Can marine reserves restore lost ecosystem functioning? A global synthesis

Running head: can reserves restore lost function?

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Abstract

Marine protected areas (MPAs) have grown exponentially, emerging as a widespread tool to conserve biodiversity and enhance fisheries production. Although numerous empirical studies and global syntheses have evaluated the effects of MPAs on community structure (e.g., biodiversity), no broad assessment concerning their capacity to influence ecological processes (e.g., species interactions) exists. Here, we present meta-analyses that compare rates of predation and herbivory on a combined 32 species across 30 MPAs spanning 85° of latitude. Analyzing the fate of 15,225 field experimental assays, we show that MPAs greatly increased predation intensity on animals but not herbivory on macroalgae or seagrass. Predation risk, quantified as the odds of prey being eaten, was largely determined by predator abundance and biomass within reserves. At MPAs with the greatest predator accumulation, the odds of predation increased to nearly 49:1, as opposed to 1:1 at MPAs where predators actually declined. Surprisingly, we also found evidence that predation risk declined with increased sea surface temperature. Greater predation risk within MPAs was consistent with predator and prey population estimates, where predators increased 4.4-fold within MPAs while prey decreased 2.2-fold. For herbivory, the lack of change may have been driven by functional redundancy and the inability of reserves to increase herbivore abundance relative to fished zones in our sample. Overall, this work highlights the capacity of MPAs to restore a critical ecosystem function such as predation, which mediates energy flows and community assembly within natural systems. However, our review of the literature also uncovers relatively few studies that have quantified the effects of MPAs on ecosystem function, highlighting a key gap in our understanding of how protected areas may alter ecological processes and deliver ecosystem services. From a historical perspective, these

findings suggest that modern levels of predation in the coastal oceans may currently only be a

38   fraction of the baseline prior to human exploitation.

Keywords: *consumer, ecosystem function, functional redundancy, herbivory, marine protected*

40   *area, meta-analysis, predation*

Introduction

42   One of the most pervasive and consequential human activities on Earth is the hunting of

animals, particularly large consumers (Diamond 1982, Alroy 2001). This is true in the oceans

44   (Jackson et al. 2001, McCauley et al. 2015), where estimates suggest that fishing has resulted in

the removal of two-thirds of total fish biomass over the last two centuries and a 10-50% decline

46   in predator diversity in the open ocean (Worm et al. 2005, Christensen et al. 2014, Edgar et al.

2014). Whether resulting in local, ecological, or ultimate extinction, the loss of these consumers

48   is a source of widespread concern because consumers can play a critical role in the functioning

of ecosystems by imposing strong direct and indirect effects that can permeate throughout food

50   webs (Estes et al. 2011). Consumer loss may also drive alterations in biogeochemical fluxes

(Schindler et al. 1997), disease prevalence (Lafferty 2004), susceptibility to invasion (Ling et al.

52   2009), and the coexistence of prey (Crooks and Soulé 1999).

The establishment of marine protected areas (MPAs; regions of restricted fishing or no-

54   take) often seeks to maintain the biodiversity and abundance of consumers, while promoting

sustainable fisheries (Gaines et al. 2010). Broad-scale synthetic research in this realm has largely

56   focused on quantifying reserve efficacy based on aggregate metrics and community structure,

evaluating characteristics such as abundance, biomass, size-structure, and biodiversity (Halpern

58   and Warner 2002, Micheli et al. 2004, Lester et al. 2009, Soykan and Lewison 2015). When

combined with natural history knowledge (i.e. functional roles), these metrics can be used to

60   infer ecosystem functioning, assuming that species presence or biomass is positively correlated

with function (Micheli et al. 2014). However, species interactions are subject to context-

62   dependency and behavioral modification, potentially decoupling the linkage between species

presence and ecosystem functioning. For example, grazers may be abundant within a

64   community, but fear of predation may constrain the ability of herbivores to forage on primary

producers, resulting in less than expected rates of herbivory (e.g., Madin et al. 2011). Therefore,

66   direct, process-based quantifications of MPA effects on ecosystem function (e.g., grazing assays

or predation trials) are a necessary complement to observational abundance and biomass

68   estimates. While the latter effects have been synthesized both regionally and globally, to our

knowledge, there has been no direct global test for the consistency of MPA effects ecosystem

70   functioning, despite a considerable body of empirical research highlighting this linkage

(McClanahan and Muthiga 1989, Shears and Babcock 2002, Guidetti 2006). Here, we consider

72   consumer interactions (predation and herbivory) as key components of ecosystem functioning

because they are integrative processes that mediate energy flows, secondary production, and

74   community structure (Jax 2005).

        Species loss from extraction may greatly reduce ecosystem functioning if individual

76   species are unique in fulfilling their respective functional roles within a community, that is, if

marine ecosystems exhibit limited functional redundancy (Bellwood et al. 2003, Micheli and

78   Halpern 2005). In this case, protection within reserves would be expected to increase ecosystem

functioning relative to fished areas, provided that the targeted species recover (Bellwood et al.

80   2003, D'Agata et al. 2016). This is supported by the observation that fishing tends to eliminate

entire functional groups (Micheli and Halpern 2005, Micheli et al. 2014). In contrast, functional

82   redundancy may exist, such that compensatory mechanisms buffer against species loss and the

subsequent reductions in ecosystem function (Walker 1992). For example, on Pacific coral reefs,

84   the loss of large parrotfishes from fishing was partially compensated for by population increases

of small parrotfishes not targeted by fisheries (Bellwood et al. 2012). Here, some ecosystem

86   functions (grazing and sediment removal), were unaffected by fishing, while other functions

(bioerosion and coral predation) were eliminated. This functional redundancy can arise from the

88   'portfolio effect' (Figge 2004), which occurs when ecosystem functions are stabilized because

species abundances within a functional group are asynchronous (Thibaut et al. 2012), in this

90   case, differentially sensitive to disturbances such as fishing removal (Schindler et al. 2015).

        Marine reserve characteristics such as MPA age, size, and enforcement may also

92   influence ecosystem functioning (Halpern 2003, Claudet et al. 2008, Edgar et al. 2014), as these

features are well known to affect the population trajectories and accumulation of biomass for

94   both targeted and non-targeted species (Micheli et al. 2004, Lester et al. 2009, Babcock et al.

2010). Additionally, consumptive activities such as herbivory and predation may be driven by

96   prey taxonomy, habitat structure, predation refuge, and biogeographic features (e.g., latitude,

temperature; Schemske et al. 2009, Ling and Johnson 2012, Poore et al. 2012, Reynolds et al.

98   2018). These characteristics appear to have contributed to variation in empirically measured

predation and herbivory intensity, resulting in context dependent and complex MPA effects on

100   ecosystem functioning (Mislan and Babcock 2008, Cook and Vanderklift 2011, Vergés et al.

2012, Ory et al. 2012, Boada et al. 2015).

102   To determine whether MPAs generally influence ecosystem functioning, we used a meta-

analysis to conduct a global synthesis of MPA effects on two consumption-based processes,

104   predation and herbivory. We address three key questions: (1) What is the global effect of MPAs

on ecosystem functioning (predation and herbivory) in coastal ecosystems? (2) Do MPA

106   characteristics, environmental factors (e.g., temperature and habitat structure), or experimental

procedures explain additional variation in these ecosystem functions? (3) Is greater predation risk

108   supported by patterns of increased predator and decreased prey population estimates?

Methods

Data Sources and Inclusion Criteria

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To identify candidate publications, we searched the Web of Science (Clarivate Analytics,

112   Philadelphia, USA) on 1 April 2018 using the topic keywords: ("marine reserve" or "marine

protected area") AND (herbivor* or graz* or tether* or predat*). For a publication to be included

114   in our meta-analysis it must have satisfied the following criteria: (1) the study conducted a field

experiment explicitly comparing an MPA to a reference fished area and (2) the experiment

116   quantified (e.g., counts of survivors, biomass loss) the fate of an experimentally deployed

resource (e.g., animal prey, seagrass or algae). For each publication that met the above criteria,

118   we also performed backwards and forwards citation searches for additional candidate papers. In

total, we screened 529 publications that measured predation or herbivory intensity within marine

120   ecosystems. Of this pool of candidate publications, we identified 29 unique studies for our meta-

analysis that quantified species interactions in both an MPA and control fished area (Table 1).

122   The predation analysis includes 23 studies measuring consumption on 20 animal species

(echinoids, bivalves, crustaceans, gastropods) residing in 23 MPAs from 43°N to 43°S (Fig. 1,

124   Table 1). The herbivory analysis includes 9 studies assaying 12 primary producers (seagrass and

macroalgae) residing in 14 MPAs from 43°N to 35°S (Fig. 1, Table 1).

126   *Calculation of Effect Sizes*

We analyzed the predation and herbivory data with different effect size metrics because

128   of intrinsic differences in the properties of the data. Most predation studies measured prey

survival where the data was binomial (i.e., prey are alive or dead). Therefore, we extracted these

130   binomial counts from the text, tables, or figures of each publication. In cases when the authors

presented average survival (or mortality), we digitally extracted the mean and estimated the

132   counts by multiplying the mean estimate by the sample size within a given treatment level. This

data extraction approach is accurate when validated against published raw datasets (Cheng and

134   Brandl *in revision*). For each study, we then constructed a 2 x 2 matrix describing prey recovered

as dead or alive from inside or outside of the MPA. From this matrix, we calculated the effect

136   size as the log-odds ratio (OR), which is given as:

$$ln\,(OR) = ln\frac{p_1/(1-p_1)}{p_2/(1-p_2)}$$

138   The numerator is the probability of mortality (p_1) divided by the probability of survival

($1-p_1$) within the MPA. The denominator is the probability of mortality (p_2) divided by the

140   probability of survival ($1-p_2$) in fished areas. If MPAs enhance the probability of prey death (i.e.,

ecosystem function), the log-odds ratio is greater than 0. If MPAs decrease the probability of

142   prey death, the log-odds ratio is less than 0. After calculation of these effect sizes, we used them

in meta-regression described below.

144   Investigators measured the effect of herbivory by deploying algal or seagrass assays and

measuring the loss of tissue or proportion of assays with grazing marks. We calculated herbivory

146   effect sizes utilizing Hedges *d*, a standardized comparison of means with a small sample size bias

correction (Scheiner and Gurevitch 2001). For each predation and herbivory effect size, we

148   paired each MPA site with the nearest control fished site. In instances where there were several

potential control sites of similar distance from the MPA site, we randomly selected a control site.

150   For studies that reported repeated measures of predation or herbivory on the same assay, we

extracted the last measure for analysis. For studies that sampled predation or herbivory within

152   the same MPA but with different assays over time, we extracted all data points.

Predation Modeling

154   In the predation meta-regression, we used eight predictors, including MPA characteristics

(age, size, type, and MPA specific predator response), environmental features (sea surface

156   temperature, habitat), and experimental variables (prey type, availability of refuge). Due to

extensive discussion regarding reserve age and size as correlates of MPA efficacy, we used MPA

158   age (years at time of experimentation) and MPA size (km^2) as predictors of ecosystem function

(Halpern 2003, Claudet et al. 2008, Edgar et al. 2014). We also modeled MPA type (full no-take

160   versus partial reserves that allow limited recreational or commercial fishing). To address the role

of MPAs established in name only ('paper parks'), we used the natural log response ratio of

162   predators in MPA versus fished areas (counts or biomass) as a measure of MPA efficacy and

tested its effect on prey mortality. For four studies lacking this data, we located predator data

164   from other published studies for the same MPAs (all within 2-3 years of measurement of prey

survival; often by the same authors in a different publication). If a paper presented both count

166   and biomass data, we selected biomass because it incorporates an aspect of predator body size,

which can be a determinant of predator-prey dynamics (Cohen et al. 1993).

168   Additional predictors included habitat type (temperate reef, coral reef, soft-sediment),

prey taxon (urchins, lobsters, bivalves, shrimp or gastropods pooled as 'other'). We modeled

170   prey refuge (no cover, algal cover, hard shelter) because investigators varied in the provisioning

of experimental animals with access to *in situ* structural refuge (i.e., hard substrate shelters, algal

172   canopies, or no refuge). We also used temperature to test for biogeographic patterns in ecosystem

function because theory suggests that strong species interaction strengths may be a driver of

174 greater biodiversity in tropical ecosystems (Schemske et al. 2009). We extracted sea surface

temperature from the Bio-ORACLE raster dataset (Tyberghein et al. 2012). Here, temperature

176 was remotely sensed using Aqua-MODIS satellite data at 5 arcminute resolution and was

calculated as the mean temperature from years 2002-2009. We elected to use the mean

178 temperature over this time period because evolutionary hypotheses for stronger consumptive

activities in the tropics invoke long-term climatological explanations for latitudinal gradients in

180 species diversification rates (Mittelbach et al. 2007).

To test whether heightened predation intensity inside of MPAs in our meta-analysis

182 translated to population patterns of known predator and prey pairs, we extracted population

estimates for the subset of studies reporting this data. Here, we hypothesized that MPAs should

184 lead to increased predator populations and concomitant declines in prey populations, relative to

fished areas. To visualize this data, we generated a scatterplot of known predator and prey log

186 response ratios (LnRR; natural log of predator or prey abundance within reserves divided by

their respective abundance at fished sites).

188 *Herbivory Modeling*

Due to data reporting differences, we quantified the effect of MPAs on herbivory with a

190 separate analysis using Hedges *d*, a standardized difference of means (Scheiner and Gurevitch

2001). Because of the limited sample size of herbivory studies, we restricted this analysis to four

192 additive predictors: the change in herbivore abundance within MPAs (LnRR), MPA size, MPA

age, and plant type. As previously discussed, we modeled MPA age and size due to the

194 importance of temporal and spatial processes in mediating MPA response and because

considerable discussion has focused on these features of MPA design to optimize conservation

196   goals. We also included plant type as a predictor because of evidence suggesting phylogenetic

conservatism in marine plant susceptibility to grazing (Poore et al. 2012).

198   *Statistical Analysis*

We used a weighted and unweighted approach to quantify MPA effects on ecosystem

200   function. For the weighted analysis, we used inverse-variance random effect meta-regression

(Cooper et al. 2009). This approach weights effect sizes such that studies with greater variance

202   are weighted less as opposed to studies with less variance that are more heavily used in the

analysis. For the unweighted approach, we used generalized linear mixed models. For both

204   weighted and unweighted analyses, we used a model selection and averaging approach using

AICc to evaluate model performance (Burnham and Anderson 2002). Here, we constructed all

206   possible candidate models with additive predictors because sample size precluded the use of

interaction terms. Both approaches revealed broad agreement in the importance of key predictors

208   (overall MPA effects for predation but not herbivory) but differed with respect to specific

moderator variables (e.g., sea surface temperature and refuge availability; Appendices S1-S3).

210   Therefore, we present the more conservative weighted analyses here and the unweighted

analyses in the supplemental materials (further detail in Appendices S2, S3). In the weighted

212   analysis, we calculated variable importance as the proportion of all models in which a moderator

has been included, weighted by Akaike weight. We then averaged all possible candidate models

214   into one model, for which we extracted parameter estimates and 95% confidence intervals for

comparison across predictors (Burnham and Anderson 2002). To assess the possibility of

216   publication bias that could skew the meta-analysis towards studies with significant results, we

calculated Rosenberg's fail-safe number (Rosenberg 2005). This fail-safe number represents the

218   number of nonsignificant, unpublished studies that would be need to be added to the meta-

analysis to change it from statistical significance to non-significance. We used a threshold fail-

220   safe number of 5n + 10 (n = number of original studies) to determine the potential presence of

publication bias. Prior to analysis, we centered and scaled continuous predictors except for

222   predator and herbivore LnRR. We conducted all analyses within R (version 3.5; R Core Team

2018) using the packages 'metafor', 'glmulti', 'raster', 'lme4', 'MuMin', and 'ggplot2'. We

224   performed graphical data extraction with 'WebPlotDigitizer' version 4.0 (Rohatgi 2017).

Results

226   *Predation*

MPAs had consistent and predictable effects on predation but not herbivory (Figs. 2, 3).

228   For predation, five moderators (Predator LogRR, temperature, habitat, and MPA age, from

highest to lowest) had high variable importance, appearing in greater than 80% of all models

230   (Appendix S1). Of these moderators, only three parameter estimates from the averaged model

deviated from zero. Of greatest variable importance was Predator LogRR, where greater predator

232   accumulation increased predation risk for prey (Fig. 4A, estimate = 0.86, $\pm$95% CI = 0.46, 1.25).

At MPAs with the greatest predator accumulation, the odds of predation were 49:1, as opposed

234   to odds of predation that were essentially 1:1 at MPAs with predator declines as compared to

fished areas. Temperature was the second most important variable, with greater temperatures

236   associated with decreased predation risk for prey (Fig. 4B, estimate = -1.37, $\pm$95% CI = -2.13, -

0.61). Predation risk was also greater on coral reefs (estimate = 2.48, $\pm$95% CI = 1.01, 3.96) as

238   opposed to temperate reefs and soft-sediment systems, but there was no difference between

temperate reefs and soft-sediment systems (Appendix S1). MPA age exhibited high variable

240   importance but did not have a significant effect (estimate = 0.32, $\pm$95% CI = -0.068, 0.72, mean

MPA age = 17.0 years). MPA size, MPA type (full no-take vs. partial), prey refuge availability,

242 and prey taxon did not affect predation risk (Appendix S1). We calculated Rosenberg's fail-safe

number as 10,463 non-significant studies that would need to be added to the meta-analysis to

244 alter the result from statistical significance to non-significance, which vastly exceeds the

threshold number 115 studies, suggesting that publication bias was not present.

246   When considering population level data for predator and prey, the observed increase in

predation risk within MPAs was consistent with greater predator populations (4.4-fold increase

248 on average) and diminished prey populations (2.2-fold decline on average; Fig. 4) for studies

within our meta-analysis. One exception was the La Jolla Ecological Reserve (Loflen and Hovel

250 2010), where both predatory fish and prey lobsters increased within this MPA (Fig. 4; red circle).

Herbivory

252   We located 9 studies that measured herbivory on seagrasses (e.g., *Thalassia* spp.) or

macroalgae (e.g., *Ulva* sp.) in 14 MPA and fished comparisons in temperate and tropical

254 ecosystems (Table 1). In contrast to predation, herbivory was unaffected by MPA age, MPA size,

herbivore LogRR, or plant type (Fig. 3, Appendix S1). This result may be driven by a lack of an

256 herbivore abundance response within these MPAs, which showed little change relative to fished

sites (Appendix S3, herbivore mean LnRR = -0.19).

258 **Discussion**

      The establishment of marine reserves has grown exponentially (Worm 2017) and a wide

260 body of literature has synthesized the effects of MPAs using aggregate community level metrics

such as biodiversity and biomass (Halpern and Warner 2002, Micheli et al. 2004, Lester et al.

262 2009, Soykan and Lewison 2015). In contrast, to our knowledge, there has not been a synthetic

assessment of MPA effects on process-based metrics such as ecosystem functioning, despite

264 some empirical research suggesting cascading effects of predator protection on prey species

(e.g., Edgar et al. 2014). Synthesizing data across a global scale, our findings demonstrate that

266 increased predation intensity within reserves is a general and widespread result arising from

predator accumulation within marine reserves. This clearly reveals that the effects of overfishing

268 on an ecosystem function such as predation are reversible. In turn, population estimates from

reserves within our meta-analysis verify that greater predation intensity leads to community

270 restructuring, with greater predator and diminished prey abundance within reserves. Greater

predation risk for prey residing in MPAs arises because of an increase in predator abundance

272 inside reserves shown here and elsewhere (Lester et al. 2009, Babcock et al. 2010, Edgar et al.

2014) and also because MPAs can increase predator body sizes (Micheli et al. 2004, Lester et al.

274 2009), diminishing the possibility of a prey size refuge. Overall, these results provide evidence

that human induced trophic cascades (Steneck 1998) can at least be partially reversed through the

276 protection of marine predators. Our results indicate that overfishing by humans removes

predators, decreases prey mortality, and thereby allows prey populations to increase. MPAs

278 reverse this process, allowing predators to accumulate, which increases predation intensity and

thereby decreases prey abundance.

280 Our analysis also provides insights into the processes governing ecosystem functioning

within reserves. We found that predation intensity was driven by predator accumulation within

282 reserves (Fig. 4A) but not MPA age or size (Appendix S1). We do not interpret this as evidence

suggesting that MPA age or size are unimportant, given that they are known to be key predictors

284 of differences in community restructuring (Babcock et al. 2010, Edgar et al. 2014). Rather, in

this context, MPA age and size are proxies for the potential for management to alter ecosystem

286 structure and function, whereas predator accumulation is a more direct ecological predictor of

predation risk for prey. This analysis also highlights the fact that MPAs did not always result in

288   greater predator abundance relative to control fished sites; in some cases, predator abundance

actually decreased within MPAs (Fig. 4). A decline of predators within reserves may reflect

290   deficiencies in staffing and financial resources or the establishment of reserves that are legislated

but not enforced ('paper parks'; Gill et al. 2017). In one case, the abundance of both predatory

292   fish and their prey (lobster) increased within the MPA (Fig. 5 red circle; Loflen and Hovel 2010),

a pattern seen in other MPAs (Barrett et al. 2009). Although lobsters experience high predation

294   risk within the reserve, they are targeted by fisheries outside the reserve and their elevated MPA

abundance suggests that fishery impacts outweigh the effect of predation by fishes.

296   At first glance, our finding of decreased predation risk with greater temperature (Fig. 4B)

seems incompatible with the observation of increased predation risk on coral reefs. This is

298   explained by the inclusion of tropical soft-sediment habitat, which reported diminished predation

intensity relative to coral reefs. However, we note relatively fewer tropical studies as compared

300   to work in temperate systems (Table 1, Fig. 1). If the pattern is robust, decreases in predation risk

with greater temperature is consistent with a global analysis of herbivory in marine systems

302   (Poore et al. 2012). One possibility that could explain diminished predation risk at warmer

temperatures is the presence of a seasonal bias in field sampling, where both temperate and

304   tropical studies typically quantified predation risk in warmer months when biological activity

was likely greatest. If temperate systems exhibit more pronounced seasonality than tropical

306   systems, as is the case with other ecological processes such as recruitment (Connolly et al. 2001),

this could produce the observation of decreased interaction strength at warmer temperatures.

308   The lack of an MPA effect on herbivory suggests that this ecosystem function may

exhibit some degree of functional redundancy. This is consistent with other studies that have

310   found compensation for herbivore loss from perturbations (Bellwood et al. 2012, Nash et al.

2016) and evidence for asynchronous responses of herbivores to environmental stochasticity

312   ('response diversity'; Thibaut et al. 2012). In these former cases, herbivores insensitive to the

original perturbations (fishing and heat waves), increased in abundance or biomass, resulting in

314   no change in overall herbivory. In our synthesis, the lack of an herbivory effect is perhaps not

surprising given that our analysis found herbivore abundance was not altered by MPA status (i.e.

316   herbivory density was not different in MPAs or fished sites). This may have been partly driven

by the suppression of herbivorous prey by the recovery of predators. However, it is unclear why

318   we did not observe lower herbivore abundances as seen in several well studied marine reserves

(Babcock et al. 2010). The herbivore abundance signal may have been further masked because

320   not all herbivores are harvested and some experience differential susceptibility to predation

(Mumby 2006). One possibility is that these MPAs were of insufficient age to allow for

322   herbivores to recover. However, this seems unlikely because prior work identified an average of

13.1 years to initial detection of indirect effects (Babcock et al. 2010), whereas the average MPA

324   age for herbivory studies within our analysis was 19.3 years. Overall, given the limited number

of studies quantifying herbivory in MPAs and fished zones, we interpret the lack of an herbivory

326   effect with caution and suggest further evaluation is needed to assess functional redundancy.

The vast majority of MPA research has focused on evaluating reserve effects on

328   aggregate metrics and community structure. Although this focus has been critical in establishing

biological baselines and documenting reserve efficacy, we suggest a path forward in MPA

330   research that complements these metrics with assessments of ecosystem function, in order to

provide an understanding of the ecological mechanisms underlying management outcomes.

332   While we found general evidence for higher predator abundances within MPAs that increased

predation intensity and depleted prey populations, the multifaceted nature of predator-prey

334   interactions may drive the emergence of complex non-linear ecological responses. For example,

predator accumulation may increase the potential for intraguild predation, thereby reducing

336   consumptive pressure on prey at lower trophic levels (Polis et al. 1989). Depleted prey

populations may also experience relief from consumption pressure depending on the shape of

338   predator functional responses and the diversity of prey species. While consumptive processes

mediate energy flows and biomass production, other ecosystem functions may be altered within

340   MPAs, such as calcification and bioerosion that can govern the construction of habitat structure

(Bellwood et al. 2003, 2012, Davidson et al. 2018). Yet, our understanding of MPA effects on

342   these ecological processes and overall ecosystem multifunctionality is minimal. This is

surprising, given that biodiversity conservation is a major goal of MPA establishment and the

344   broad evidence linking biodiversity and ecosystem function (Cardinale et al. 2006).

        From a historical perspective, our results imply that modern predatory interactions in the

346   sea may currently be a small fraction of the baseline prior to overfishing. Evidence from the

fossil record and comparisons to extant species indicate an escalation of predation intensity from

348   the Jurassic until the recent past (Vermeij et al. 1981, Aronson 1987). This escalation, or enemy

driven evolution, is characterized by enhanced power of predators and defensive traits of prey

350   (Vermeij 2013). However, the global-scale extraction of predator biomass by humans in recent

centuries (Edgar et al. 2014, Christensen et al. 2014) appears to have rapidly reversed this trend

352   and caused radically altered predation dynamics in the coastal oceans (Jackson et al. 2001). This

suggests that modern investigations of ecological processes in fished habitats may reflect greatly

354   skewed trophic structure, with fewer predators and potentially more prey (Duffy 2003).

Therefore, caution is required when using modern ecological processes to infer the mechanisms

356   that gave rise to existing biological phenomena. For example, stronger species interaction

strengths in the tropics has been invoked to partly explain the latitudinal diversity gradient

358   (Schemske et al. 2009). Where key predatory species in marine communities have been

extirpated by fishing, measuring interaction strengths may greatly underestimate the importance

360   of predators with a geographic bias according to habitats and regions that have been more

heavily fished. The corollary is that in addition to their role in restoring marine species and

362   ecosystem function, MPAs may be a useful means of gaining insight into the ecological and

evolutionary dynamics that gave rise to biodiversity in the sea.

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Table 1. Summary of studies included in the meta-analysis of MPA effects on predation and
600   herbivory. '#' is the MPA number mapped in Fig. 1. 'Year' refers to the year that the MPA was
established. 'Age' is years of MPA establishment at the time of study. Multiple years are
602   reported if there were multiple studies at different times. We preferentially used year and area
data that was provided by the authors, however if this data was unreported, we digitally extracted
604   the area using manuscript figures or park maps.

#	Country	MPA	Year	Age	Km²	Resource	Species	Citation
1	Australia	Armstrong Bay Sanctuary Zone	2007	4	0.82	alga	*Ulva* sp.	Ferguson et al. 2017
2	Australia	Crayfish Point Marine Reserve	1971	29	0.58[a]	urchin	*Heliocidaris erythrogramma*	Pederson and Johnson 2006
				33		urchin	*Centrostephanus rodgersii*	Ling et al. 2009
3	Australia	Green Island Sanctuary Zone	2007	4	0.92	alga	*Ulva* sp.	Ferguson et al. 2017
4	Australia	Kingston Reef Sanctuary Zone	1988	17	1.29[a]	urchin	*Heliocidaris erythrogramma*	Cook and Vanderklift 2011
						urchin	*Centrostephanus tenuispinus*	Cook and Vanderklift 2011
						snail	*Turbo intercostalis*	Cook and Vanderklift 2011
						snail	*Turbo torquatus*	Cook and Vanderklift 2011
5	Australia	Maria Island Marine Reserve	1992	9	7.2[a]	urchin	*Heliocidaris erythrogramma*	Pederson and Johnson 2006
				12		urchin	*Centrostephanus rodgersii*	Ling et al. 2009, Ling and Johnson 2012
6	Australia	Moreton Bay Marine Park	1997	17	5.26	seagrass	*Sargassum flavicans*	Yabsley et al. 2016
						alga	Unidentified algal turf	Yabsley et al. 2016
7	Australia	Parker Point Sanctuary Zone	1998	23	0.89	alga	*Ulva* sp.	Ferguson et al. 2017
8	Belize	Glover's Reef Atoll	1995	13	70.8	urchin	*Echinometra viridis*	McClanahan et al. 2011

						seagrass	*Thalassia testudinum*	McClanahan et al. 2011
9	Chile	Caleta Totoral Managed Area	na	na	na	shrimp	*Rhynchocinetes typus*	Ory et al. 2012
10	Chile	El Frances Managed Area	na	na	na	shrimp	*Rhynchocinetes typus*	Ory et al. 2012
11	Chile	Punta Choros Managed Area	na	na	na	shrimp	*Rhynchocinetes typus*	Ory et al. 2012
12	France	Banyuls MPA	1974	31	0.65	seagrass	*Posidonia oceanica*	Prado et al. 2008
13	France	Cap Roux MPA	2003	4	4.1[a]	urchin	*Paracentrotus lividus*	Seytre et al. 2013
						urchin	*Arbacia lixula*	Seytre et al. 2013
14	France	Port-Cros MPA	1963	44	12.8	seagrass	*Posidonia oceanica*	Prado et al. 2008
15	Italy	Torre Guaceto Marine Reserve	1992	11	22.2	urchin	*Arbacia lixula*	Guidetti 2006
						urchin	*Paracentrotus lividus*	Guidetti 2006
16	Kenya	Kisite Marine Park	1978	18, 26	10	urchin	*Echinometra viridis*	McClanahan et al. 2006
17	Kenya	Malindi Marine Park	1968	20	213[a]	urchin	*Echinometra mathaei*	McClanahan and Muthiga 1989
						seagrass	*Thalassia hemprichii*	McClanahan 2008
18	Kenya	Mombasa Marine Park	1995	11	210[a]	urchin	*Tripneustes gratilla*	Eklöf et al. 2009
			20, 11			seagrass	*Thalassia hemprichii*	McClanahan 2008, Eklöf et al. 2009
			11			seagrass	*Thalassodendron ciliatum*	Eklöf et al. 2009
19	Kenya	Watamu Marine Park	1968	20, 35	10[a]	urchin	*Echinometra mathaei*	McClanahan and Muthiga 1989, Eklöf et al. 2009

				35		urchin	*Tripneustes gratilla*	Eklöf et al. 2009
				20, 35		seagrass	*Thalassia hemprichii*	McClanahan 2008, Eklöf et al. 2009
20	New Zealand	Leigh Marine Reserve	1976	17, 23	5.5	urchin	*Evechinus chloroticus*	Shears and Babcock 2002, Cole and Keuskamp 1998
				23		lobster	*Jasus edwardsii*	Mislan et al. 2008
				21		bivalve	*Dosinia subrosea*	Langlois et al. 2006
21	New Zealand	Tawharanui Marine Park	1982	17	3.5	urchin	*Evechinus chloroticus*	Shears and Babcock 2002
				17		lobster	*Jasus edwardsii*	Mislan et al. 2008
				21		bivalve	*Dosinia subrosea*	Langlois et al. 2006
22	Spain	Cabrera National Park	1991	16	68.3[a]	urchin	*Paracentrotus lividus*	Vergés et al. 2012
				16		alga	*Cystoseira amentacea*	Vergés et al. 2012
23	Spain	Graciosa Marine Reserve	1990	12.7[b]	707	urchin	*Diadema antillarum*	Clemente et al. 2011
24	Spain	La Palma MPA	1996	12.7[b]	37.2	urchin	*Diadema antillarum*	Clemente et al. 2011
25	Spain	Mar de Las Calmas	1991	12.7[b]	7.8	urchin	*Diadema antillarum*	Clemente et al. 2011
26	Spain	Medes Islands MPA	1983	22	0.73	bivalve	*Mytilus galloprovincialis*	Ruis and Zabala 2008
				17, 28		urchin	*Paracentrotus lividus*	Hereu et al. 2005, Verges et al. 2012, Boada et al. 2015
				11		lobster	*Palinurus elephas*	Diaz et al. 2005
				22		seagrass	*Posidonia oceanica*	Prado et al. 2008

				25		alga	*Cystoseira mediterranea*	Vergés et al. 2012
27	Spain	Menorca MPA	1999	9	27.5	urchin	*Paracentrotus lividus*	Vergés et al. 2012
						alga	*Cystoseira stricta*	Vergés et al. 2012
28	USA	Catalina Marine Science Center Reserve	1988	22	0.13	urchin	*Mesocentrotus franciscanus*	Selden et al. 2017
						urchin	*Strongylocentrot us purpuratus*	Selden et al. 2017
29	USA	La Jolla Ecological Reserve	1973	33	2.2	lobster	*Panulirus interruptus*	Loflen and Hovel 2010
30	USA	Florida Keys Protection Areas	1997	7	0.39	seagrass	*Thalassia testudinum*	Kramer and Heck 2007
						alga	*Acanthophora spicifera*	Kramer and Heck 2007
						alga	*Laurencia papillosa*	Kramer and Heck 2007

Notes:

606   a – MPA area estimated with published map and image analysis software

b – data reported in aggregate form, mean MPA age used

608   na – not available, MPA age or boundaries not given and not available in MPA Atlas

Figure Legends

Figure 1. Global coverage of studies that measured predation or herbivory in MPAs and control

fished sites. Numbers refer to MPAs listed in Table 1.

Figure 2. Predation forest plot depicting individual study effect sizes (log odds ratios $\pm$95% CI).

Studies are ranked in order (top to bottom) of increasing mean effect size. Sample size for

each study is given at right (e.g., number of tethered prey).

Figure 3. Herbivory forest plot depicting individual study effect sizes (Hedges d $\pm$95% CI).

Studies are ranked in order (top to bottom) of increasing mean effect size. Sample size for

each study is given at right (e.g., number of algal or seagrass assays).

Figure 4. Meta-analytic scatterplots of effect sizes as a function of predator accumulation within

MPAs and sea surface temperature. Positive log-odds ratios indicate increased predation risk

for prey within MPAs whereas negative values indicate decreased predation risk. Point

estimates are weighted by size (i.e. larger symbols have greater weight because of less

variance). Model predictions and 95% confidence intervals are from the top performing

model. (A) Predation risk increases with greater predator accumulation within MPAs

(positive values of predator logRR). (B) Predation risk within MPAs decreases at higher sea
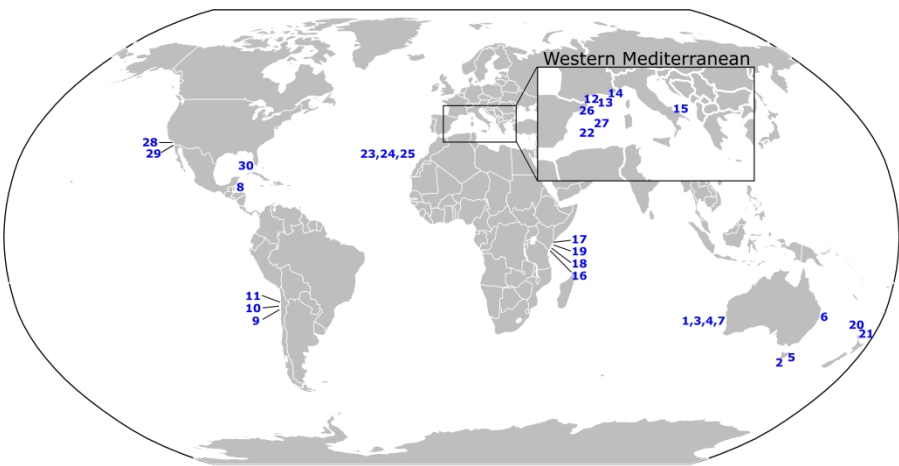
surface temperatures.

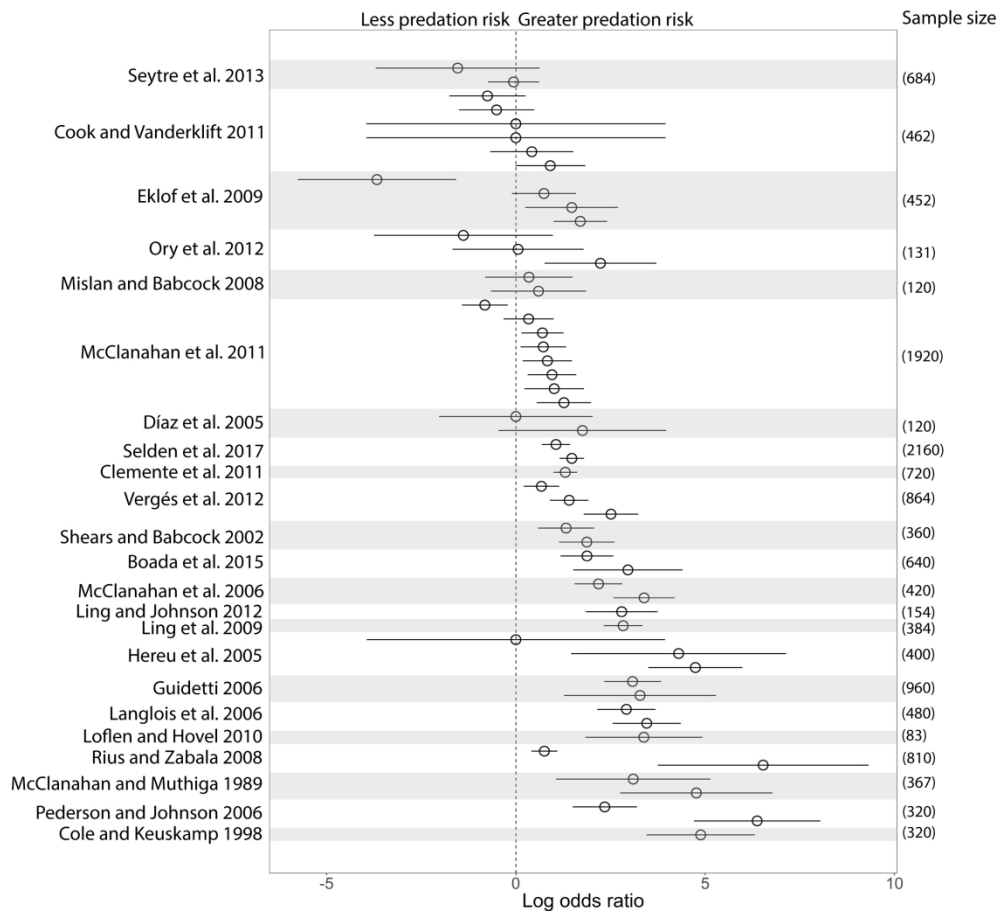**Figure 5.** The effect of MPAs on the abundance of known predator-prey pairs. Positive values

indicate that the population increased within the reserve whereas negative values indicate a

decrease. In most cases, predator populations increased whereas prey populations declined.

Global coverage of studies that measured predation or herbivory in MPAs and control fished sites. Numbers refer to MPAs listed in Table 1.

Predation forest plot depicting individual study effect sizes (log odds ratios +95% CI). Studies are ranked in order (top to bottom) of increasing mean effect size. Sample size for each study is given at right (e.g., number of tethered prey).

218x202mm (300 x 300 DPI)
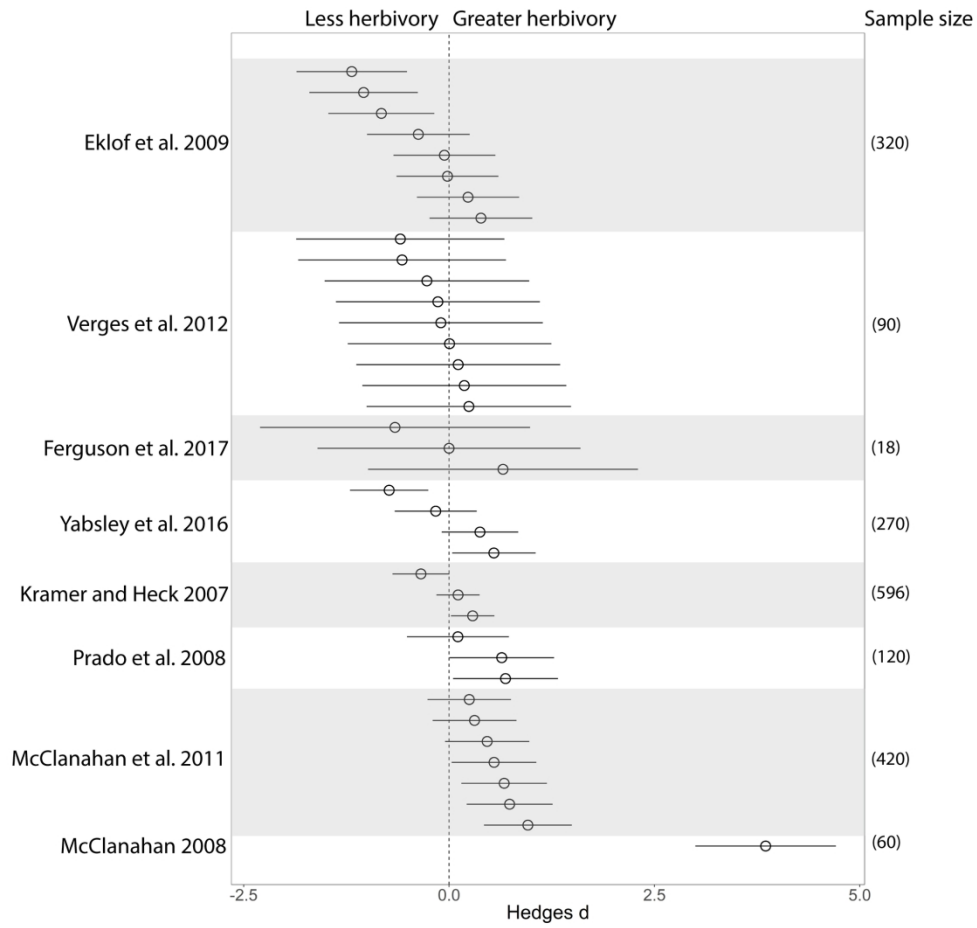
Herbivory forest plot depicting individual study effect sizes (Hedges d +95% CI). Studies are ranked in order (top to bottom) of increasing mean effect size. Sample size for each study is given at right (e.g., number of algal or seagrass assays).

189x177mm (300 x 300 DPI)
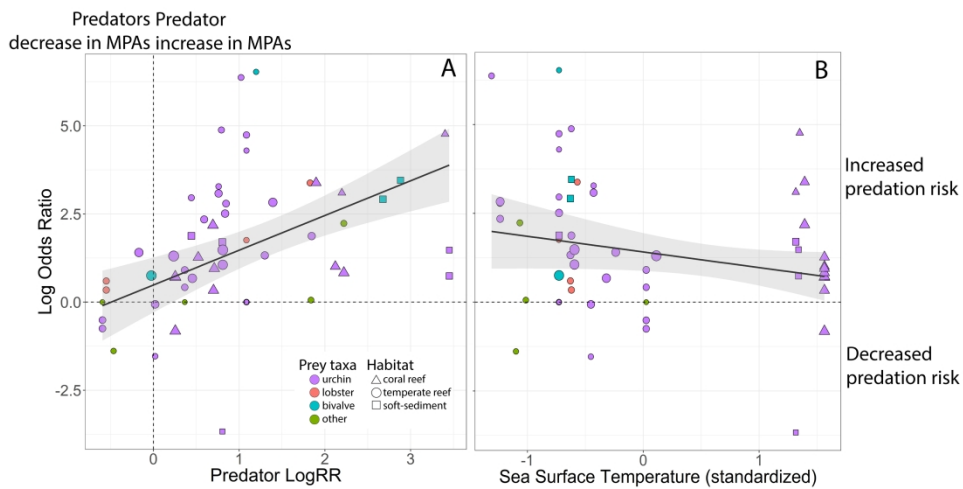
Meta-analytic scatterplots of effect sizes as a function of predator accumulation within MPAs and sea surface temperature. Positive log-odds ratios indicate increased predation risk for prey within MPAs whereas negative values indicate decreased predation risk. Point estimates are weighted by size (i.e. larger symbols have greater weight because of less variance). Model predictions and 95% confidence intervals are from the top performing model. (A) Predation risk increases with greater predator accumulation within MPAs (positive values of predator logRR). (B) Predation risk within MPAs decreases at higher sea surface temperatures.

321x158mm (300 x 300 DPI)
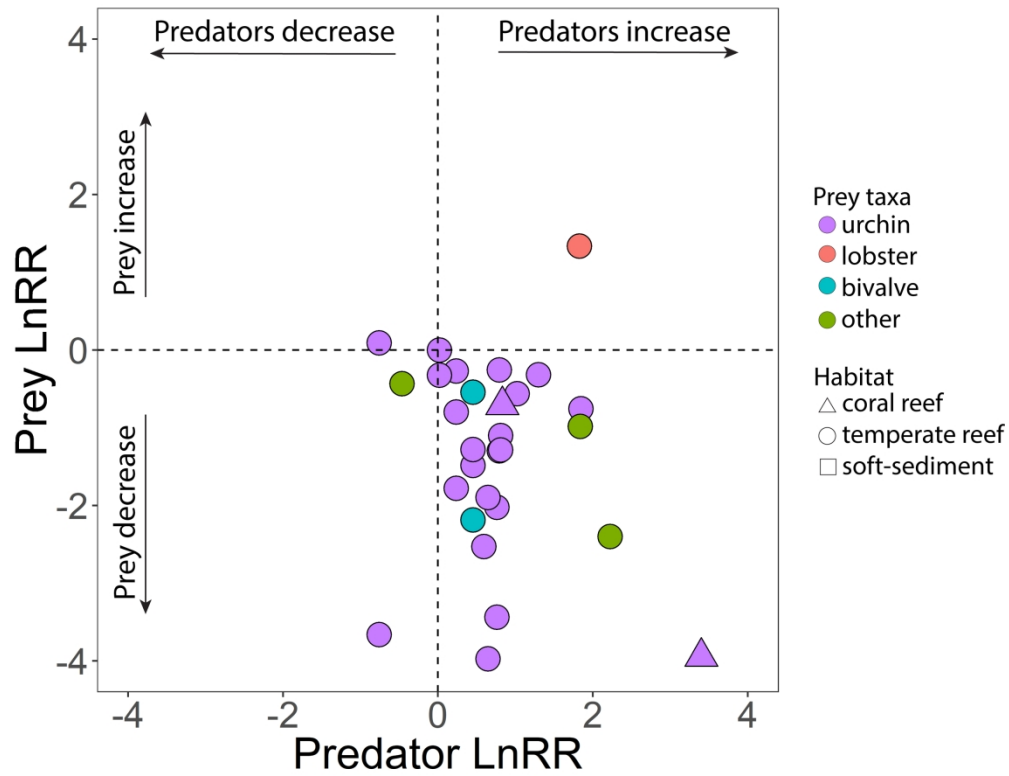
The effect of MPAs on the abundance of known predator-prey pairs. Positive values indicate that the population increased within the reserve whereas negative values indicate a decrease. In most cases, predator populations increased whereas prey populations declined.

242x189mm (300 x 300 DPI)