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# Assessing spillover from marine protected areas and its drivers: A meta-analytical approach

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## Abstract

Overfishing may seriously impact fish populations and ecosystems. Marine protected areas (MPAs) are key tools for biodiversity conservation and fisheries management, yet the fisheries benefits remain debateable. Many MPAs include a fully protected area (FPA), restricting all activities, within a partially protected area (PPA) where potentially sustainable activities are permitted. An effective tool for biodiversity conservation, FPAs, can sustain local fisheries via spillover, that is the outward export of individuals from FPAs. Spillover refers to both: "ecological spillover": outward net emigration of juveniles, subadults and/or adults from the FPA; and "fishery spillover": the fraction of ecological spillover that directly benefits fishery yields and revenues through fishable biomass. Yet, how common is spillover remains controversial. We present a meta-analysis of a unique global database covering 23 FPAs worldwide, using published literature and purposely collected field data, to assess the capacity of FPAs to export biomass and whether this response was mediated by specific FPA features (e.g. size, age) or species characteristics (e.g. mobility, economic value). Results show fish biomass and abundance outside FPAs was higher: (a) in locations close to FPA borders (<200 m) than further away (>200 m); (b) for species with a high commercial value; and (c) in the presence of PPA surrounding the FPA. Spillover was slightly higher in FPAs that were larger and older and for more mobile species. Based on the broadest data set compiled to date on marine species ecological spillover beyond FPAs' borders, our work highlights elements that could guide strategies to enhance local fishery management using MPAs.

KEYWORDS

coral reef, fully protected area, marine reserve, no-take zone, small-scale fisheries, temperate reef

## 1 | INTRODUCTION



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

Although marine protected areas (MPAs) are widely recognized as an important tool for biodiversity conservation (Claudet et al., 2008; Edgar et al., 2014; Giakoumi et al., 2017) and fisheries management (Abesamis, Russ, & Alcala, 2006; Goñi et al., 2008; Russ & Alcala, 2011), the prevalence of fisheries benefits delivered by MPAs is still largely debated (Hilborn, 2016; Kerwath, Winker, Götz, & Attwood, 2013; Sale et al., 2005). Many MPAs embed a fully protected area (FPA), aiming to preserve natural populations and ecosystems, within a partially protected area (PPA) where potentially sustainable activities are allowed. There is a body of evidence suggesting that FPAs can play an important role for fisheries management, especially for SSFs (Di Franco et al., 2016; Januchowski-Hartley, Graham, Cinner, & Russ, 2013; Russ & Alcala, 2011). Two ecological processes can drive fishery benefits of FPAs: population replenishment through larval subsidies (Manel et al., 2019; Marshall, Gaines, Warner, Barneche, & Bode, 2019) and the spillover of fish biomass from protected areas to surrounding fishing grounds (Rowley, 1994). While both processes require populations to firstly recover within the boundaries of the FPAs, generally the former is key to the long-term persistence of exploited populations also at relatively large distances from the MPA (i.e. hundreds of kilometres, Manel et al., 2019), while the latter produces faster benefits to fisheries mainly across shorter distances (Halpern, Lester, & Kellner, 2010). The spatio-temporal scale of these two processes is species-specific (Green et al., 2015; McCauley et al., 2015).

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

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

The overall relative contribution of potential drivers of spillover is poorly known. Two main categories of drivers may facilitate spillover: (a) MPA features—age, design (e.g. size, shape, location), presence of PPAs, the level of enforcement and habitat continuity/discontinuity across FPA borders (Goñi et al., 2008; Harmelin-Vivien et al., 2008; Kaunda-Arara & Rose, 2004; Kay, Lenihan, Kotchen, & Miller, 2012); and (b) species characteristics—the species-specific ability to move across the FPA borders related, for example, to the intraspecific behaviour of individuals, habitat preferences, species mobility, commercial value and fishing pressure (Kaunda-Arara & Rose, 2004). Some studies reported that spillover may require many years (>10 years) to take place after a FPA is established (Abesamis et al., 2006; Harmelin-Vivien et al., 2008; Russ & Alcala, 1996; Russ, Alcala, & Maypa, 2003), while others detected spillover after only a few years from FPA establishment (<5 years) (Francini-Filho & Moura, 2008; Guidetti, 2007). Spillover has been observed from FPAs surrounded or not by a PPA (Abesamis et al., 2006; Francini-Filho & Moura, 2008; Harmelin-Vivien et al., 2008; Zeller, Stoute, & Russ, 2003) and detected from both small (< 1km$^2$) (Abesamis et al., 2006; Harmelin-Vivien et al., 2008; Russ & Alcala, 1996; Russ et al., 2003) and large FPAs (Ashworth & Ormond, 2005; Fisher & Frank, 2002; Stobart et al., 2009). Habitat continuity inside and outside the FPA is thought to facilitate spillover (Abesamis & Russ, 2005; Kaunda-Arara & Rose, 2004), but several studies detected spillover also where the habitat was discontinuous across FPA borders (Goñi, Quetglas, & Reñones, 2006; Guidetti, 2007; Harmelin-Vivien et al., 2008; Kay et al., 2012).

Spillover is expected to mostly occur for relatively mobile species (Buxton, Hartmann, Kearney, & Gardner, 2014; Halpern et al., 2010), but some studies showed that also sedentary species (Chapman & Kramer, 1999; Eggleston & Parsons, 2008; Forcada et al., 2009; Goñi et al., 2006, 2008; Zeller et al., 2003), as well as vagile (Abesamis et al., 2006; Forcada, Bayle-Sempere, Valle, & Sánchez-Jerez, 2008; Guidetti, 2007) and highly vagile species (Chapman & Kramer, 1999; Kaunda-Arara & Rose, 2004; Stobart et al., 2009), may spillover beyond FPA borders.

Here, we performed a meta-analysis to (a) investigate the extent of spillover occurrence from FPAs globally and (b) assess which FPA features and species characteristics mainly drive spillover. To do so, we compiled the most complete global database on spillover to date, covering 23 FPAs in 12 countries, combining information from reviewed literature and data gathered from underwater visual census samplings purposely carried out in the field.

## 2 | METHODS

### 2.1 | Data collection

We assembled our data set using two different approaches: extracting data from existing literature and performing ad hoc field activities to collect new data.

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

**TABLE 1** Empirical studies and data that met the selection criteria of our meta-analysis

| Fully protected area name (Country) | Years since enforcement | Enforcement level | Reserve Size (km$^2$) | Presence of a partially protected area (PPA) | Number of studied species | Source |
|---|---|---|---|---|---|---|
| Apo (Philppines) | 16 | High | 0.11 | No | 1, Assemblage | 1,2,3,4,5 |
| Asinara (Italy) | 9 | Medium | 2.45 | Yes | 17 | 6 |
| Balicasag (Philppines) | 16 | High | 0.08 | No | 1 | 4 |
| Barbados (Caribbean) | 15 | High | 2.3 | No | Assemblage | 7 |
| Bonifacio (France) | 19 | High | 0.74 | Yes | 13 | 6 |
| Cabo de Palos (Spain) | 23 | High | 2.68 | Yes | 18 | 6 |
| Cabrera (Spain) | 22 | High | 0.85 | Yes | Assemblage | 8,9 |
| Cap Roux (France) | 15 | Low | 0.44 | No | 12 | 6 |
| Capo Carbonara (Italy) | 6 | Medium | 0.6 | Yes | 16 | 6 |
| Channel Islands (California) | 7 | High | 3807.2 | No | 1 | 10 |
| Columbretes (Spain) | 12 | High | 44 | No | 1 | 11 |
| Cote Bleue (France) | 32 | High | 0.85 | No | 12 | 6 |
| Egadi (Italy) | 27 | High | 6.63 | Yes | 13 | 6 |
| Mombasa (Kenya) | 6 | High | 10 | No | Assemblage | 12 |
| Portofino (Italy) | 19 | High | 0.18 | Yes | 15 | 6 |
| Pupukea-Waimea (Hawaii) | 17 | High | 0.71 | No | Assemblage | 13 |
| Strunjan (Slovenia) | 10 | High | 0.46 | Yes | 7 | 6 |
| Su Pallosu (Italy) | 11 | High | 4 | No | 1 | 14 |
| Tabarca (Spain) | 20 | High | 14 | Yes | 1 | 15 |
| Telascica (Croatia) | 30 | Medium | 0.12 | Yes | 13 | 6 |
| Tonga (Tonga) | 7 | High | 18.35 | No | 1 | 16 |
| Torre Guaceto (Italy) | 18 | High | 1.38 | Yes | 12 | 17,6 |
| Zakyntos (Greece) | 19 | Medium | 8 | Yes | 10 | 6 |

*Note:* For further details, see the Supporting Information. Source: (1) Russ & Alcala (1996); (2) Russ et al. (2003); (3) Abesamis and Russ (2005); (4) Abesamis et al. (2006); (5) Russ and Alcala (2011); (6) Data collection; (7) Chapman & Kramer (1999); (8) Harmelin-Vivien et al. (2008); (9) Bellier et al. (2013); (10) Kay et al. (2012); (11) Goñi et al. (2006); (12) McClanahan and Mangi (2000); (13) Stamoulis & Friedlander (2013); (14) Follesa et al. (2011); (15) Forcada et al. (2008); (16) Davidson et al. (2002); and (17) Guidetti (2007). Information on enforcement level was obtained from primary literature, from Giakoumi et al. (2017) and, when no information was available, from expert judgement by the authors.

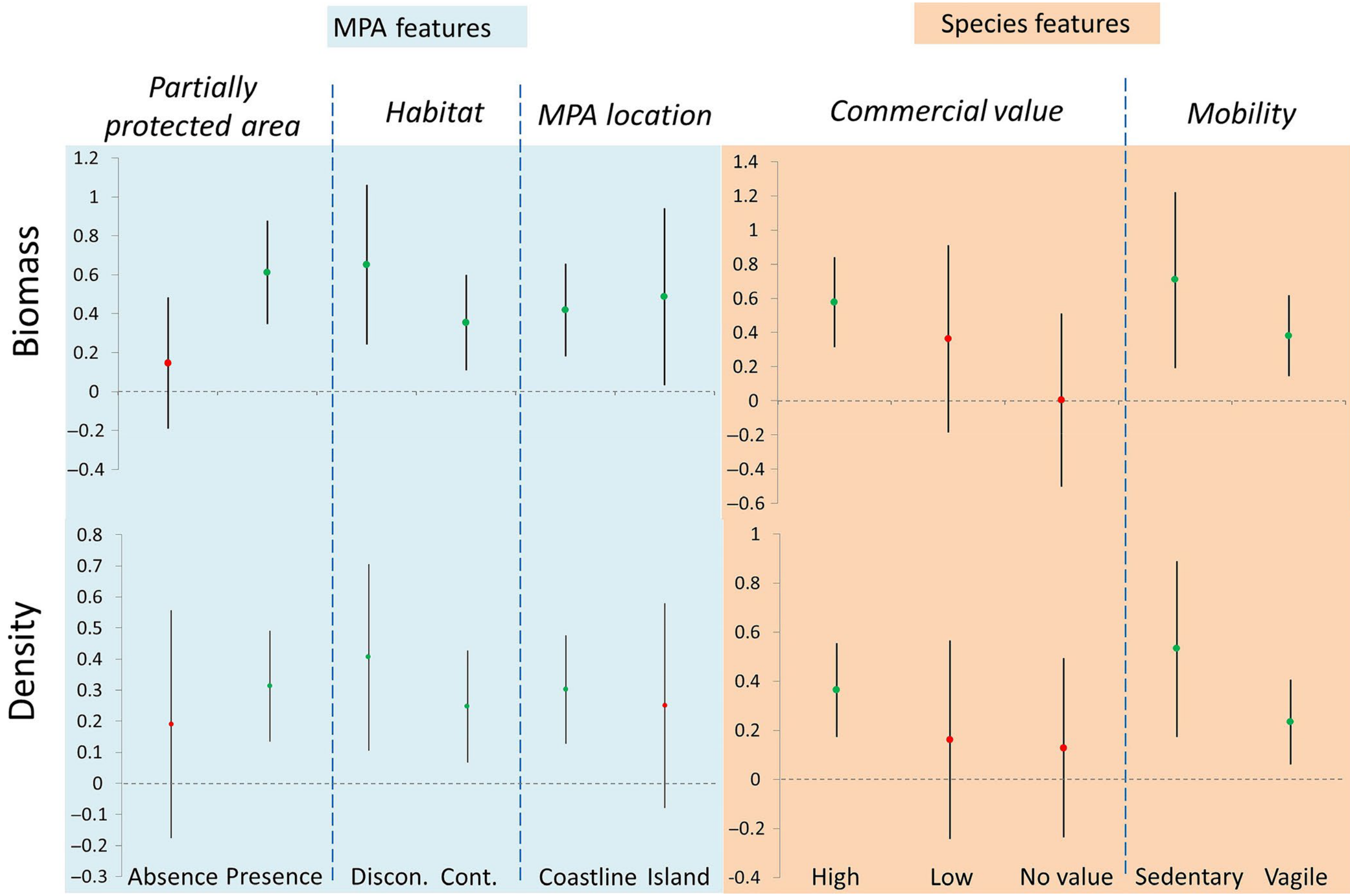


**FIGURE 1** MPA-level and species-level drivers of spillover. The spillover indicator is the log-transformed ratio of fish biomass or abundance between close and far from fully protected area boundaries (average weighted effect size ± 95% CI). Green dots indicate effect sizes that do not overlap zero and red dots those that overlap zero. Cont., continuous; Discon., discontinuous. Figure appears in colour in the online version only. [Colour figure can be viewed at wileyonlinelibrary.com]

were found. They were either based on underwater visual census, catch or tagging abundance and/or biomass data. Spillover has been modelled in various ways in the literature, such as using linear gradients of abundance/biomass decline from FPA borders (e.g. Goñi et al., 2006; Harmelin-Vivien et al., 2008) or tracking individual movements across FPA borders (Afonso, Morato, & Santos, 2008; Barrett, Buxton, & Gardner, 2009; Follesa et al., 2011; Kay et al., 2012; Kerwath et al., 2013). In order to keep the maximum number of studies, we built a model of spillover that would be as inclusive as possible in terms of different measurements and ways to report the data. Data from papers were extracted either from tables or from graphs using ImageJ (http://imagej.nih.gov/ij). Contextual information about the FPAs was recorded from the articles and/or by contacting their authors: FPA age and size, whether the FPA was situated on an island or along a coastline, presence of PPA surrounding the FPA and habitat continuity/discontinuity along FPA borders (Table 1). Information on species mobility (sedentary or vagile) and economic value (commercial, low commercial or not commercial) was also collected from the papers or FishBase (http://www.fishbase.org). It is worth noting that this study focused only on species that benefit most from protection and that are also targeted by SSFs; thus included only sedentary and vagile species. Mobility was not used when data were reported for higher taxonomic levels than genus. Subadults of target species were also included in the low commercial category as during that life stage they are not fishery targets.

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

Only one study used fisheries yield to assess spillover. Due to the absence of replication, we could not account for fisheries spillover and had to restrict our analysis to ecological spillover (Di Lorenzo et al., 2016). A total of 334 assessments from 23 MPAs (most of them reported as having a high level of enforcement Table 1) and 31 taxonomic groups (including species, genus or family) worldwide were finally used in the meta-analysis (Table 1; Table S1).

## 2.2 | Data analysis

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

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

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

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

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

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

All effect sizes were weighted, accounting for both the within- and among-study variance components (Hedges & Vevea, 1998). Models were fitted, and heterogeneity tests were run to assess how MPA-level (FPA age and size, island or coastline FPA, presence of a PPA, habitat continuity/discontinuity along FPA borders) and species-level (mobility and economic) drivers could mediate spillover from FPAs (Table 1). All analyses were done in R (R Core Team 2016) and weighted mixed-effects model fitting, and heterogeneity tests were carried out using the metaphor package (Viechtbauer, 2015).

# 3 | RESULTS

Overall, we found 33% higher fish abundance and 54% higher biomass close to the FPA borders (<200 m) compared to further away ($\bar{R}$ = 0.29 ± 0.15 95% CI and $\bar{R}$ = 0.43 ± 0.21 95% CI, respectively), indicating the general occurrence of spillover. However, effect sizes were heterogeneous across assessments ($Q_T$ = 7,314, $df$ = 167, $p$ < .001; $Q_T$ = 7,777, $df$ = 164, $p$ < .001, respectively) (Table S2).

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

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

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

Habitat continuity/discontinuity across FPA borders did not seem to affect the occurrence of spillover, for both abundance ($Q_E$ = 6,767.35; $df$ = 165; $p$ = .0001) and biomass ($Q_E$ = 7,299.05; $df$ = 163; $p$ = .0001; Figure 1).

Spillover density and biomass was detected for both sedentary and vagile species (Figure 1; Table S1). Only species with high commercial value showed a spillover effect from FPAs both in terms of abundance and biomass (Figure 1; Table S1).

# 4 | DISCUSSION

Our results showed that spillover of marine species, both in terms of abundance and biomass, can be expected as a general response of FPAs. Based on the data collected, the present study focused on ecological spillover (sensu Di Lorenzo et al., 2016). We showed that both fish biomass and abundance outside FPAs are higher in locations close to FPA borders (<200 m) than in locations further away (>200 m), for species with a high commercial value, and that it is occurring more in the presence of a partially protected area (PPA) surrounding the FPA. Spillover was slightly higher for larger and older FPAs and for more mobile species.

To the best of our knowledge, this is the first study using a meta-analytical approach considering the presence of PPAs as a potential driver of spillover, as well as benthic habitat continuity. Our findings suggest that the presence of a PPA might help detect the net export of biomass and fish abundance through spillover from the FPA. However, it is crucial to highlight that these patterns can be affected/altered by the magnitude of fishing effort around FPAs

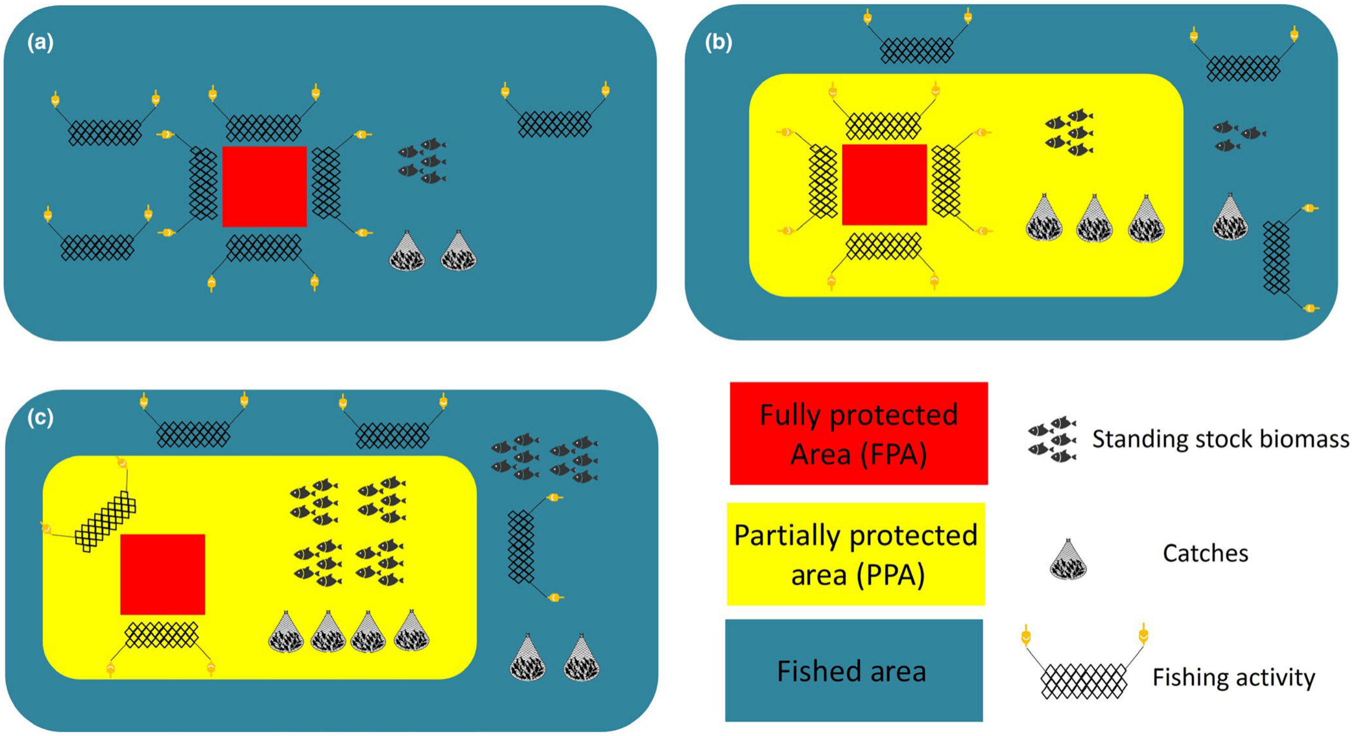


**FIGURE 2** This generic conceptual framework illustrates the potential effects of presence and absence of partially protected areas (PPAs) surrounding fully protected areas (FPAs) for spillover. Three different scenarios are shown: (a) high fishing pressure could reduce the ecological and fishery spillover recorded in fished areas around FPAs; (b) high fishing pressure in weakly regulated PPA could reduce the ecological (standing stock biomass) and fishery (catches) spillover recorded within PPAs surrounding the FPAs and nullifies both spillover recorded in fished area; and (c) low fishing pressure could increase the ecological and fishery spillover recorded within PPAs surrounding the FPAs and enhances ecological and fishery spillover assessment in the fished area. Figure appears in colour in the online version only. [Colour figure can be viewed at wileyonlinelibrary.com]

(in PPAs or in unprotected areas, depending on MPA zonation schemes). Fishing the line, that is fishers' tendency to fish close to the boundaries of FPAs (Kellner, Tetreault, Gaines, & Nisbet, 2007), is a recognized activity occurring around FPAs. In the absence of a PPA, fishery activities around FPAs' borders are not subject to strict spatially explicit regulations beside the ones imposed by national and international laws, generally resulting in a higher concentration of the fishing effort close to the FPA borders (Abesamis & Russ, 2005; Chapman & Kramer, 1999; Davidson, Villouta, Cole, & Barrier, 2002; Follesa et al., 2011; Russ & Alcala, 2011; Stamoulis & Friedlander, 2013). The recorded magnitude of ecological spillover can be reduced by fishing pressure in the unprotected areas (Nillos Kleiven et al., 2019), but high fishing effort can also be concentrated within PPAs (in the absence of specific regulations limiting the fishing effort) which also has negative consequences for potential ecological and fishery spillover (Figure 2) (Zupan, Bulleri, et al., 2018).

Our findings can shed light on the results observed in a recent global meta-analysis assessing the ecological effectiveness of different levels of protection (highly, moderately and weakly) in PPAs (Zupan, Fragkopoulou, et al., 2018). While the authors observed that fully and highly protected PPAs harbour higher fish abundance and biomass than surrounding unprotected areas, they found that moderately PPAs are effective only when adjacent to a FPA (Zupan, Fragkopoulou, et al., 2018). A possible explanation for this could be that in the absence of a FPA providing spillover, such moderately protected areas permit too much fishing to be effective. Spillover can thus be an important component driving the effectiveness of multizoned MPAs, allowing combinations of protection levels (including FPAs and PPAs) to favour both conservation and fisheries outcomes (Zupan, Bulleri, et al., 2018).

We observed a slight influence of time since protection (i.e. MPA age) on ecological spillover, in agreement with what has been observed for the response to protection within the FPA boundaries (Claudet et al., 2008; Edgar et al., 2014; Molloy, McLean, & Côté, 2009).

The fact that only species with a high commercial value display spillover is not surprising as they are the ones responding more favourably to protection and most rapidly to MPA establishment (Babcock et al., 2010; Claudet, Pelletier, Jouvenel, Bachet, & Galzin, 2006; Kerwath et al., 2013) hence the ones most likely exporting adults from the FPA boundaries. An important difference between our synthesis and a previous meta-analysis by Halpern et al. (2010) is that while their study focussed on highly valued fish species only, our analysis, for the first time, integrated data from three commercial value categories of species (i.e. no value, low and high).

A slight effect of FPA size on spillover was also found; it suggests that the set of MPAs included in our study covers a range of sizes representing a trade-off between the inclusion of the home ranges of most species and the optimal size for spillover to neighbouring areas. In fact, the size of a FPA should include the full home ranges of the species that you intend to protect in order to obtain high conservation benefits (Di Franco et al., 2018; Weeks, Green, Joseph, Peterson, & Terk, 2017).

While several experimental studies have shown that habitat continuity inside and outside FPAs may play a role in facilitating spillover (Forcada et al., 2008; Goñi et al., 2008; Halpern et al., 2010; Kaunda-Arara & Rose, 2004), our meta-analysis showed that spillover could occur where the habitat across FPA borders is either continuous or discontinuous. Landscape connectivity theory ("the degree to which the landscape facilitates or impedes movement among resource patches"; Taylor, Fahrig, Henein, & Merriam, 1993) suggests that similar habitat types across FPAs and fished areas may enhance the border permeability (Bartholomew et al., 2008). However, our results suggest that the likelihood that fish cross a different habitat rather than the preferred one also depends on how fish can perceive and respond behaviourally to integrate the patched habitat to minimize overall costs (Bélisle, 2005; Wiens, 2008). Therefore, although different habitats outside FPAs could be a barrier to fish movements (due, e.g., to the increased risk of predation), individuals may be able to move beyond FPA borders when a threshold level of population density/biomass (i.e. competition for local resources such as preys and refuges) is exceeded.

Here, we observed that species, regardless of their mobility, are able to perform spillover. The fact that any species with different mobility levels can display spillover may support the use of FPA for SSF management, as these fisheries are multispecific and usually target both sedentary and vagile species (Claudet, Guidetti, Mouillot, & Shears, 2011).

As in any qualitative review or quantitative synthesis or meta-analysis, our study may have a publication bias. For example, studies supporting spillover could be more likely to be published than those where no spillover is observed and this would therefore translate in some overestimation of spillover. However, the way we modelled spillover is rather conservative in the sense that it favours false negatives over false positives (see Section 2.2). In addition, our sample covers a large array of species, MPA types, and biogeographic regions and is well representative of spillover assessment in marine protection worldwide. We are thus quite confident that MPAs, through spillover and larval subsidy (Marshall et al., 2019), can play a significant role in replenishing surrounding areas, therefore enhancing fisheries and non-extractive activities that may benefit from increased fish density and biomass (e.g. scuba diving and tourism in general).

In terms of socio-economic implications, the potential benefits induced by spillover could raise expectations in stakeholders (e.g. fishers, divers, tourists) that, if shattered, could induce a negative attitude and finally reduce support towards conservation initiatives and potentially foster non-compliant behaviours (e.g. poaching) (Bergseth, Russ, & Cinner, 2015; Di Franco et al. 2020). In our study, we use a conservative approach to assess spillover occurrence (i.e. spillover might have been underestimated in some cases), and in addition, we point out the circumstances under which spillover could occur, which is more appropriate from a management point of view as deception can be dramatic when a management tool is oversold (Chaigneau & Brown, 2016; Hogg, Gray, Noguera-Méndez, Semitiel-García, & Young, 2019). This can allow a clear message to be delivered to stakeholders and avoid overselling the occurrence of spillover, preventing unrealistic expectations, and as a consequence help foster support to conservation initiatives (Bennett et al., 2019; Di Franco et al. 2020).

Our findings highlight under which conditions ecological spillover may be expected, allowing MPA managers and policy-makers to develop sound strategies to eventually maximize the exploitation of fishable biomass exported by FPAs. While the foundation for the ecological effectiveness of full protection is clearly evidenced (i.e. the removal of fishing mortality; Claudet et al., 2008; Lester et al., 2009), how to adapt in each partially protected area, the types of use that are allowed or not (Zupan, Fragkopoulou, et al., 2018) and their respective intensity (Zupan, Bulleri, et al., 2018) remain unclear. Globally PPAs include a variety of management measures that range from almost unprotected areas (with no regulations implemented) to practically FPAs (Horta e Costa et al., 2016; Zupan, Fragkopoulou, et al., 2018). From this perspective, an effort should be made through further research to assess under which conditions PPAs can benefit local communities within multiuse MPAs. Here, all MPAs with multiple zones had a fully protected area, surrounded by at least a highly protected area (Claudet, Loiseau, Sostres, & Zupan, 2020). Future investigations that include the different levels of fishing intensity inside these areas based on the current regulations and levels of enforcement would help guide more effective management strategies. As PPAs currently lack a consistent and well-designed set of regulations worldwide (Horta e Costa et al., 2016), MPAs, mainly aimed to maximize fishery benefits, should assess the fisheries yield within PPAs and fished areas integrated with fishing effort data in order to optimize spillover (Figure 2).

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data are available upon a formal request to the lead author.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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