1 **Drivers of ecological effectiveness in marine partially protected areas**

2 Mirta Zupan^{1*}, Eliza Fragkopoulou^{1,2*}, Joachim Claudet^{3,4}, Karim Erzini², Bárbara
3 Horta e Costa^{1,2,3,4§}, Emanuel J. Gonçalves^{1§#}

4 ¹ MARE - Marine and Environmental Sciences Centre, ISPA – Instituto Universitário,
5 Rua Jardim do Tabaco 34, 1149-041, Lisboa, Portugal

6 ² Centre of Marine Sciences, CCMAR, University of Algarve, Campus de Gambelas,
7 8005-139 Faro, Portugal

8 ³ National Center for Scientific Research, CRIOBE, USR 3278 CNRS-EPHE-UPVD,
9 66860 Perpignan, France

10 ⁴ Laboratoire d'Excellence CORAIL, France

11 * - These authors contributed equally to this work.

12 § - joint senior authorship

13 **E-mail addresses:** M. Zupan: mirtazupan@gmail.com; E. Fragkopoulou:
14 eli_frag@hotmail.com; J. Claudet: joachim.claudet@gmail.com; K. Erzini:
15 kerzini@ualg.pt; B. Horta e Costa: barbarahcosta@gmail.com; E.J. Gonçalves:
16 emmanuel@ispa.pt

17 **Running title:** Effectiveness of marine partially protected areas

18

19

20 **KEYWORDS:** Abundance, Biomass, Commercial fish, Fully protected areas,
21 Impact assessment, Marine protected areas, Meta-analysis, Regulation-Based
22 Classification System

23 **Type of article:** *Research Communication*

24 150 words in the Abstract, 2303 words in total, 20 References, 3 Figures, 2 Web-only
25 Tables.

26 **Corresponding author:**

27 Emanuel J. Gonçalves

28 MARE - Marine and Environmental Sciences Centre, ISPA – Instituto Universitário,
29 Rua Jardim do Tabaco 34, 1149-041, Lisboa, Portugal

30 Tel: +351 218811700; fax: +351 218860954; E-mail: emanuel@ispa.pt

31 **ABSTRACT**

32 The global number of marine protected areas grew exponentially in the last decade to
33 meet international targets. Most of them are partially protected areas (PPAs). Yet,
34 their ecological effectiveness remains unclear due to the high variability of allowed
35 uses. Here, we performed the first global meta-analysis of PPAs following a new
36 regulation-based classification system, to assess their ecological effectiveness.
37 Overall, PPAs are effective relative to unprotected areas but allowed uses are the key
38 feature determining their performance. Highly and moderately regulated PPAs
39 provide higher biomass and abundance of commercial fish species, while weakly
40 regulated PPAs do not exhibit differences relative to unprotected areas. Importantly,
41 the effectiveness of some PPAs can be enhanced by the presence of an adjacent fully
42 protected area (no-take zone). We conclude that limited and well-regulated uses in
43 PPAs and the presence of an adjacent fully protected area confer ecological benefits,
44 on which socio-economic advantages are derived.

INTRODUCTION

Coastal zones are experiencing increasing human and environmental pressures and they are in need of strategic management decisions (Halpern *et al.* 2015). The implementation of marine protected areas (MPAs) is a commonly used tool for conservation, food security and fisheries management (Gaines *et al.* 2010). The ecological effects of fully protected areas (FPAs, ie no-take areas) are well studied: they can usually increase abundance and size of species within (eg Claudet *et al.* 2008) and in some cases outside the FPAs (eg Caselle *et al.* 2015), and contribute to recover populations and communities and to preserve habitat structure (White & Costello 2014).

On the downside, the establishment of FPAs has shown conflicts between conservation and socio-economic objectives, especially in areas with numerous users and uses (Fox *et al.* 2011). Hence, the implementation of partially protected areas (PPAs), where some extractive activities may be allowed, has become a preferable option as a compromise in such social-ecological systems, since they are easier to implement. Simultaneously, in response to international agreements and commitments, more and more MPAs are established, most of them being PPAs of an ever-increasing variety (Lubchenco & Grorud-Colvert 2015). Therefore, it is urgent to identify which types of PPAs can provide socio-economic benefits while still protecting biodiversity.

PPAs are context-dependent, and their regulations vary with their management objectives. In turn, these regulations will likely affect their ecological effectiveness. Only a handful of studies examined the effects of different levels of protection (eg Di

Franco *et al.* 2009; Ban *et al.* 2014; Sciberras *et al.* 2015), yet none followed a systematic classification for the different protection zones leading to variable results which are difficult to generalize.

A recently published regulation-based classification system for MPAs (Horta e Costa *et al.* 2016) presents a new way to classify both MPAs and each zone within them, according to the uses they allow. Understanding the ecological responses of various types of PPAs is essential, since most MPAs are multiple-use and the ecological effects each PPA provides are likely linked to different regulatory regimes (Fox *et al.* 2011).

We present the first assessment of the ecological effectiveness of different types of PPAs through a global meta-analysis, using the regulation-based classification (Horta e Costa *et al.* 2016). We also examined how design characteristics that are known to affect the effectiveness of no-take areas, such as age and size (Claudet *et al.* 2008), or that are specific to multiple-use MPAs, such as the presence of an adjacent fully protected area, may also mediate the effectiveness of PPAs.

METHODS

Data selection: response variables and covariates

We built our database based on studies compiled by Sciberras *et al.* (2015) and Horta e Costa *et al.* (2016), updated with recent peer reviewed literature resulting from a database search following the methods of Sciberras *et al.* (2015). We limited our analyses to studies that reported values for abundance and/or biomass of fisheries targeted species and that compared these ecological variables between PPAs and the

surrounding areas outside, which in this study we will refer to as unprotected areas (UPAs). We only retained studies that reported ecological responses for a particular PPA when compared to UPAs, but not cases where biological responses were aggregated for an entire multiple-use MPA. When studies reported ecological responses for PPAs with different protection levels, we included them separately in the database, since they represent different types of PPAs. In cases where more than one study investigated the effect of protection of a given PPA, only the most recent one was retained, unless different metrics were used.

The studies had to report the mean of the response variable, sample size (eg number of transects) and an appropriate error measure (eg variance). If the study assessed abundance and biomass of targeted fish species over some other variables (eg depth, habitat types), data were averaged over these. When data were collected over time, only the most recent results were extracted, as they represent the longest duration of protection. However, when data were reported over several times within a year, results were averaged for that year in order to minimize seasonal effects associated with sampling period. Similarly, when data were reported for multiple targeted species k , we calculated the overall mean ($\bar{X}$) and standard deviation (sd) for the study as:

$$(1) \bar{X} = \frac{\sum_{j=1}^k n_j \bar{x}_j}{\sum_{j=1}^k n_j} \quad \text{and} \quad (2) \text{sd} = \sqrt{\frac{1}{k^2} \sum_{j=1}^k \text{sd}_j^2}$$

where $\bar{x}$ is the mean biomass or abundance for species j ; sd and n_j are the standard deviation and sample sizes (eg number of transects) associated with $\bar{x}_j$.

We classified each PPA based on Horta e Costa *et al.* (2016) where each PPA type allows different activities, ranging from closed areas, to areas where only low impact

non-extractive activities are allowed, and areas with very high impact extractive activities, resulting in five classes of PPAs: i) highly regulated, ii) moderately regulated, iii) weakly regulated, iv) very weakly regulated, and v) unregulated.

Moreover, we recorded the age (years since establishment), size, and the presence or absence of an adjacent FPA (when the FPA and PPA were part of a multiple-use MPA). We also scored the capacity to implement regulations in each PPA following Mora *et al.* (2009). These range from 0 to 1, with 0 representing low capacity and 1 representing high capacity. This index was obtained for fisheries at a national level, and is here assumed as a proxy for MPA enforcement regarding fisheries regulations.

The final database resulted in 26 peer-reviewed research articles and 47 case studies of PPAs worldwide (WebTable 1). Out of the 47 PPAs, 24 were characterized as highly regulated, 15 as moderately regulated, 7 as weakly regulated and 1 as very weakly regulated. We restricted our analysis to the first three classes.

Meta- analysis

To assess the ecological effectiveness of PPAs we used a weighted random-effect meta-analysis. The effect size R_i for each PPA i was modeled as a natural logarithm (Ln) response ratio of the mean ($\bar{X}_i$) abundance or biomass estimates measured inside and outside the PPA (Osenberg *et al.* 1997; Hedges *et al.* 1999):

$$(3) R_i = \ln \frac{\bar{X}_{PPA_i}}{\bar{X}_{UPA_i}}$$

where $\bar{X}_{PPA}$ and $\bar{X}_{UPA}$ are the mean abundance or biomass inside and outside the PPA

of the study i . The variance v_i of the effect sizes, the within study variance, was calculated as follows:

$$(4) v_i = \frac{sd_{PPA_i}^2}{n_{PPA_i} * \bar{X}_{PPA_i}^2} + \frac{sd_{UPA_i}^2}{n_{UPA_i} * \bar{X}_{UPA_i}^2}$$

where $\bar{X}_{PPA}$ and $\bar{X}_{UPA}$ are the mean abundance or biomass inside and outside the PPA of the study i , sd_{PPA} , sd_{UPA} , are the standard deviations associated with $\bar{X}_{PPA}$ and $\bar{X}_{UPA}$ of the study i , and n_{PPA} and n_{UPA} are the sample sizes of the study i for the estimation of the mean (eg number of transects). As in traditional random-effect meta-analysis, our weights w_i included both the within- and among-study variances as follows:

$$(5) w_i = \frac{1}{v_i + vA}$$

where v_i is defined as above and vA is the among-study variance.

We investigated if different types of PPAs show different levels of ecological effectiveness. In addition, we assessed if different PPA features were mediating the response to protection, namely: i) age, ii) size (measured in km² and log-transformed in the analyses), iii) the capacity to implement regulations, and iv) the presence/absence of an adjacent FPA. The interactions between PPA class and each of the PPA features were also tested. All analyses were conducted with the statistical software environment R (R Development Core Team 2016).

RESULTS

Both abundance and biomass of targeted fish species were significantly higher inside PPAs compared to the UPAs: on average 2.4 and 2.9 times higher, respectively (Figure 1). The effectiveness of PPAs, however, was variable across studies, both when considering abundance ($Q_t = 961$, $df=35$, $p<0.001$) or biomass ($Q_t=2197$, $df=38$, $p<0.001$). In fact, different classes of PPAs showed different levels of effectiveness (abundance $Q_m=11.35$, $p=0.0034$; biomass $Q_m=6.6636$, $p=0.048$). When compared to unprotected areas, highly regulated PPAs exhibited 2.9 and 3 times higher fish abundances and biomass, respectively, and moderately regulated PPAs exhibited 2.9 and 4.2 times higher abundances and biomasses, respectively. However, in weakly regulated PPAs, abundance and biomass did not differ from the surrounding UPAs (Figure 1).

Ecological effectiveness of PPAs increased with PPA age, size and the capacity to implement regulations (Figure 2, WebTable 2.1). Each year after implementation, abundance and biomass of targeted fish species increased on average by 5.1 and 4.6%, respectively, relative to the UPAs. For every 10-fold increase in the size of a PPA, fish abundance and biomass increased by 37 and 46%, respectively. Further, increasing the implementation capacity of a PPA by 10% resulted in a 4.3 and 6.4-fold increase in, respectively, the abundance and biomass of targeted fish species. The effect of age, size and capacity to implement regulations did vary with the PPA class, yet these interactions were significant only for the abundance of targeted fish species and not for biomass (see WebTable 2.1). The response of target species inside moderately and highly regulated PPAs was positively affected by age, size and the

capacity to implement regulations, whereas no significant effect was detected on weakly regulated PPAs (Figure 2).

Finally, the presence of a fully protected area (FPA) adjacent to a PPA played a role in making the PPA more ecologically effective (abundance $Q_m=2.05$, $p=0.15$; biomass $Q_m=5.47$ $p=0.082$). Fish abundance and biomass were on average 1.6 and 2.1 times higher, respectively, within PPAs with an adjacent FPA than in single PPAs (Figure 3). The effects of the presence of the FPA varied across the three PPA classes (abundance $Q_m=22.07$, $p=0.0005$; biomass $Q_m=12.59$ $p=0.096$), with moderately regulated PPAs showing positive ecological benefits only when adjacent to an FPA (Figure 3, WebTable 2.2) and weakly regulated PPAs not showing any benefit.

DISCUSSION

Our most important finding is that the regulations of PPAs are the key feature determining their ecological effectiveness. Moderately and highly regulated PPAs are effective at harboring more target fish abundance and biomass when compared to unprotected areas (UPAs), whereas weakly regulated PPAs do not show ecological benefits. Highly and moderately regulated PPAs allow for a limited amount of extractive uses (maximum of five and ten gears allowed, respectively) that have minimal (eg lines and traps) or moderate (eg gillnets) impact on the ecosystem compared to weakly regulated PPAs where more gears and/or with greater negative environmental impacts (eg trawling) are allowed (Horta e Costa *et al.* 2016).

Additionally, we show that combining a fully protected area (FPA) with moderately regulated PPAs confers considerable positive benefits. This class of PPAs is

commonly used and therefore siting these areas adjacent to a FPA is an important option to consider, since it increases the ecological benefits of these PPAs. Highly and weakly regulated PPAs are less sensitive to a presence of an adjacent FPA for different reasons. The former most likely due to the limited amount of extractive activities permitted within them which already confer high conservation benefits, and the latter due a large number of activities occurring within them with significant impacts. Even if, in the moderately regulated PPAs, regulations alone may not be sufficient to significantly enhance populations of targeted fish species, spill-over effects from an adjacent no-take area may increase their ecological effectiveness (eg Hackradt *et al.* 2014).

We also show that the effectiveness of protection is positively correlated with PPA age and size, demonstrating that these variables matter in partial protection and not only for no-take areas (Claudet *et al.* 2008; Edgar *et al.* 2014). Moreover, the higher the capacity to implement regulations the greater the ecological effectiveness of PPAs, confirming that investment in control and surveillance mechanisms should be a high priority when establishing and managing MPAs (Mora *et al.* 2009; Edgar *et al.* 2014). Likewise, Guidetti *et al.* (2008) demonstrated that the patterns of fish recovery within protected areas were linked to the enforcement and compliance levels of the associated MPA. The positive ecological effects associated with larger, older and better-enforced PPAs are, however, negatively correlated with the increasing number of extractive activities allowed within those PPAs.

Here, we confirm that some types of partial protection can provide both fisheries and conservation benefits (eg Hackradt *et al.* 2014), particular for populations of targeted

fish species. Sciberras *et al.* (2015) also detected some variability in the response to partial protection of targeted fish species in relation to a broad categorization of protection regimes. Fernández-Chacón *et al.* (2015) demonstrated empirically that by excluding a number of fishing gears inside PPAs, fish species targeted by those gears benefit from protection when compared to UPAs.

Most of the studies included in this analysis were for PPA classes where extraction is limited (highly and moderately regulated PPAs) and, therefore, stronger responses are to be expected, whereas only a handful of studies reported results for PPAs with lower levels of protection (weakly and very weakly regulated PPAs). Publication bias (ie scientists tend to sample where it is likely to record an effect and journals tend to favor the publication of positive results) can explain why we were only able to find 47 case studies while there are more than 13,000 MPAs listed globally (MPA Atlas: www.mpatlas.org). However, although caution is needed when generalizing our results, it is important to note that it is very likely that we have captured the most effective PPAs, likely, leading to conservative results. Such syntheses can provide solid insights on the effectiveness of PPAs and may provide baseline guidelines for managers and policy-makers.

The implementation of MPAs requires the integration of conservation, social, economic and political goals and their design should be driven by the management objectives. A regulation-based classification system as the one used in this study (Horta e Costa *et al.* 2016) provides an adequate tool to test not only aspirational goals, based on objectives, but concrete impacts as predicted by regulations of uses. Our results can assist policy-makers and managers to determine appropriate levels of

protection to reach specific goals by accounting for the type of regulations adopted in each MPA.

ACKNOWLEDGEMENTS

We thank C.W. Osenberg for fruitful discussion in the early stages of this manuscript. This research was funded by the ERA-Net BiodivERsA project “BUFFER—Partially protected areas as buffers to increase the linked social-ecological resilience”, with the national funders ANR (France), FCT (Portugal), FOR-MAS and SEPA (Sweden) and RCN (Norway). B.H.C. was supported by a grant under the project BUFFER, a FCT grant (SFRH/BPD/100377/2014), and a Fernand Braudel IFER fellowship (Fondation Maison des Sciences de l’Homme). FCT supported this work under the strategic project UID/MAR/04292/2013.

REFERENCES

- Ban NC, McDougall C, Beck M, *et al.* 2014. Applying empirical estimates of marine protected area effectiveness to assess conservation plans in British Columbia, Canada. *Biol Conserv* **180**: 134–148.
- Caselle JE, Rassweiler A, Hamilton SL, *et al.* 2015. Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. *Sci Rep* **5**: 14102.
- Claudet J, Osenberg CW, Benedetti-Cecchi L, *et al.* 2008. Marine reserves: size and age do matter. *Ecol Lett* **11**: 481–489.

293 Di Franco A, Bussotti S, Navone A, *et al.* 2009. Evaluating effects of total and partial
 294 restrictions to fishing on Mediterranean rocky-reef fish assemblages. *Mar Ecol Prog*
 295 *Ser* **387**: 275–285.

296

297 Edgar GJ, Stuart-Smith RD, Willis TJ, *et al.* 2014. Global conservation outcomes
 298 depend on marine protected areas with five key features. *Nature* **506**: 216–220.

299

300 Fernández-Chacón A, Moland E, Espeland SH, *et al.* 2015. Demographic effects of
 301 full vs. partial protection from harvesting: inference from an empirical before-after
 302 control-impact study on Atlantic cod. *J Appl Ecol* **52**: 1206–1215.

303

304 Fox HE, Mascia MB, Basurto X, *et al.* 2011. Reexamining the science of marine
 305 protected areas: linking knowledge to action. *Conserv Lett* **5**: 1–10.

306

307 Gaines SD, White C, Carr MH, *et al.* 2010. Designing marine reserve networks for
 308 both conservation and fisheries management. *Proc Natl Acad Sci U.S.A.* **107**: 18286–
 309 18293.

310

311 Guidetti P, Milazzo M, Bussotti S, *et al.* 2008. Italian marine reserve effectiveness:
 312 Does enforcement matter? *Biol Conserv* **141**: 699–709.

313

314 Hackradt CW, Garcia-Charton JA, Harmelin-Vivien M, *et al.* 2014. Response of
 315 rocky reef top predators (Serranidae: Epinephelinae) in and around marine protected
 316 areas in the Western Mediterranean Sea. *PLoS One* **9**: e98206.

317

318 Halpern BS, Frazier M, Potapenko J, *et al.* 2015. Spatial and temporal changes in
319 cumulative human impacts on the world's ocean. *Nat Commun* **6**: 7615.
320

321 Hedges LV, Gurevitch J and Curtis PS, *et al.* 1999. The meta-analysis of response
322 ratios in experimental ecology. *Ecology* **80**: 1150–1156.
323

324 Horta e Costa B, Claudet J, Franco G, *et al.* 2016. A regulation-based classification
325 system for Marine Protected Areas (MPAs). *Mar Policy* **72**: 192–198.
326

327 Lester S and Halpern B. 2008. Biological responses in marine no-take reserves versus
328 partially protected areas. *Mar Ecol Prog Ser* **367**: 49–56.
329

330 Lubchenco J and Grorud-Colvert K. 2015. Making waves: The science and politics of
331 ocean protection. *Science* **350**: 382–383.
332

333 Mora C, Myers RA, Coll M, *et al.* 2009. Management Effectiveness of the World's
334 Marine Fisheries. *PLoS Biol* **7**: e1000131.
335

336 Osenberg CW, Sarnelle O and Cooper SD. 1997. Effect size in ecological
337 experiments: the application of biological models in meta-analysis. *Am Nat* **150**: 798–
338 812.
339

340 R Core Team. 2016. R: A language and environment for statistical computing.
341 Foundation for Statistical Computing, Vienna, Austria.
342

343 Sciberras M, Jenkins SR, Mant R, *et al.* 2015. Evaluating the relative conservation
344 value of fully and partially protected marine areas. *Fish Fish* **16**: 58–77.
345
346 White C and Costello C. 2014. Close the high seas to fishing? *PLoS Biol* **12**:
347 e1001826.

FIGURE CAPTIONS

Figure 1: Ecological effectiveness of partially protected areas (PPAs) for abundance (a) and biomass (b) of targeted fish species for all PPAs combined and for PPAs grouped by classes (sensu Horta e Costa *et al.* 2016). The horizontal dotted line at 1 represents equal fish abundance or biomass inside and outside the PPA. Values higher than 1 mean more fish (or biomass) inside the PPA and values below 1 mean fewer fish (or biomass) inside the PPA. The bars represent 95% confidence intervals. The sample size of each group is indicated.

Figure 2: Ecological effectiveness of the classes of partially protected areas (PPAs) as mediated by PPA age, PPA size and capacity to implement regulations for abundance (top panel) and biomass (bottom panel) of target fish species. The horizontal dotted line at 1 represents equal fish abundance (a-c) or biomass (d-f) inside and outside of the PPA. Values higher than 1 mean more fish (or biomass) inside the PPA and values below 1 mean fewer fish (or biomass) inside the PPA. The fitted lines are regressions of each PPA class and the corresponding feature (solid line: significant regression, $p < 0.05$; dashed line: non-significant regression, $p > 0.05$).

Figure 3: Ecological effectiveness of classes of partially protected areas (PPAs) for the abundance (a) and biomass (b) of targeted fish species as mediated by the presence of a fully protected area (open symbols). The horizontal dotted line at 1 represents equal fish abundance inside and outside of the PPA. Values higher than 1 mean more fish (or biomass) inside the PPA and values below 1 mean fewer fish (or biomass) inside the PPA. The bars represent 95% confidence intervals. The sample size of each group is indicated.

Relative fish abundance

Relative fish biomass

The class of the partially protected area

- Highly regulated partially protected areas
- Moderately regulated partially protected areas
- Weakly regulated partially protected areas

● All
partially protected areas

● Highly regulated
partially protected areas

● Moderately regulated
partially protected areas

● Weakly regulated
partially protected areas

Supporting Information
APPENDIX 1
Database of partially protected area indicators of ecological effectiveness

WebTable 1: Database of the characteristics of each partially protected area (PPA) included in the weighted meta-analysis investigating the effects of partial protection for abundance and/or biomass of targeted fish (PPA class following Horta e Costa *et al.* 2016; Implementation capacity score from Mora *et al.* (2009); FPA considered present when attached to or embedded within the PPA; Metrics: A - abundance, B - biomass; Number of Species Combined: the number of targeted fish species reported in the study, NA when the study reported targeted fish species as assemblage).

PPA name	PPA class	Location	Age PPA	PPA size (km ²)	Implementation capacity	FPA presence	Metrics	Number of Species Combined	Reference
Kisite	Highly regulated	Kenya	18	11	0.14	No	B	12	McClanahan <i>et al.</i> 2006
Tanga	Moderately regulated	Tanzania	18	1914	0.4	No	B	12	McClanahan <i>et al.</i> 2006
US Virgin Islands	Highly regulated	USA	2	51	0.56	No	B	4	Monaco <i>et al.</i> 2007
Isla Mona a	Highly regulated	Puerto Rico	5	5.8	0.42	No	A;B	NA	Mateos-Molina <i>et al.</i> 2014
Isla Mona b	Highly regulated	Puerto Rico	5	9	0.42	No	A;B	NA	Mateos-Molina <i>et al.</i> 2014
Easter group	Highly regulated	Australia	8	22.43	0.7	No	A	2	Nardi <i>et al.</i> 2004
Abrolhos	Highly regulated	Australia	8	27.6	0.7	No	A	2	Nardi <i>et al.</i> 2004
Wallabi group	Highly regulated	Papua New Guinea	60	0.33	0.54	No	B	NA	Cinner <i>et al.</i> 2005
Abrolhos	Highly regulated	Britain	10	4	0.4	Yes	A;B	3	Tupper & Rudd 2002

PPA name	PPA class	Location	Age PPA	PPA size (km ²)	Implementation capacity	FPA presence	Metrics	Number of Species Combined	Reference
Pedra Vermelha	Moderately regulated	Brazil	8	73	0.26	No	A	7	de Carvalho Teixeira Chaves & Monteiro-Neto 2008
Arraial do Cabo	Moderately regulated	Brazil	8	517	0.26	No	A	7	de Carvalho Teixeira Chaves & Monteiro-Neto 2008
Achang preserve	Highly regulated	Guam US	2	4.8	0.82	No	B	5	Tupper 2007
Piti preserve	Highly regulated	Guam US	2	3.6	0.82	No	B	5	Tupper 2007
Tumon preserve	Highly regulated	Guam US	2	4.5	0.82	No	B	5	Tupper 2007
Abrolhos Bank	Moderately regulated	Brazil	5	50	0.26	Yes	B	7	Francini-Filho & de Moura 2008
Pupukea	Highly regulated	USA	5	0.17	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007
Keakakekua Bay C	Weakly regulated	USA	5	5.65	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007
Keakakekua Bay B	Moderately regulated	USA	37	1.24	0.7	No	A	NA	Friedlander <i>et al.</i> 2007
Folkstone	Highly regulated	Barbados	15	2.2	0.24	No	A	10	Chapman & Kramer 1999
Yamoto Lase	Highly regulated	Fiji	3	0.13	0.48	Yes	B	NA	Jupiter & Egli 2011
Nakali	Highly regulated	Fiji	4	0.77	0.75	No	B	NA	Jupiter & Egli 2011
Lapakahi	Highly regulated	USA	30	0.54	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007
Old Kona Airport x	Weakly regulated	USA	5	7.32	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007
Old Kona Airport x	Moderately regulated	USA	12	1.06	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007

PPA name	PPA class	Location	Age PPA	PPA size (km ²)	Implementation capacity	FPA presence	Metrics	Number of Species Combined	Reference
Waialea	Moderately regulated	USA	19	0.14	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007
Manele	Moderately regulated	USA	28	1.12	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007
Molokini	Highly regulated	USA	27	0.36	0.7	No	A;B	NA	Friedlander <i>et al.</i> 2007
Waikiki	Weakly regulated	USA	5	11.2	0.7	Yes	A;B	NA	Friedlander <i>et al.</i> 2007
Loreto Bay National Park	Weakly regulated	Mexico	7	1835.7	0.34	Yes	B	4	Rife <i>et al.</i> 2013
Cerbere-Banyuls	Moderately regulated	France	24	5.85	0.64	Yes	B	3	Forcada <i>et al.</i> 2009
Portofino zone B	Moderately regulated	Italy	7	11.91	0.5	Yes	A;B	3	La Mesa & Vacchi 1999
Portofino zone C	Moderately regulated	Italy	7	19.4	0.5	Yes	A;B	3	La Mesa & Vacchi 1999
Scandola	Moderately regulated	France	37	6.5	0.64	Yes	A;B	1	Harmelin-Vivien <i>et al.</i> 2015
Tabarca	Moderately regulated	Spain	17	4.8	0.52	Yes	A;B	3	Hackradt <i>et al.</i> 2014
Tavolara zone B	Moderately regulated	Italy	2	31.13	0.5	Yes	A;B	5	Di Franco <i>et al.</i> 2009
Tavolara zone C	Moderately regulated	Italy	2	117.15	0.5	Yes	A;B	5	Di Franco <i>et al.</i> 2009
Sugar Loaf SLICA	Highly regulated	New Zealand	12	7.49	0.52	No	A	3	Miller <i>et al.</i> 2005
Sugar Loaf SLIPPA	Highly regulated	New Zealand	12	7.49	0.52	No	A	3	Miller <i>et al.</i> 2005
Gulf of Maine	Very weakly regulated	USA	7	3100	0.56	No	A	1	Smith <i>et al.</i> 2008
La Jolla	Highly regulated	USA	24	1.85	0.54	No	A;B	3	Tetreault & Ambrose 2007

PPA name	PPA class	Location	Age PPA	PPA size (km ²)	Implementation capacity	FPA presence	Metrics	Number of Species Combined	Reference
Isla La Graciosa	Highly regulated	Spain	9	609.95	0.54	Yes	A;B	4	Tuya <i>et al.</i> 2006
Punta La Restiga zone A	Highly regulated	Spain	8	1.8	0.54	No	A;B	4	Tuya <i>et al.</i> 2006
Punta La Restiga zone B	Highly regulated	Spain	8	4.8	0.54	No	A;B	4	Tuya <i>et al.</i> 2006
Georges Bank- CA1	Weakly regulated	USA	5	3960	0.56	No	A;B	13	Link <i>et al.</i> 2005
Georges Bank- CA2	Weakly regulated	USA	4	3880	0.56	No	A;B	15	Link <i>et al.</i> 2005
Gordons Bay	Highly regulated	Australia	12	1.64	0.7	No	A	2	Curley <i>et al.</i> 2013
Batemans*	Weakly regulated	Australia	5	365.5	0.7	Yes	A	1	Coleman <i>et al.</i> 2013
Cabo de Palos	Moderately regulated	Spain	8	16.8	0.52	Yes	A;B	3	Hackradt <i>et al.</i> 2014
Cabrera	Moderately regulated	Spain	12	7.4	0.52	No	A;B	3	Hackradt <i>et al.</i> 2014

References

- Chapman, M.R. & Kramer, D.L. (1999). Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Mar Ecol Prog Ser* **181**, 81–96.
- Cinner, E. J., J, M.M. & R, M.T. (2005). Judicious use of multiple hypothesis tests. *Conserv Biol* **19**, 261–267.
- Coleman, M.A., Palmer-Brodie, A. & Kelaher, B.P. (2013). Conservation benefits of a network of marine reserves and partially protected areas. *Biol Conserv* **167**, 257–264.
- Curley, B.G., Glasby, T.M., Curley, A.J., Creese, R.G. & Kingsford, M.J. (2013). Enhanced numbers of two temperate reef fishes in a small, partial-take marine protected area related to spearfisher exclusion. *Biol Conserv* **167**, 435–445.
- de Carvalho Teixeira Chaves, L. & Monteiro-Neto, C. (2008). Comparative analysis of rocky reef fish community structure in coastal islands of south-eastern Brazil. *J Mar Biol Ass* **89**, 609–11.
- Di Franco, A., Bussotti, S., Navone, A., Panzalis, P. & Guidetti, P. (2009). Evaluating effects of total and partial restrictions to

- fishing on Mediterranean rocky-reef fish assemblages. *Mar Ecol Prog Ser* **387**, 275–285.
- Forcada, A., Valle, C., Bonhomme, P., Crique, G., Cadiou, G., Lenfant, P. & Sánchez-Lizaso, J. (2009). Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar Ecol Prog Ser* **379**, 197–211.
- Francini-Filho, R.B. & de Moura, R.L. (2008). Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conserv* **18**, 1166–1179.
- Friedlander, A.M., Brown, E.K. & Monaco, M.E. (2007). Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. *Ecol Appl* **17**, 715–730.
- Hackradt, C.W., Garcia-Charton, J.A., Harmelin-Vivien, M., Pérez-Ruzafa, Á., Le Diréach, L., Bayle-Sempere, J., Charbonnel, E., Ody, D., Reñones, O., Sanchez-Jerez, P. & Valle, C. (2014). Response of rocky reef top predators (Serranidae: Epinephelinae) in and around marine protected areas in the Western Mediterranean Sea. *PLoS One* **9**, e98206.
- Harmelin-Vivien, M., Cottalorda, J.-M., Dominici, J.-M., Harmelin, J.-G., Le Diréach, L. & Ruitton, S. (2015). Effects of reserve protection level on the vulnerable fish species *Sciaena umbra* and implications for fishing management and policy. *Global Ecol Conserv* **3**, 279–287.
- 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). *Mar Policy* **72**, 192–198.
- Jupiter, S.D. & Egli, D.P. (2011). Ecosystem-Based Management in Fiji: Successes and Challenges after Five Years of Implementation. *J Mar Biol* **2011**, 1–14.
- La Mesa, G. & Vacchi, M. (1999). An Analysis of the Coastal Fish Assemblage of the Ustica Island Marine Reserve (Mediterranean Sea). *Mar Ecol* **20**, 147–165.
- Link, J., Almeida, F., Valentine, P., Auster, P., Reid, R. & Vitaliano, J. (2005). The Effects of Area Closures on Georges Bank. *Am Fish Soc Symp* **41**, 345–368.
- Mateos-Molina, D., Schärer-Umpierre, M.T., Appeldoorn, R.S. & Garcia-Charton, J.A. (2014). Measuring the effectiveness of a Caribbean oceanic island no-take zone with an asymmetrical BACI approach. *Fish Res* **150**, 1–10.
- McClanahan, T.R., Verheij, E. & Maina, J. (2006). Comparing the management effectiveness of a marine park and a multiple-use collaborative fisheries management area in East Africa. *Aquatic Conserv* **16**, 147–165.
- Miller, R., Williams, B. & Duffy, C. (2005). Reef fish of the Sugar Loaf Islands (Ngā Motu) Marine Protected Area, New Zealand. DOC Research & Development Series 226. Department of Conservation, Wellington. 26 p.
- Monaco, M.E., Friedlander, A.M., Caldow, C., Christensen, J.D., Rogers, C., Beets, J., Miller, J. & Boulon, R. (2007). Characterising reef fish populations and habitats within and outside the US Virgin Islands Coral Reef National Monument: A lesson in marine protected area design. *Fish Manag Ecol* **14**, 33–40.

- Mora, C., Myers, R.A., Coll, M., Libralato, S., Pitcher, T.J., Sumaila, R.U., Zeller, D., Watson, R., Gaston, K.J. & Worm, B. (2009). Management Effectiveness of the World's Marine Fisheries. *PLoS Biol* **7**, e1000131.
- Nardi, K., Jones, G.P., Moran, M.J. & Cheng, Y.W. (2004). Contrasting effects of marine protected areas on the abundance of two exploited reef fishes at the sub-tropical Houtman Abrolhos Islands, Western Australia. *Environ Conserv* **31**, 160–168.
- Rife, A.N., Aburto-Oropeza, O., Hastings, P.A., Erisman, B., Ballantyne, F., Wielgus, J., Sala, E. & Gerber, L. (2013). Long-term effectiveness of a multi-use marine protected area on reef fish assemblages and fisheries landings. *J Environ Manag* **117**, 276–283.
- Smith, M.D., Grabowski, J.H. & Yund, P.O. (2008). The role of closed areas in rebuilding monkfish populations in the Gulf of Maine. *ICES J Mar Sci* **65**, 1326–1333.
- Tetreault, I. & Ambrose, R.F. (2007). Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. *Ecol Appl* **17**, 2251–2267.
- Tupper, M.H. (2007). Spillover of commercially valuable reef fishes from marine protected areas in Guam, Micronesia. *Fish Bull*, 105, 527–537.
- Tupper, M.H. & Rudd, M.A. (2002). Species-specific impacts of a small marine reserve on reef fish production and fishing productivity in the Turks and Caicos Islands. *Environ Conserv* **29**, 484–492.
- Tuya, F., Espino, F. & Haroun, R.J. (2006). Assessment of the effectiveness of two marine reserves in the Canary Islands (eastern Atlantic). *Cienc Mar* **32**, 505–522.

Supporting Information

APPENDIX 2

Statistical outputs of the meta-analysis

WebTable 2.1 Summary of the weighted model of age (years of enforcement), size (log km²) and capacity to implement regulations (Mora *et al.* 2009) on targeted fish species abundance and biomass effect sizes comparing partially protected areas (PPAs) to unprotected areas.

PPA feature	Ecological response							
	Abundance				Biomass			
	Estimate	Lower limit CI	Upper limit CI	P value	Estimate	Lower limit CI	Upper limit CI	P value
Age	0.05	0.03	0.07	<0.0001	0.05	0.02	0.07	0.0001
Size	0.37	0.11	0.63	0.054	0.46	0.16	0.76	0.0026
Implementation	1.43	0.89	1.98	<0.0001	1.65	1.055	2.29	<0.0001

WebTable 2.2 Heterogeneity statistics for the interaction model of the class of the partially protected area (PPA) with the PPA characteristics: age (years), size (log km²), capacity to implement regulations (Mora *et al.* 2009) and the presence of a fully protected area (FPA).

Ecological response						
Interaction of PPA class and PPA feature	Abundance			Biomass		
	Q _m	df	P	Q _m	df	P
Age	11.25	3	0.0104	4.92	3	0.1670
Size	9.9	3	0.0195	5.42	3	0.2096
Implementation Capacity	11.51	3	0.0092	7.37	3	0.0538
FPA presence	22.07	6	0.0005	12.59	6	0.0906