

ORIGINAL ARTICLE



WILEY

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

Manfredi Di Lorenzo^{1,2} | Paolo Guidetti^{2,3} | Antonio Di Franco^{2,3,4} |
Antonio Calò^{2,3,5} | Joachim Claudet^{6,7}

¹Institute for Biological Resources and Marine Biotechnologies, National Research Council, (IRBIM-CNR), Via Luigi Vaccara, 61, Mazara del Vallo, Italy

²CoNISMa, Interuniversity National Consortium for Marine Sciences, Rome, Italy

³ECOSEAS Lab. UMR 7035, Université Côte d'Azur, CNRS, Parc Valrose 28, Avenue Valrose, 06108, Nice, France

⁴Department of Integrative Marine Ecology, Sicily, Stazione Zoologica Anton Dohrn, Lungomare Cristoforo Colombo (complesso Roosevelt), 90149, Palermo, Italy

⁵Dipartimento di Scienze della Terra e del Mare (DiSTeM), Università di Palermo, Palermo, Italy

⁶National Center for Scientific Research, PSL Université Paris, CRILOBE, USR 3278 CNRS-EPHE-UPVD, Maison des Océans, Paris, France

⁷Laboratoire d'Excellence CORAIL, Moorea, French Polynesia

Correspondence

Manfredi Di Lorenzo, Institute for Biological Resources and Marine Biotechnologies, National Research Council, Via Luigi Vaccara, 61 - 91026 Mazara del Vallo, Italy. Email: manfredi.dilorenzo@libero.it

Funding information

FishMPABlue 2 project (Interreg Mediterranean programme); Italian Marine Strategy monitoring; Prince Albert II of Monaco Foundation; Luigi and Francesca Brusarosco grant; Total Corporate Foundation; Foundation de France (INTHENSE); Agence Nationale de la Recherche, Grant/Award Number: ANR-14-CE03-0001-01; ERA-Net BiodivERsA

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,

1 INTRODUCTION	907
2 METHODS	909
2.1. Data collection	909
2.2. Data analysis	910
3 RESULTS	911
4 DISCUSSION	911
ACKNOWLEDGEMENTS	913
CONFLICT OF INTEREST	913
DATA AVAILABILITY STATEMENT	913
REFERENCES	913
SUPPORTING INFORMATION	915

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 (< 1 km²) (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 (Philippines)	16	High	0.11	No	1, Assemblage	1,2,3,4,5
Asinara (Italy)	9	Medium	2.45	Yes	17	6
Balicasag (Philippines)	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
Zakynthos (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.

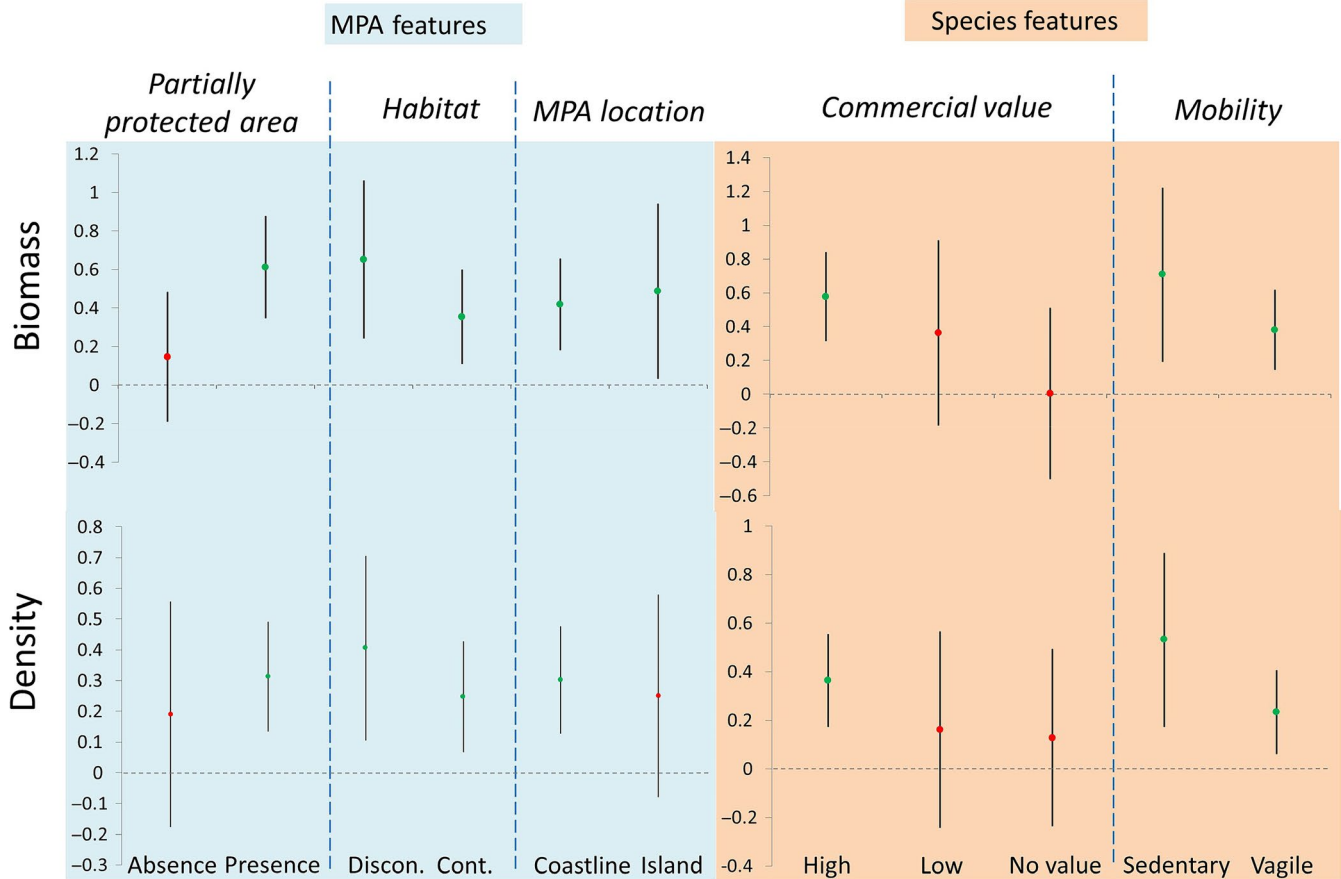


FIGURE 1 MPA-level and species-level drivers of spillover. The spillover indicator is the log-transformed ratio of fish biomass or abundance between close and far from fully protected area boundaries (average weighted effect size \pm 95% CI). Green dots indicate effect sizes that do not overlap zero 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 assess 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:

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

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

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

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 where $n_{close,i}$ and $n_{far,i}$ 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 ($\bar{R} = 0.29 \pm 0.15$ 95% CI and $\bar{R} = 0.43 \pm 0.21$ 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 ($\bar{R} = 0.008 \pm 0.007$ 95% CI) and biomass ($\bar{R} = 0.014 \pm 0.010$ 95% CI). The effect of the size of the FPA played a limited but detectable role only in the case of abundance ($\bar{R} = 0.04 \pm 0.03$ 95% CI for abundance; $\bar{R} = 0.02 \pm 0.03$ 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/alterd by the magnitude of fishing effort around FPAs

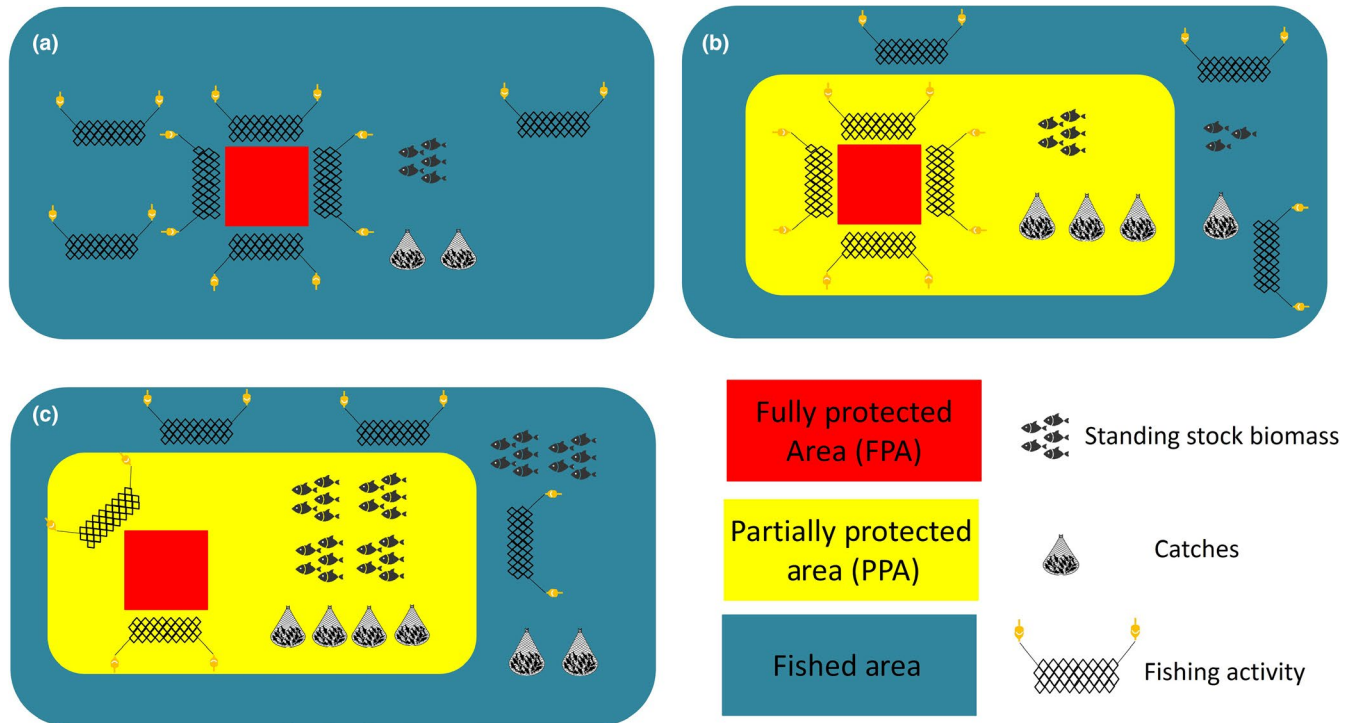


FIGURE 2 This generic conceptual framework illustrates the potential effects of presence and absence of partially protected areas (PPAs) surrounding fully protected areas (FPAs) for spillover. Three different scenarios are shown: (a) high fishing pressure could reduce the ecological and fishery spillover 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 & Alcalá, 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).

ACKNOWLEDGEMENTS

We wish to thank N. Barrett, C. Bené, J. Bohnsack, E. Brunio, R. Cole, R. Davidson, D. Eggleston, R. Francini-Filho, D. Freeman, E. Hardman, F.A. Januchowski-Hartley, M. Kay, S. Kerwath, D.L. Kramer, D. Malone, R. Ormond, M. Readdie, C. Roberts, A. Tewfik, K. Turgeon, M. Young, C. Wilcox and D. Zeller for sharing information about habitat types across MPAs borders. Special thanks to Gabriele Turco and Carlo Cattano for assistance in improving the graphics. The authors would like to thank P. Hart, E. Moland and the three anonymous referees for their constructive comments on an earlier draft of this manuscript. We are grateful to Kate Hogg (<https://katehogg.org>) for her suggestions and editing of the English of the MS. MDL was supported by a "Luigi and Francesca Brusarosco" grant. Thanks to FishMPABlue 2 project (Interreg Mediterranean programme), Italian Marine Strategy monitoring, Foundation de France (INTENSE), the ERA-Net

BiodivERsA (BUFFER) and the Agence Nationale de la Recherche (ANR-14-CE03-0001-01) for the Prince Albert II of Monaco Foundation (FPAIL, Monaco) and the Total Corporate Foundation (France) for financial support. Moreover, we are very grateful to all the MPAs directors and staff for their assistance with logistics and field support.

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.

ORCID

Manfredi Di Lorenzo  <https://orcid.org/0000-0003-3786-5772>

Paolo Guidetti  <https://orcid.org/0000-0002-7983-8775>

Antonio Di Franco  <https://orcid.org/0000-0003-3411-7015>

Antonio Calò  <https://orcid.org/0000-0001-6703-6751>

Joachim Claudet  <https://orcid.org/0000-0001-6295-1061>

REFERENCES

- Abesamis, R., & Russ, G. R. (2005). Density-dependent spillover from a marine reserve: Long-term evidence. *Marine Ecology Progress Series*, 15(5), 1798–1812.
- Abesamis, R. A., Russ, G. R., & Alcala, A. C. (2006). Gradients of abundance of fish across no-take marine reserve boundaries: Evidence from Philippine coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16(4), 349–371. <https://doi.org/10.1002/aqc.730>
- Afonso, P., Morato, T., & Santos, R. S. (2008). Spatial patterns in reproductive traits of the temperate parrotfish *Sparisoma cretense*. *Fisheries Research*, 90(1–3), 92–99. <https://doi.org/10.1016/j.fishres.2007.09.029>
- Ashworth, J. S., & Ormond, R. F. G. (2005). Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. *Biological Conservation*, 121(3), 333–344. <https://doi.org/10.1016/j.biocon.2004.05.006>
- Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., ... Russ, G. R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences of the United States of America*, 107(43), 18256–18261. <https://doi.org/10.1073/pnas.0908012107>
- Barrett, N., Buxton, C., & Gardner, C. (2009). Rock lobster movement patterns and population structure within a Tasmanian Marine Protected Area inform fishery and conservation management. *Marine and Freshwater Research*, 60(5), 417. <https://doi.org/10.1071/MF07154>
- Bartholomew, A., Bohnsack, J. A., Smith, S. G., Ault, J. S., Harper, D. E., & McClellan, D. B. (2008). Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. *Landscape Ecology*, 23(Suppl. 1), 55–65. <https://doi.org/10.1007/s10980-007-9136-0>
- Bélisle, M. (2005). Measuring landscape connectivity: The challenge of behavioral landscape ecology. *Ecology*, 86(8), 1988–1995. <https://doi.org/10.1890/04-0923>
- Bellier, E., Neubauer, P., Monestiez, P., Letourneur, Y., Ledireach, L., Bonhomme, P., Bachet F. (2013). Marine reserve spillover: Modelling from multiple data sources. *Ecological Informatics*, 18, 188–193. <http://dx.doi.org/10.1016/j.ecoinf.2013.09.004>
- Bennett, N. J., Di Franco, A., Calò, A., Nethery, E., Niccolini, F., Milazzo, M., & Guidetti, P. (2019). Local support for conservation is associated with perceptions of good governance, social impacts, and ecological effectiveness. *Conservation Letters*, 12, 1–10. <https://doi.org/10.1111/conl.12640>
- Bergseth, B. J., Russ, G. R., & Cinner, J. E. (2015). Measuring and monitoring compliance in no-take marine reserves. *Fish and Fisheries*, 16(2), 240–258. <https://doi.org/10.1111/faf.12051>
- Buxton, C. D., Hartmann, K., Kearney, R., & Gardner, C. (2014). When is spillover from marine reserves likely to benefit fisheries? *PLoS One*, 9(9), 1–7. <https://doi.org/10.1371/journal.pone.0107032>
- Chaigneau, T., & Brown, K. (2016). Challenging the win-win discourse on conservation and development: Analyzing support for marine protected areas. *Ecology and Society*, 21(1), <https://doi.org/10.5751/ES-08204-210136>
- Chapman, M., & Kramer, D. (1999). Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: Effects of reserve protection and habitat characteristics. *Marine Ecology Progress Series*, 181, 81–96. <https://doi.org/10.3354/meps181081>
- Cisneros-Montemayor, M., Pauly, D., & Weatherdon, L. V. (2016). A global estimate of seafood consumption by coastal indigenous peoples. *PLoS One*, 11(12), e0166681. <https://doi.org/10.1371/journal.pone.0166681>
- Claudet, J., Guidetti, P., Mouillot, D., & Shears, N. T. (2011). *Marine protected areas – A multidisciplinary approach*. Cambridge, UK: Cambridge University Press – Ecology Biodiversity and Conservation Series.
- Claudet, J., Loiseau, C., Sostres, M., & Zupan, M. (2020). Underprotected marine protected areas in a global biodiversity hotspot. *One Earth*, 2(4), 380–384. [10.1016/j.oneear.2020.03.008](https://doi.org/10.1016/j.oneear.2020.03.008)
- Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-Ruzafa, Á., ... Planes, S. (2008). Marine reserves: Size and age do matter. *Ecology Letters*, 11(5), 481–489. <https://doi.org/10.1111/j.1461-0248.2008.01166.x>
- Claudet, J., Pelletier, D., Jouvenel, J.-Y., Bachet, F., & Galzin, R. (2006). Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation*, 130(3), 349–369. <https://doi.org/10.1016/j.biocon.2005.12.030>
- da Silva, I. M., Hill, N., Shimadzu, H., Soares, A. M. V. M., & Dornelas, M. (2015). Spillover effects of a community-managed marine reserve. *PLoS One*, 10(4), e0111774.
- Davidson, R. J., Villouta, E., Cole, R. G., & Barrier, R. G. F. (2002). Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine Reserve, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 12(2), 213–227. <https://doi.org/10.1002/aqc.505>
- Di Franco, A., Plass-Johnson, J. G., Di Lorenzo, M., Meola, B., Claudet, J., Gaines, S. D., ... Guidetti, P. (2018). Linking home ranges to protected area size: The case study of the Mediterranean Sea. *Biological Conservation*, 221, 175–181. <https://doi.org/10.1016/j.biocon.2018.03.012>
- Di Franco, A., Thiriet, P., Di Carlo, G., Dimitriadis, C., Francour, P., Gutiérrez, N. L., ... Guidetti, P. (2016). Five key attributes can increase marine protected areas performance for small-scale fisheries management. *Scientific Reports*, 6(1), 38135. <https://doi.org/10.1038/srep38135>
- Di FrancoAntonio, Hogg Katie E., Calò Antonio, Bennett Nathan J., Sévin-Allouet Marie-Aude, Esparza Alaminos Oscar, Lang Marianne, Koutsoubas Drosos, Prvan Mosor, Santarossa Luca, Niccolini Federico, Milazzo Marco, Guidetti Paolo (2020). Improving marine protected area governance through collaboration and co-production. *Journal of Environmental Management*, 269, 110757. <http://dx.doi.org/10.1016/j.jenvman.2020.110757>
- Di Lorenzo, M., Claudet, J., & Guidetti, P. (2016). Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery

- component. *Journal for Nature Conservation*, 32, 62–66. <https://doi.org/10.1016/j.jnc.2016.04.004>
- Díaz, S., Settele, J., Brondizio, E. S., Ngo, H. T., Agard, J., Arneeth, A., ... Zayas, C. N. (2019). Pervasive human-driven decline of life on earth points to the need for transformative change. *Science*, 366(6471), eaax3100. <https://doi.org/10.1126/science.aax3100>
- Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., ... Thomson, R. J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, 506(7487), 216–220. <https://doi.org/10.1038/nature13022>
- Eggleston, D., & Parsons, D. M. (2008). Disturbance-induced “spill-in” of Caribbean spiny lobster to marine reserves. *Marine Ecology Progress Series*, 371, 213–220. <https://doi.org/10.3354/meps07699>
- Fisher, J., & Frank, K. (2002). Changes in finfish community structure associated with an offshore fishery closed area on the Scotian Shelf. *Marine Ecology Progress Series*, 240, 249–265. <https://doi.org/10.3354/meps240249>
- Follesa, M. C., Cannas, R., Cau, A., Cuccu, D., Gastoni, A., Ortu, A., ... Cau, A. (2011). Spillover effects of a Mediterranean marine protected area on the European spiny lobster *Palinurus elephas* (Fabricius, 1787) resource. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 21(6), 564–572. <https://doi.org/10.1002/aqc.1213>
- Forcada, A., Bayle-Sempere, J. T., Valle, C., & Sánchez-Jerez, P. (2008). Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. *Marine Environmental Research*, 66(5), 536–547. <https://doi.org/10.1016/j.marenvres.2008.08.003>
- Forcada, A., Valle, C., Bonhomme, P., Criquet, G., Cadiou, G., Lenfant, P., & Sánchez-Lizaso, J. (2009). Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Marine Ecology Progress Series*, 379, 197–211. <https://doi.org/10.3354/meps07892>
- Francini-Filho, R. B., & Moura, R. L. (2008). Evidence for spillover of reef fishes from a no-take marine reserve: An evaluation using the before-after control-impact (BACI) approach. *Fisheries Research*, 93(3), 346–356. <https://doi.org/10.1016/j.fishres.2008.06.011>
- Gaines, S. D., Lester, S. E., Grorud-Colvert, K., Costello, C., & Pollnac, R. (2010). Evolving science of marine reserves: New developments and emerging research frontiers. *Proceedings of the National Academy of Sciences of the United States of America*, 107(43), 18251–18255. <https://doi.org/10.1073/pnas.1002098107>
- Giakoumi, S., Scianna, C., Plass-Johnson, J., Micheli, F., Grorud-Colvert, K., Thiriet, P., ... Guidetti, P. (2017). Ecological effects of full and partial protection in the crowded Mediterranean Sea: A regional meta-analysis. *Scientific Reports*, 7(1), 1–12. <https://doi.org/10.1038/s41598-017-08850-w>
- Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., ... Planes, S. (2008). Spillover from six western Mediterranean marine protected areas: Evidence from artisanal fisheries. *Marine Ecology Progress Series*, 366, 159–174. <https://doi.org/10.3354/meps07532>
- Goñi, R., Quetglas, A., & Reñones, O. (2006). Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Marine Ecology Progress Series*, 308, 207–219. <https://doi.org/10.3354/meps308207>
- Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., ... White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, 90(4), 1215–1247. <https://doi.org/10.1111/brv.12155>
- Guidetti, P. (2007). Potential of marine reserves to cause community-wide changes beyond their boundaries. *Conservation Biology*, 21(2), 540–545. <https://doi.org/10.1111/j.1523-1739.2007.00657.x>
- Gurevitch, J., & Hedges, L. V. (1999). Statistical issues in ecological meta-analysis. *Ecology*, 80(4), 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)
- Halpern, B. S., Lester, S. E., & Kellner, J. B. (2010). Spillover from marine reserves and the replenishment of fished stocks. *Environmental Conservation*, 36(4), 268–276. <https://doi.org/10.1017/S0376892910000032>
- Harmelin-Vivien, M., Le Diréach, L., Bayle-Sempere, J., Charbonnel, E., García-Charton, J. A., Ody, D., ... Valle, C. (2008). Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? *Biological Conservation*, 141(7), 1829–1839. <https://doi.org/10.1016/j.biocon.2008.04.029>
- Hedges, L. V., & Vevea, J. L. (1998). Fixed- and random-effects models in meta-analysis. *Psychological Methods*, 3, 486–504. <https://doi.org/10.1037/1082-989X.3.4.486>
- Hilborn, R. (2016). Marine biodiversity needs more than protection. *Nature*, 535, 224–226. <https://doi.org/10.1038/535224a>
- Hogg, K., Gray, T., Noguera-Méndez, P., Semitiel-García, M., & Young, S. (2019). Interpretations of MPA winners and losers: A case study of the Cabo De Palos- Islas Hormigas Fisheries Reserve. *Maritime Studies*, 18(2), 159–171. <https://doi.org/10.1007/s40152-019-00134-5>
- Horta e Costa, B., Claudet, J., Franco, G., Erzini, K., Caro, A., & Gonçalves, E. J. (2016). A regulation-based classification system for Marine Protected Areas (MPAs). *Marine Policy*, 72, 192–198. <https://doi.org/10.1016/j.marpol.2016.06.021>
- Januchowski-Hartley, F. A., Graham, N. A. J., Cinner, J. E., & Russ, G. R. (2013). Spillover of fish naïveté from marine reserves. *Ecology Letters*, 16(2), 191–197. <https://doi.org/10.1111/ele.12028>
- Jupiter, S. D., Epstein, G., Ban, N. C., Mangubhai, S., Fox, M., & Cox, M. (2017). A social-ecological systems approach to assessing conservation and fisheries outcomes in Fijian locally managed marine areas. *Society and Natural Resources*, 30(9), 1096–1111. <https://doi.org/10.1080/08941920.2017.1315654>
- Kaunda-Arara, B., & Rose, G. A. (2004). Out-migration of tagged fishes from Marine Reef National Parks to Fisheries in Coastal Kenya. *Environmental Biology of Fishes*, 70(4), 363–372. <https://doi.org/10.1023/B:EBFI.0000035428.59802.af>
- Kay, M., Lenihan, H., Kotchen, M., & Miller, C. (2012). Effects of marine reserves on California spiny lobster are robust and modified by fine-scale habitat features and distance from reserve borders. *Marine Ecology Progress Series*, 451, 137–150. <https://doi.org/10.3354/meps09592>
- Kellner, J. B., Tetreault, I., Gaines, S. D., & Nisbet, R. M. (2007). Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications*, 17(4), 1039–1054. <https://doi.org/10.1890/05-1845>
- Kerwath, S. E., Winker, H., Götz, A., & Attwood, C. G. (2013). Marine protected area improves yield without disadvantaging fishers. *Nature Communications*, 4, 1–6. <https://doi.org/10.1038/ncomms3347>
- Lester, S. E., Halpern, B. S., Grorud-colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., ... Warner, R. R. (2009). Biological effects within no-take marine reserves: A global synthesis. *Marine Ecology Progress Series*, 384, 33–46. <https://doi.org/10.3354/meps08029>
- Manel, S., Loiseau, N., Andreollo, M., Fietz, K., Goñi, R., Forcada, A., ... Mouillot, D. (2019). Long-distance benefits of marine reserves: Myth or reality? *Trends in Ecology & Evolution*, 34, 342–354. <https://doi.org/10.1016/j.tree.2019.01.002>
- Marshall, D. J., Gaines, S., Warner, R., Barneche, D. R., & Bode, M. (2019). Underestimating the benefits of marine protected areas for the replenishment of fished populations. *Frontiers in Ecology and the Environment*, 1–7. <https://doi.org/10.1002/fee.2075>
- McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015). Marine defaunation: Animal loss in the global ocean. *Science*, 347(6219), 247–254. <https://doi.org/10.1126/science.1255641>
- McClanahan, T. R., Mangi, S. (2000). Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological*

- Applications*, 10(6), 1792–1805. [http://dx.doi.org/10.1890/1051-0761\(2000\)010\[1792:soeffa\]2.0.co;2](http://dx.doi.org/10.1890/1051-0761(2000)010[1792:soeffa]2.0.co;2).
- Micheli, F., & Niccolini, F. (2013). Achieving success under pressure in the conservation of intensely used coastal areas. *Ecology and Society*, 18(4). <https://doi.org/10.5751/ES-05799-180419>
- Molloy, P. P., McLean, I. B., & Côté, I. M. (2009). Effects of marine reserve age on fish populations: A global meta-analysis. *Journal of Applied Ecology*, 46(4), 743–751. <https://doi.org/10.1111/j.1365-2664.2009.01662.x>
- Nillos Kleiven, P. J., Espeland, S. H., Olsen, E. M., Abesamis, R. A., Moland, E., & Kleiven, A. R. (2019). Fishing pressure impacts the abundance gradient of European lobsters across the borders of a newly established marine protected area. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182455. <https://doi.org/10.1098/rspb.2018.2455>
- Osenberg, C. W., Sarnelle, O., & Cooper, S. D. (1997). Effect size in ecological experiments: The application of biological models in meta-analysis. *American Naturalist*, 150(6), 798–812. <https://doi.org/10.1086/286095>
- Roncin, N., Alban, F., Charbonnel, E., Crec'hriou, R., de la Cruz Modino, R., Culioli, J.-M., ... Boncoeur, J. (2008). Uses of ecosystem services provided by MPAs: How much do they impact the local economy? A southern Europe perspective. *Journal for Nature Conservation*, 16(4), 256–270. <https://doi.org/10.1016/j.jnc.2008.09.006>
- Rowley, R. J. (1994). Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 4, 233–254. <https://doi.org/10.1002/aqc.3270040305>
- Russ, G. R., & Alcala, A. (1996). Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series*, 132, 1–9. <https://doi.org/10.3354/meps132001>
- Russ, G. R., & Alcala, A. C. (2011). Enhanced biodiversity beyond marine reserve boundaries: The cup spillth over. *Ecological Applications: A Publication of the Ecological Society of America*, 21(1), 241–250. <https://doi.org/10.1890/09-1197.1>
- Russ, G. R., Alcala, A., & Maypa, A. (2003). Spillover from marine reserves: The case of *Naso vlamingii* at Apo Island, the Philippines. *Marine Ecology Progress Series*, 264, 15–20. <https://doi.org/10.3354/meps264015>
- Sale, P., Cowen, R., Danilowicz, B., Jones, G., Kritzer, J., Lindeman, K., ... Sadovy, Y. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, 20(2), 74–80. <https://doi.org/10.1016/j.tree.2004.11.007>
- Stamoulis, K. A., & Friedlander, A. M. (2013). A seascape approach to investigating fish spillover across a marine protected area boundary in Hawai'i. *Fisheries Research*, 144, 2–14. <https://doi.org/10.1016/j.fishres.2012.09.016>
- Stobart, B., Warwick, R., González, C., Mallol, S., Díaz, D., Reñones, O., & Goñi, R. (2009). Long-term and spillover effects of a marine protected area on an exploited fish community. *Marine Ecology Progress Series*, 384, 47–60. <https://doi.org/10.3354/meps08007>
- Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68(3), 571–573. <https://doi.org/10.2307/3544927>
- Viechtbauer, W. (2015). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36(3), 1–48. <https://doi.org/10.18637/jss.v036.i03>
- Weeks, R., Green, A. L., Joseph, E., Peterson, N., & Terk, E. (2017). Using reef fish movement to inform marine reserve design. *Journal of Applied Ecology*, 54(1), 145–152. <https://doi.org/10.1111/1365-2664.12736>
- Wiens, J. A. (2008). Landscape ecology as a foundation for sustainable conservation. *Landscape Ecology*, 24(8), 1053–1065. <https://doi.org/10.1007/s10980-008-9284-x>
- Zeller, D., Stoute, S. L., & Russ, G. R. (2003). Movements of reef fishes across marine reserve boundaries: Effects of manipulating a density gradient. *Marine Ecology Progress Series*, 254, 269–280.
- Zupan, M., Bulleri, F., Evans, J., Fraschetti, S., Guidetti, P., Garcia-Rubies, A., ... Claudet, J. (2018). How good is your marine protected area at curbing threats? *Biological Conservation*, 221, 237–245. <https://doi.org/10.1016/j.biocon.2018.03.013>
- Zupan, M., Fragkopoulou, E., Claudet, J., Erzini, K., Horta e Costa, B., & Gonçalves, E. J. (2018). Marine partially protected areas: Drivers of ecological effectiveness. *Frontiers in Ecology and the Environment*, 16(7), 381–387. <https://doi.org/10.1002/fee.1934>
- R CORE TEAM – R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, 2016 Available from: <http://www.R-project.org>.

SUPPORTING INFORMATION

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

How to cite this article: Di Lorenzo M, Guidetti P, Di Franco A, Calò A, Claudet J. Assessing spillover from marine protected areas and its drivers: A meta-analytical approach. *Fish Fish*. 2020;21:906–915. <https://doi.org/10.1111/faf.12469>