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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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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 (< 1km²; (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.

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117

118 2. METHODS

119
120

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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193
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).

219
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**

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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 ²)	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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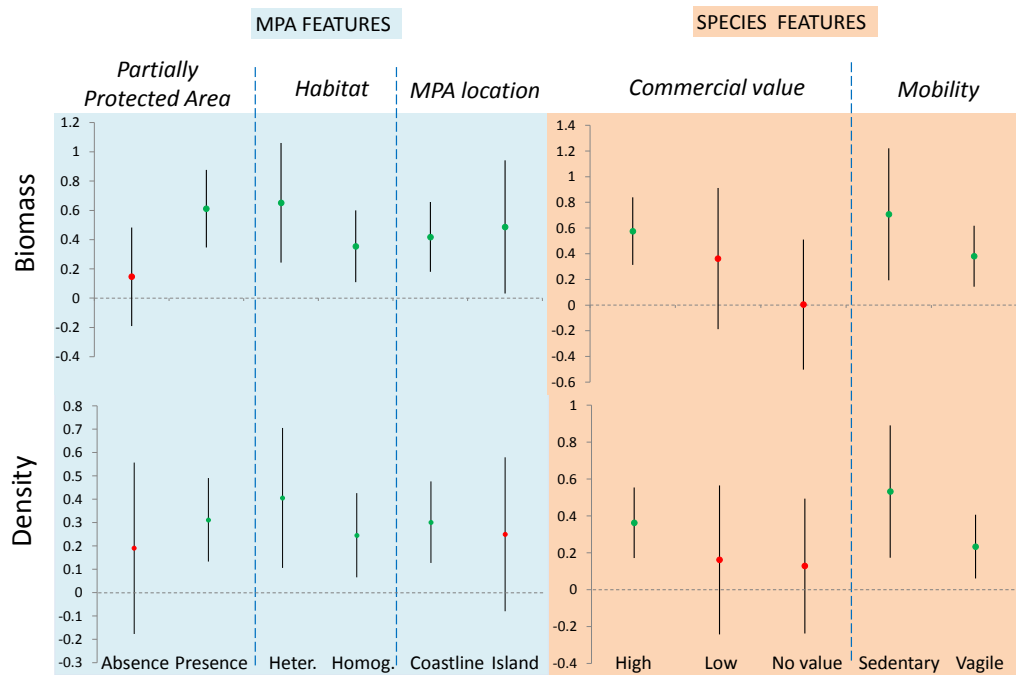
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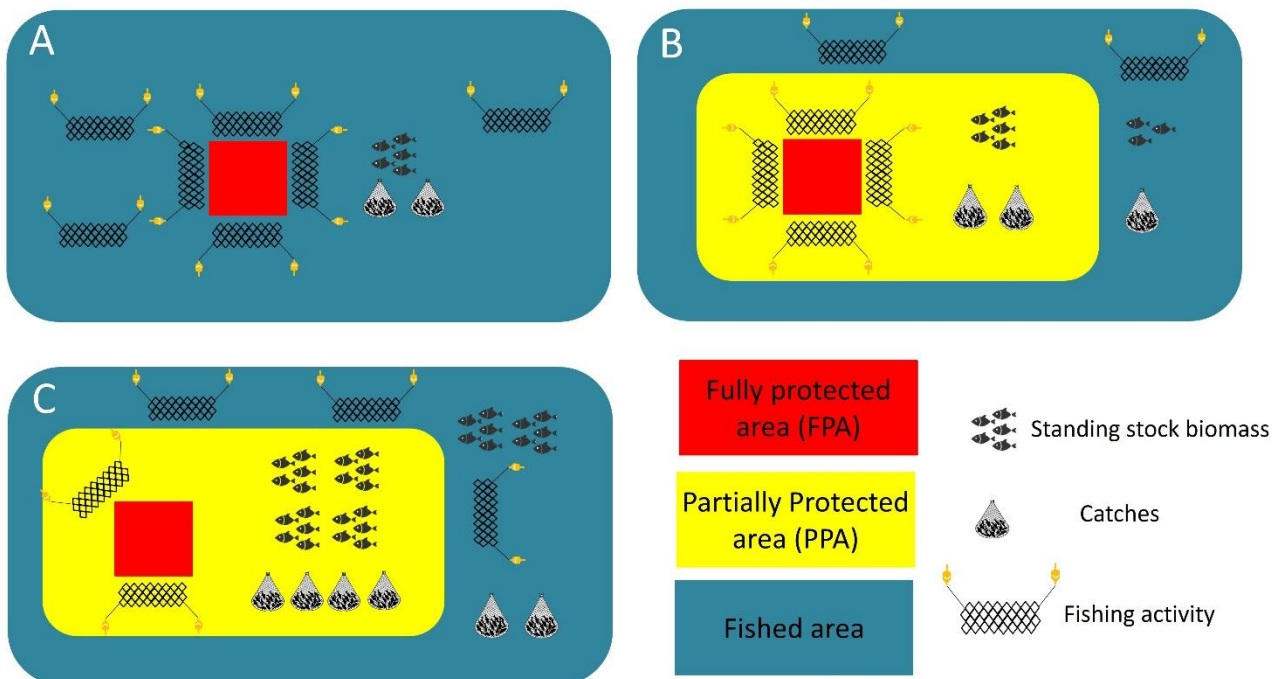
605 **Figure 1:** MPA-level and species-level drivers of spillover. The spillover indicator is the log-
 606 transformed ratio of fish biomass or abundance between close and far from fully protected
 607 area boundaries (average weighted effect size \pm 95% CI). Green dots indicate effect sizes
 608 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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