance gradient of European lobsters across the borders of a  
515 newly established marine protected area. *Proceedings of the Royal Society B: Biological*  
516 *Sciences*, 286, 20182455. <https://doi.org/10.1098/rspb.2018.2455>

517 Lester, S. E., Halpern, B. S., Grorud-colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., ...  
518 Warner, R. R. (2009). Biological effects within no-take marine reserves : a global synthesis,  
519 384, 33–46. <https://doi.org/10.3354/meps08029>

520 Manel, S., Loiseau, N., Andrello, M., Fietz, K., Goñi, R., Forcada, A., ... Mouillot, D. (2019). Long-  
521 Distance Benefits of Marine Reserves : Myth or Reality ? *Trends in Ecology & Evolution*, 1–  
522 13. <https://doi.org/10.1016/j.tree.2019.01.002>

523 Marques, I., Hill, N., Shimadzu, H., Soares, A. M. V. M., & Dornelas, M. (2015). Spillover Effects of a  
524 Community-Managed Marine Reserve, 1–18. <https://doi.org/10.1371/journal.pone.0111774>

525 Marshall, D. J., Gaines, S., Warner, R., Barneche, D. R., & Bode, M. (2019). Underestimating the  
526 benefits of marine protected areas for the replenishment of fished populations, 1–7.  
527 <https://doi.org/10.1002/fee.2075>

528 McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015).  
529 Marine defaunation: Animal loss in the global ocean. *Science*, 347(6219), 247–254.  
530 <https://doi.org/10.1126/science.1255641>

531 Micheli, F., & Niccolini, F. (2013). *Achieving success under pressure in the conservation of intensely*  
532 *used coastal areas. Ecology and Society* (Vol. 18). <https://doi.org/10.5751/ES-05799-180419>

533 Molloy, P. P., McLean, I. B., & Côté, I. M. (2009). Effects of marine reserve age on fish populations:  
534 a global meta-analysis. *Journal of Applied Ecology*, 46(4), 743–751.  
535 <https://doi.org/10.1111/j.1365-2664.2009.01662.x>

536 Osenberg, C. W., Sarnelle, O., & Cooper, S. D. (1997). Effect Size in Ecological Experiments: The  
537 Application of Biological Models in Meta-Analysis. *The American Naturalist*, 150(6), 798–812.  
538 <https://doi.org/10.1086/286095>

539 Roncin, N., Alban, F., Charbonnel, E., Crec’hriou, R., de la Cruz Modino, R., Culioli, J.-M., ...  
540 Boncoeur, J. (2008). Uses of ecosystem services provided by MPAs: How much do they impact  
541 the local economy? A southern Europe perspective. *Journal for Nature Conservation*, 16(4),  
542 256–270. <https://doi.org/10.1016/j.jnc.2008.09.006>

543 Russ, G. R. & Alcala, A. (1996). Do marine reserves export adult fish biomass? Evidence from Apo

544 Island , central Philippines. *Marine Ecology Progress Series*, 132, 1–9.

545 Russ, G. R., Alcala, A., & Maypa, A. (2003). Spillover from marine reserves: the case of *Naso*  
546 *vlamingii* at Apo Island, the Philippines. *Marine Ecology Progress Series*, 264, 15–20.  
547 <https://doi.org/10.3354/meps264015>

548 Russ, G. R., & Alcala, A. C. (2011). Enhanced biodiversity beyond marine reserve boundaries: the  
549 cup spillith over. *Ecological Applications : A Publication of the Ecological Society of America*,  
550 21(1), 241–50. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/21516901>

551 Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., ... Steneck, R.  
552 S. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology &*  
553 *Evolution*, 20(2), 74–80. <https://doi.org/10.1016/j.tree.2004.11.007>

554 Stamoulis, K. A., & Friedlander, A. M. (2013). A seascape approach to investigating fish spillover  
555 across a marine protected area boundary in Hawai'i. *Fisheries Research*, 144, 2–14.  
556 <https://doi.org/10.1016/j.fishres.2012.09.016>

557 Stobart, B., Warwick, R., González, C., Mallol, S., Díaz, D., Reñones, O., & Goñi, R. (2009). Long-  
558 term and spillover effects of a marine protected area on an exploited fish community. *Marine*  
559 *Ecology Progress Series*, 384, 47–60. <https://doi.org/10.3354/meps08007>

560 Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of  
561 landscape structure. *Oikos*, 68(3), 571–573. <https://doi.org/10.2307/3544927>

562 Viechtbauer, W. (2015). Conducting Meta-Analyses in R with the metafor Package . *Journal of*  
563 *Statistical Software*, 36(3). <https://doi.org/10.18637/jss.v036.i03>

564 Weeks, R., Green, A. L., Joseph, E., Peterson, N., & Terk, E. (2017). Using reef fish movement to  
565 inform marine reserve design. *Journal of Applied Ecology*, 54(1), 145–152.  
566 <https://doi.org/10.1111/1365-2664.12736>

567 Wiens, J. A. (2008). Landscape ecology as a foundation for sustainable conservation. *Landscape*

568 *Ecology*, 24(8), 1053–1065. <https://doi.org/10.1007/s10980-008-9284-x>

569 Zeller, D., Stoute, S. L., & Russ, G. R. (2003). Movements of reef fishes across marine reserve  
570 boundaries : effects of manipulating a density gradient, *254*(Pdt 1990), 269–280.

571 Zupan, M., Bulleri, F., Evans, J., Fraschetti, S., Guidetti, P., Garcia-Rubies, A., ... Claudet, J. (2018).  
572 How good is your marine protected area at curbing threats? *Biological Conservation*, *221*,  
573 237–245. <https://doi.org/10.1016/j.biocon.2018.03.013>

574 Zupan, M., Fragkopoulou, E., Claudet, J., Erzini, K., Horta e Costa, B., & Gonçalves, E. J. (2018).  
575 Marine partially protected areas: drivers of ecological effectiveness. *Frontiers in Ecology and*  
576 *the Environment*, *16*(7), 381–387. <https://doi.org/10.1002/fee.1934>

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#### 581 **SUPPORTING INFORMATION**

582 Additional supporting information may be found online in the Supporting Information section  
583 at the end of the article.

584

585 **Table 1. Empirical studies and data that met the section criteria of our meta-analysis. For further details, see the**  
 586 **supplementary material.**

587

588 N/A: Data Not Available

Fully protected area name (Country)	Years since enforcement	Reserve Size (km <sup>2</sup> )	Presence of a partially protected area (PPA)	Number of species	Source
Apo (Philippines)	16	0.11	No	1	Russ and Alcala 1996; Russ <i>et al.</i> 2003, 2004; Abesamis and Russ 2005; Abesamis <i>et al</i> 2006; Russ and Alcala 2011
Asinara (Italy)	9	2.45	Yes	17	data collection
Balicasag (Philippines)	16	0.08	No	1	Abesamis <i>et al</i> 2006
Barbados (Caribbean)	15	2.3	No	Assemblage	Chapman and Kramer 1999
Bonifacio (France)	19	0.74	Yes	13	data collection
Cabo de Palos (Spain)	23	2.68	Yes	18	data collection
Cabrera (Spain)	22	0.85	Yes	Assemblage	Harmelin Vivien <i>et al</i> 2008; Bellier <i>et al</i> 2013
Cap Roux (France)	15	0.44	No	12	data collection
Capo Carbonara (Italy)	6	0.6	Yes	16	data collection
Channel Islands (California)	7	N/A	No	1	Kay <i>et al</i> 2012a
Columbretes (Spain)	12	44	No	1	Goni <i>et al</i> 2006
Cote Bleue (France)	32	0.85	No	12	data collection
Egadi (Italy)	27	6.63	Yes	13	data collection
Mombasa (Kenya)	6	10	No	Assemblage	McClanahan and Mangi 2000
Portofino (Italy)	19	0.18	Yes	15	data collection
Pupukea-Waimea (Hawaii)	17	0.71	No	Assemblage	Stamoulis and Friedlander 2013
Strunjan (Slovenia)	10	0.46	Yes	7	data collection
Su Pallosu (Italy)	11	4	No	1	Follesa <i>et al</i> 2011
Tabarca (Spain)	20	14	Yes	1	Forcada 2008
Telascica (Croatia)	30	0.12	Yes	13	data collection
Tonga (Tonga)	7	18.35	No	1	Davidson <i>et al.</i> 2002
Torre Guaceto (Italy)	18	1.38	Yes	12	Guidetti <i>et al.</i> 2007; data collection
Zakyntos (Greece)	19	8	Yes	10	data collection

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599 Figure Captions

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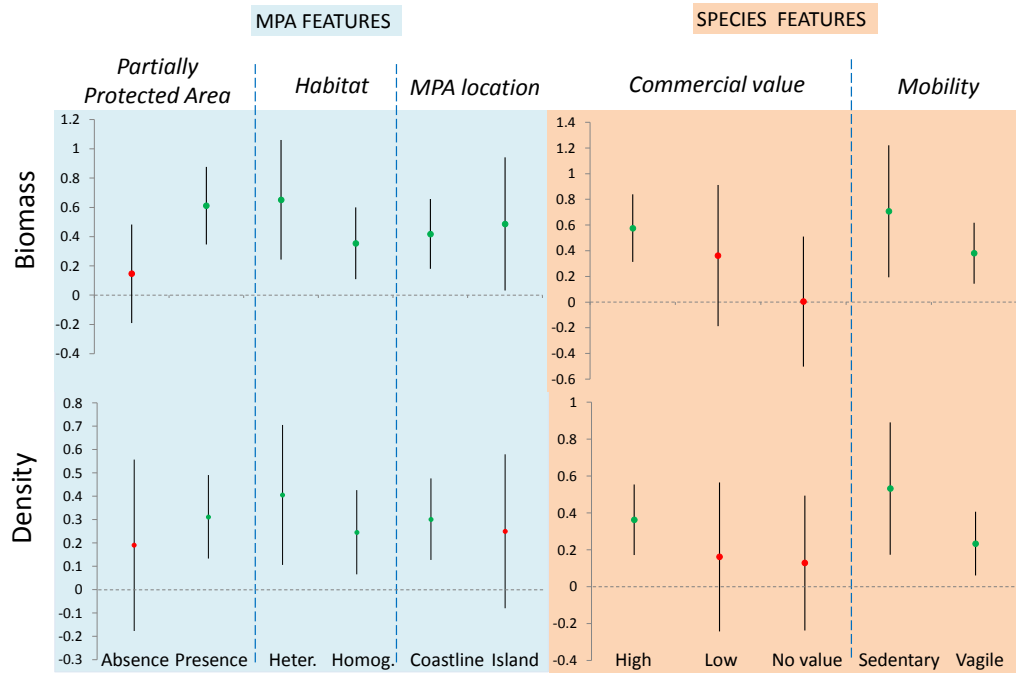
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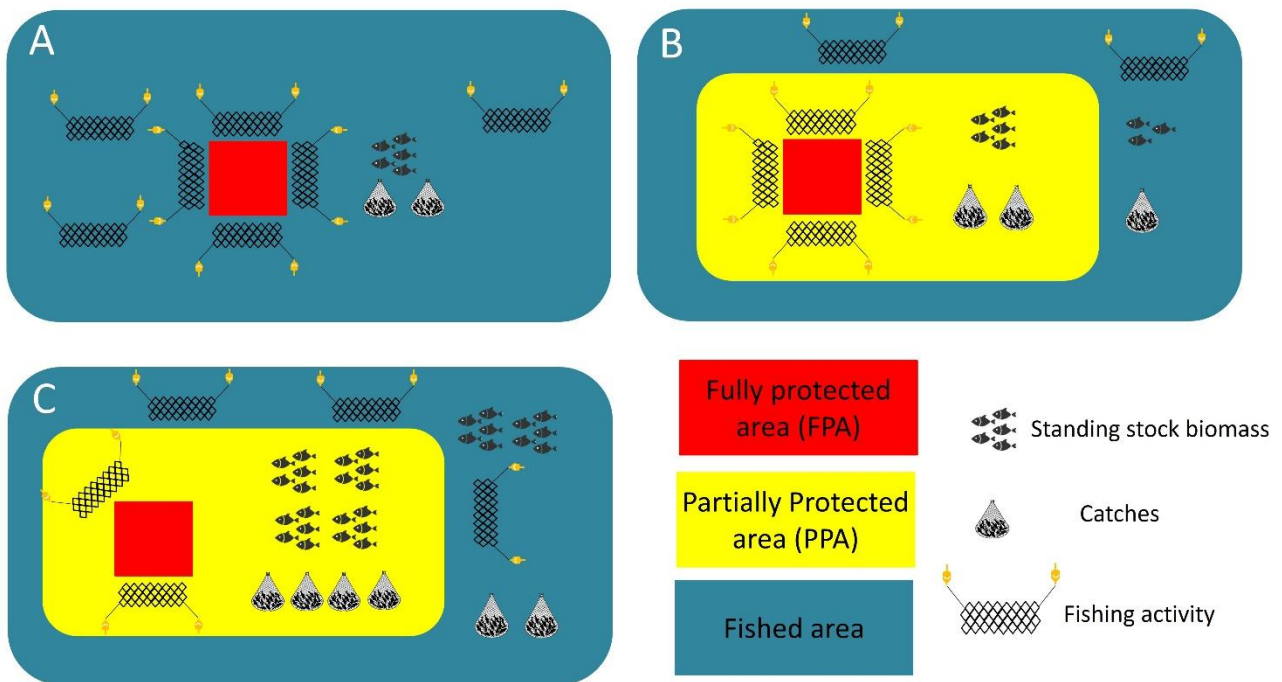
605 **Figure 1:** MPA-level and species-level drivers of spillover. The spillover indicator is the log-  
 606 transformed ratio of fish biomass or abundance between close and far from fully protected  
 607 area boundaries (average weighted effect size  $\pm$  95% CI). Green dots indicate effect sizes  
 608 that do not overlap zero and red dots those that overlap zero.  
 609 Heter.: Heterogeneous; Homog.: Homogeneous



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**Figure 2:** This generic conceptual framework illustrates the potential effects of presence and absence of partially protected area (PPA) surrounding fully protected area (FPA) on spillover. Three different scenarios are shown: A) high fishing pressure could reduce the ecological and fishery spillover assessment in fished area around FPA; B) high fishing pressure could reduce the ecological (standing stock biomass) and fishery (catches) spillover assessment within PPA surrounding the FPA and nullifies both spillover assessment in fished area; C) low fishing pressure could increase the ecological and fishery spillover assessment within PPA surrounding the FPA and enhances ecological and fishery spillover assessment in the fished area



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