Global Ecology and Conservation 2 (2014) 289–299

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Review paper

Meta-analysis indicates habitat-specific alterations to primary producer and herbivore communities in marine protected areas

Ben L. Gilby *, Tim Stevens

Griffith School of Environment and Australian Rivers Institute - Coasts and Estuaries, Griffith University, Gold Coast Campus, QLD 4222, Australia

ARTICLE INFO

Article history:
Received 8 October 2014
Accepted 10 October 2014
Available online 27 October 2014

Keywords:
Meta-analysis
MPAs
Fishing
Trophic cascades
Herbivores
Macroalgae

ABSTRACT

Understanding changes in trophic group interactions following the implementation of marine protected areas (MPAs) is critical in understanding their success, or otherwise. A systematic review and meta-analysis was used to determine trends in the effects of MPAs on primary producers and herbivores from 57 locations throughout the world. On coral reefs, macroalgal coverage and sea urchin density were significantly ($p < 0.05$) lower within MPAs, with 79% and 83% of MPAs reporting smaller populations of these groups, respectively. Conversely, in kelp/algal habitats, where habitat-forming macroalgae are beneficial, no statistical differences were found in either algal coverage or herbivore density, however, 70% of MPAs reported lower densities of urchins. Finally, we found that the literature conveyed a significant negative relationship between grazer density effect sizes and macroalgal coverage effect sizes. Our results indicate that the tropho-dynamics of recovering fish populations in disparate habitats is likely to be more complex than initially thought, and partly driven by differential fisheries and habitat effects. This study highlights the importance of selecting MPAs based on the processes that assist in the recovery of ecosystems in the aftermath of fishing, in addition to habitat quality and representativeness.
© 2014 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/3.0/).

Contents

1. Introduction 290
2. Material and methods 290
3. Results 292
   3.1. Included papers 292
   3.2. MPA characteristics 292
   3.3. Primary producers 293
   3.4. Herbivores 294
   3.5. Trophic cascades 295
4. Discussion 295
Acknowledgements 297
Appendix A. Supplementary data 297
References 297

* Corresponding author. Tel.: +61 4 23507003.
E-mail address: b.gilby@griffith.edu.au (B.L. Gilby).

http://dx.doi.org/10.1016/j.gecco.2014.10.005
2351-9894/© 2014 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/3.0/).

1. Introduction

The design, development and implementation of marine protected areas (MPAs) aim to address human-induced and natural alterations to marine habitats and biodiversity, especially overfishing and associated cascading effects on biodiversity and reduced resilience to natural disturbances (Kelleher, 1999; Ballantine and Langlois, 2008; Game et al., 2009; Steneck et al., 2009; Graham et al., 2011). Historically, management of MPAs has largely been by restricting extractive activities, principally fishing, through complete bans within designated "no-take" areas. The establishment of MPAs primarily aims to facilitate the recovery of habitats towards a more resilient and biodiverse state, and to protect areas that represent the range of identified habitats (Stevens, 2002; Leslie, 2005). Further fishery and ecosystem functioning benefits arise from this primary aim (Stevens, 2002; Almany et al., 2009; Coleman et al., 2011).

Most commonly, predatory fishes are the targets of fishing (Pauly, 1998; Kellner et al., 2010; Madin et al., 2010; Mumby et al., 2012). Top-down trophic restructuring suggests that MPAs should aid in restoration towards the pre-impacted state (or at least to a more resilient and biodiverse assemblage; Hughes et al., 2007a; Pressey et al., 2007; Lester et al., 2009). This trophic cascade allows the return of predatory fish populations, which increases predation pressure on herbivores and indirectly relieves herbivory pressure on primary producers (Shears and Babcock, 2002; Duffy, 2003; Mumby et al., 2006; Hughes et al., 2007b). Primary producer groups, especially macroalgae, react strongly and quickly to changes in abiotic and biotic factors, meaning community composition can change and biomass can increase rapidly (Shears et al., 2008; Anderson et al., 2009; Fulton et al., 2014). Such lifecycles and interactions make them an ideal indicator group in assessments of MPA effectiveness.

However, different ecosystems react differently to the formation or reversal of trophic cascades (Micheli et al., 2004a; Borer et al., 2005; Knight et al., 2005). For example, reductions in urchin populations on subtropical and temperate rocky reefs following the return of predators result in the return of habitat forming algae, (especially kelps, e.g. McClanahan, 1995a; Micheli et al., 2005; Babcock et al., 2010). Predator removal also impacts herbivore populations on coral reefs, resulting in varied impacts on macroalgal abundance, depending on fishing pressures, herbivore community structure and individual trophic relationships (Mumby, 2006; Mumby and Harborne, 2010; McClanahan, 2014). For example, on coral reefs, phase shifts to macroalgal dominance occur when overall herbivore biomass (fish and urchins) decreases below a threshold (Hughes et al., 2007b) and may be influenced by the direct removal of herbivores by targeted fisheries (Mumby and Harborne, 2010; Mumby et al., 2012). Due to these important differences in how different ecosystem types are likely to react to MPA implementation, there are likely to be dangers in inferring protection effects across ecosystems (Babcock et al., 2010). For example, urchin dominated grazing (in kelp forests) and combined urchin and fish grazing (on coral reefs) should not be viewed as equal in nature, scale or relative importance (McClanahan et al., 2002; O'Leary and McClanahan, 2010).

Quantitative meta-analytical review approaches have been applied extensively to trophic interactions in terrestrial areas (e.g. Hillebrand, 2002; Shurin et al., 2002), but are yet to be applied specifically to trophic structure in MPAs, despite meta-analyses assessing the efficacy of MPAs (e.g. Micheli et al., 2004b; Maliao et al., 2009; Molloy et al., 2009; Huijbers et al., 2014) and traditional reviews on overall MPA and fishery impacts on trophic interactions (e.g. Valentine and Heck, 2005; Salomon et al., 2010). Therefore, we carried out a quantitative review and meta-analysis on the effects of MPAs on the two lowest trophic levels (primary producers and herbivores) to examine global trends (sensu Babcock et al., 2010, as opposed to time series) in trophic sequences and to support future management decisions. Specifically, we aimed to:

- Quantify the effect of MPA implementation on primary producers and herbivores (including key fish families and urchins), given the trophic alterations that occur within MPAs and the importance of these groups in habitat recovery,
- Determine differences in MPA responses between coral reef and kelp habitats and;
- Identify critical gaps in the literature pertaining to primary producers and herbivores within MPAs, from ecological and methodological points of view.

In this study, we use the means and 95% confidence intervals (CIs; calculated from random effects meta-analysis models) surrounding individual trophic or niche groups collated from numerous studies, which increases the accuracy and global generalisation of effect sizes. Using 95% CIs provides a conservative estimate of MPA effectiveness over global and habitat scales (Payton et al., 2000). MPA design for different benthic habitat types, for example between coral reefs and hard substrate algal habitats, demands sophisticated understanding of relevant trophic cascades and rates of herbivory. Given the changes in trophic relationships resulting from the implementation of no-take MPAs, and the importance of these processes in habitat restoration, we expect differing habitats to exhibit differing interactions between primary producers and herbivores according to benthic habitat type and desired habitat goals (e.g. higher macroalgal coverage in kelp habitats and lower macroalgal cover on coral reefs; (Guidetti, 2006; Mumby et al., 2006).

2. Material and methods

Full methodological approaches and justifications can be found in the supplementary material (Appendix A). We used a systematic review process (Pullin and Stewart, 2006) to access peer reviewed sources (journal articles and postgraduate theses), for potential inclusion in the study. Appendix A provides detailed information regarding databases and search terms

used during this process. Studies were included in the final meta-analysis database only if they met **all** of the following criteria:

- Article published online prior to the 24th October 2012.
- MPA reported as a well-enforced, complete no-take MPA.
- Study design reported appropriate MPA control/impact site data.
- Data represents a single, contiguous MPA (i.e. not combined data from multiple MPAs), with protection being uninterrupted across the entire protection duration.
- For primary producer data: primary producer groups reported macroalgal percent cover data derived from either line intercept transect or quadrat-based surveys.
- For herbivore data: Herbivore abundance given as density (individuals per unit area) derived from underwater visual census (UVC) transect surveys for fish communities and UVC transect or quadrat-based surveys for urchin populations. Herbivore groups included were the fish families Acanthuridae, Kyphosidae, Siganidae and Pomacentridae, subfamily Scarinae (Labridae) and all urchin species.
- Calculations of variance (SE or SD) for each of the above metrics along with sampling effort (e.g. number of transects, quadrats) explicitly provided. Survey units were considered to be at the level of transect or quadrat as opposed to MPA or control site.

The weighting factor chosen in our meta-analysis weights studies according to sampling effort. To prevent the trivialisation of the smaller, more numerous datasets in the analysis, studies with $n > 250$ were excluded due likely non-independence of replicates at small spatial scales and exceedingly large weightings in analyses. This resulted in only two studies being excluded from each of the primary producer and herbivore datasets. All four excluded articles were conducted with very high replication ($n < 400$), whilst all others were below $n = 250$, thus $n = 250$ was chosen.

Information regarding MPA latitude, size and age was also recorded. Study extent was recorded as the area surveyed within MPAs under the assumption that surveys encompassing a larger area are likely to be more accurate indicators of individual MPA effects.

Where a study included more than one MPA or reported on different trophic groups within MPAs, these were considered as separate evaluations. This allowed us to account for the varied ways of separating results, especially for fish, which were represented by multiple families. All analyses were conducted at this 'evaluation' level. Therefore, we had notionally four sets of analyses: herbivorous fishes in coral reefs, herbivorous fishes in kelp/algal habitats, urchins in coral reefs, and urchins in coral/algal habitats. Typically, when multiple families were reported within an MPA, these were from the same replicate transect/quadrat etc. and were not a replicate from a different part of the MPA (e.g. differing distances to MPA borders). As evaluations were not strictly independent in these cases, we also conducted meta-analyses on individual fish families as well as when all herbivores were reported.

Meta-analyses were carried out using Metawin v2.1 software (Rosenberg et al., 1999) using the log response ratio effect size metric ($\ln \mathrm{RR} = \ln$ (mean inside MPA measure/mean outside MPA measure)) and a random effects model approach (which assumes differences as a result of natural variations, as opposed to observed error, and combines both information regarding within and between studies variances; (Rosenberg et al., 1999)). Ln RR sampling variance is calculated by:

$$V_{\ln RR} = \frac{(S^E)^2}{N^E(\bar{X}^E)^2} + \frac{(S^C)^2}{N^C(\bar{X}^C)^2}$$

where $v_{\ln RR}$ is the variance about ln RR, N^E and N^C are the sample sizes of the experiment (MPA, in this case) and control respectively, and S^E *and* S^C are the standard deviations of the experiment and the control, respectively (Hedges et al., 1999).

Random effects models calculate a weighting $w_{i(rand)}$ for each study by:

$$W_{i(rand)} = \frac{1}{V_i + \sigma^2_{pooled}}$$

where the term *rand* indicates the use of a random effects model, V_i is the within-study variance of i and σ^2_{pooled} is the between-study variance. This weighting system is well accepted in the meta-analytical literature, and other studies have used such an approach for similar data (e.g. Molloy et al., 2009; Vandeperre et al., 2011).

In our analyses, a positive effect size (positive ln RR) indicates MPAs have either a larger population of herbivores or greater macroalgal coverage than the controls, whereas negative effects size indicates values less than the controls. Meta-analytical effects are considered statistically significant ($p < 0.05$), either positively or negatively, if the 95% confidence intervals (CIs) do not contain zero (e.g. Hedges, 1982; Thomsen et al., 2012). Data using before–after-control-impact paired series (BACIPS; Underwood, 1991; Osenberg et al., 1994) study designs were unfortunately rarely implemented in included studies. This lack of BACIPS design means that increases or decreases in population size cannot be inferred over time and that interpretation of results was focused on differences between MPAs and fished sites along a spatial scale, rather than axes of recovery or trajectories through time. Further, caution should be taken in interpreting global trends from meta-analytical datasets due to the difficulties in inferring effects from studies using disparate methods. Although we endeavour to control for methodological differences in our inclusion criteria, conclusions should be made conservatively.

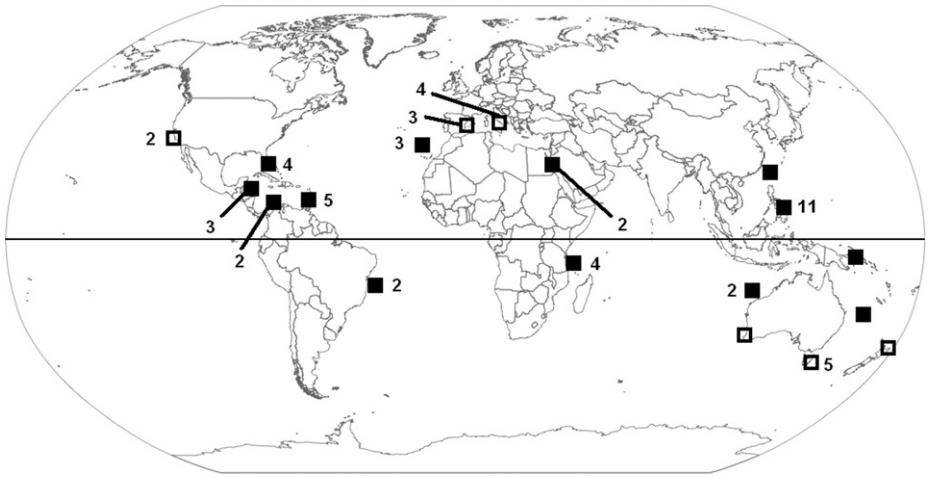

Fig. 1. Locations of included MPAs ($n = 57$). Closed boxes indicate coral reef habitats and open boxes indicate kelp/algal habitats. Numbers indicate the number of included MPAs within those symbols, with no number indicating a single MPA.

The presence of publication bias (the tendency for statistically significant studies to be preferentially published over papers with non-significant results) was estimated by the use of funnel plots, Kendall's tau (where $p < 0.05$ indicates potential bias) and Rosenthal's failsafe method in Metawin (Rosenberg et al. 1999). Relationships between effect size and reserve size or study extent, as well as relationships between primary producers and herbivores (when both are reported), were determined by un-weighted regression. Previous studies have indicated significant differences in the protection duration required for detecting differences in different types of organisms in recovering MPAs (Babcock et al., 2010; McClanahan, 2014). Therefore, MPA age was binned to enable a fully factorial analysis of variance (ANOVA) design assessing herbivore type (coral reef herbivorous fishes, coral reef urchin and kelp/algal urchin) by protection duration (classed as short (1–5 years), medium (5–10) and long (>10) durations). These analyses were conducted on unweighted Log10 transformed Ln RR to homogenise variances in IBM SPSS (v20.0.0).

3. Results

3.1. Included papers

Fifty-five searches were performed using scientific databases and 50 searches were conducted using web search utilities, resulting in a total of 476 papers considered for potential inclusion. Of these, 41 individual publications, representing 57 MPAs worldwide (Fig. 1) satisfied all the criteria for inclusion in the analyses. Studies were primarily omitted because;

- there were no appropriate control sites (118 publications),
- there were no data for our focal taxonomic groups (70), or
- sampling techniques were not quadrats or transects (68).

In total, 36 out of the 41 total publications directly addressed differences between MPAs and matching non-MPAs in their title or aims. Included papers could be broadly grouped into kelp/algal or coral reef habitats. See Appendix B for the full list of included articles.

3.2. MPA characteristics

The average age of included MPAs was 11.97 years (±1.05 years SE) with the youngest reserve having been protected for only 0.5 years (Basak, Philippines) and the oldest for 49 years (Exuma Cays, Bahamas) at the time of survey. Average MPA size was 2091 ha (±765 SE). The majority of MPAs were located in the northern hemisphere (44 north vs 13 south) and more coral reef habitats (41 MPAs for 70 total evaluations) were included in the analysis than kelp/algal habitats (16 MPAs for 30 total evaluations).

No significant effect was found for study extent (MPA survey area), MPA size or MPA age on primary producer ln RR ($p > 0.05$, Table 1), so these were excluded from subsequent analyses and were not accounted for by weighting factors. However, regression analyses showed an effect of MPA age on ln RR ($p = 0.006$, Table 1, Fig. 2) for herbivores. To further disentangle this significant relationship, a two-factor ANOVA (herbivore type (coral reef fishes/urchins) by MPA age in three age classes) was conducted. No significant effect was found for MPA age ($p = 0.8$, Table 2) on ln RR, as well as no interaction between herbivore type and MPA age ($p = 0.17$). However, a significant effect of herbivore type ($p = 0.001$) was present. Given the lack of an interaction between MPA age and herbivore type within our dataset, no weighting functions were

Table 1
Unweighted regression results for the effect of study extent (total area surveyed per protected area), marine protected area (MPA) size and MPA age on MPA effects for primary producers (PP) and herbivores.

Test	n	*p*
MPA Age on PP	39	0.28
Study Extent on PP	39	0.98
No Take Area on PP	28	0.99
MPA Age on Herbivores	63	0.01 ($R^2 = 0.12$)
Study Extent on Herbivores	62	0.38
No Take Area on Herbivores	46	0.97

Table 2
Two-factor Analysis of Variance (ANOVA) results for influence of MPA age (short (<5 years), medium (5–10) and long (>10)), and herbivore type (coral reef herbivorous fish, coral reef urchins, kelp/algal urchins) on herbivore ln RR.

Source	Sum of Sq	*df*	Mean Sq	*F*	*p*
Corrected Model	39.79	8	4.97	3.211	0.005
Intercept	22.39	1	22.39	14.459	<0.001
Herbivore Type	22.99	2	11.49	7.424	0.001
MPA Age	0.671	2	0.33	0.21	0.8
Type × MPA Age	10.42	4	2.6	1.68	0.17
Error	80.54	52	1.54		
Total	134.037	61			
Corrected Total	120.338	60			

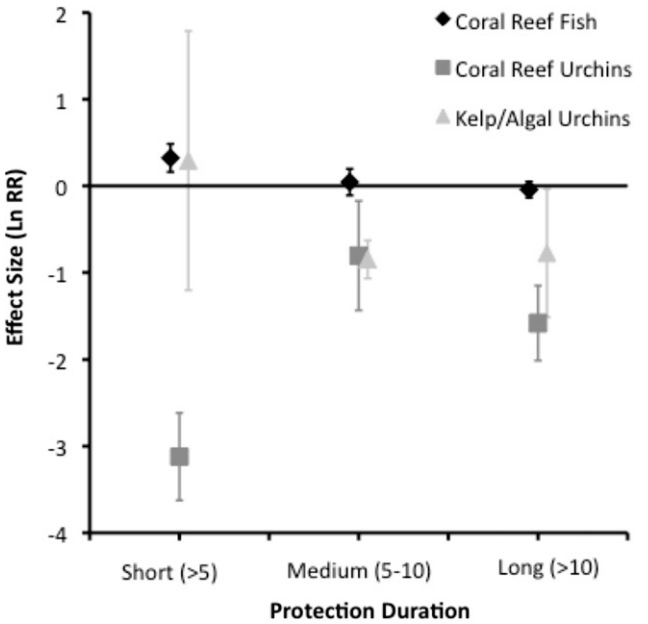

Fig. 2. Mean herbivore ln RR (± standard error) for coral reef fish ($n_{short} = 11$, $n_{medium} = 7$, $n_{long} = 8$), coral reef urchins ($n_{short} = 2$, $n_{medium} = 2$, $n_{long} = 8$) and kelp/algal urchins ($n_{short} = 6$, $n_{medium} = 7$, $n_{long} = 10$). Note that kelp/algal fish was not included as only a single study was recorded in this category. A positive ln RR value indicates a larger population within the marine protected area, and vice-versa for a negative value.

required for MPA age. This result indicates that there is some evidence of protection duration affecting Ln RR when all herbivores are pooled, but no evidence when divided by herbivore type.

3.3. Primary producers

Thirty-nine primary producer evaluations were included (34 coral reef and 5 kelp/algal). There was no statistically significant publication bias in the included primary producer studies (Fig. 3(a), Kendall's Tau, $p = 0.09$, Rosenthal's method= 2650). Primary producer coverage was lower in MPAs than in fished areas (grand mean (combining both coral reef and kelp/algal habitats); $p < 0.05$). This result was reflected on coral reefs (Fig. 4(a), mean $= -0.4581$, 95% CI [−0.6925, −0.2238]), but not in kelp/algal habitats, where no effect was found (95% CI [−0.7433, 0.9656]). Overall, primary producer

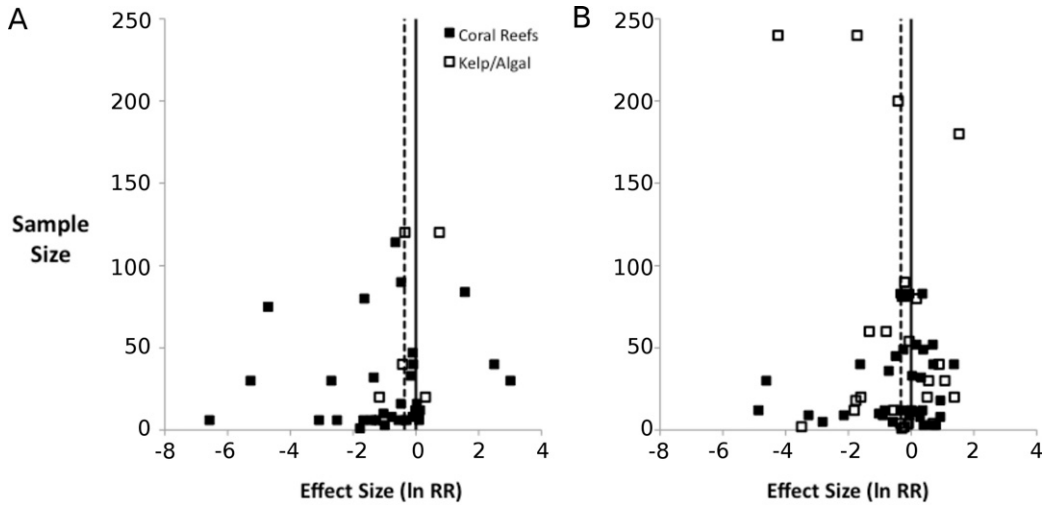

Fig. 3. Funnel plots of (A) all included primary producers and (B) all included herbivore studies. Dashed lines indicate grand mean for the respective groups.

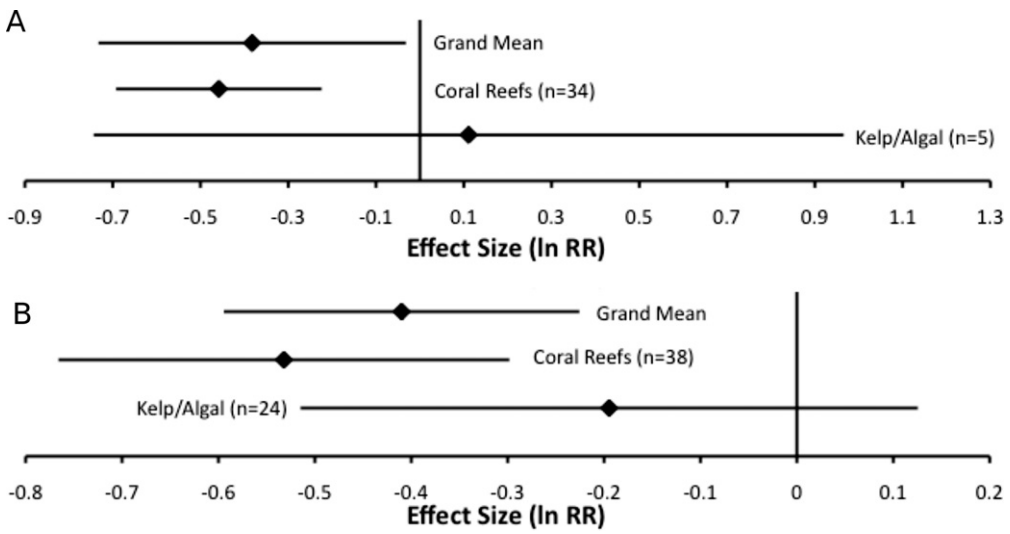

Fig. 4. Primary producer (A) and herbivore (B) grouped mean effect sizes and 95% confidence intervals for kelp/algal and coral reefs, along with the overall grand mean for each.

cover was lower inside MPAs compared to outside in 79% (29 out of 38) of included coral reef MPAs and 58% (14 out of 24) of kelp/algal MPAs.

3.4. Herbivores

Sixty-two herbivore evaluations were included (38 coral reef and 24 kelp/algal). There was no statistically significant publication bias for included herbivore evaluations (Fig. 3(b), Kendall's Tau, $p = 0.89$, Rosenthal's method $= 1551$). Only one study reported differences in fish populations for kelp/algal habitats in the appropriate form, so this category could not be used in the categorical random effects model. The grand mean (Fig. 4(b), mean $= -0.41$, 95% CI $[-0.5944, -0.2256]$) and mean effect size for coral reef herbivores (mean $= -0.5321$, 95% CI $[-0.766, -0.2982]$) indicated significantly greater herbivore abundance within MPAs, whereas there was no effect of MPA implementation on herbivores in kelp/algal habitats (mean $= -0.1947$, 95% CI $[-0.5118, 0.1255]$). Populations of urchins on coral reefs were lower within MPAs (Fig. 5(a); $p < 0.05$), whereas herbivorous fish populations did not change (Fig. 5(a): $p > 0.05$). Fifty-eight percent (15 of 26 evaluations) of evaluations of herbivorous fishes on coral reefs showed a positive response to MPAs, and 83% (13 of 16) of evaluations of urchins on coral reefs showed a negative response to MPAs. Seventy percent (16 of 23) of evaluations of urchins in kelp/algal habitat also showed a negative response. When separated by family, no individual coral reef herbivorous

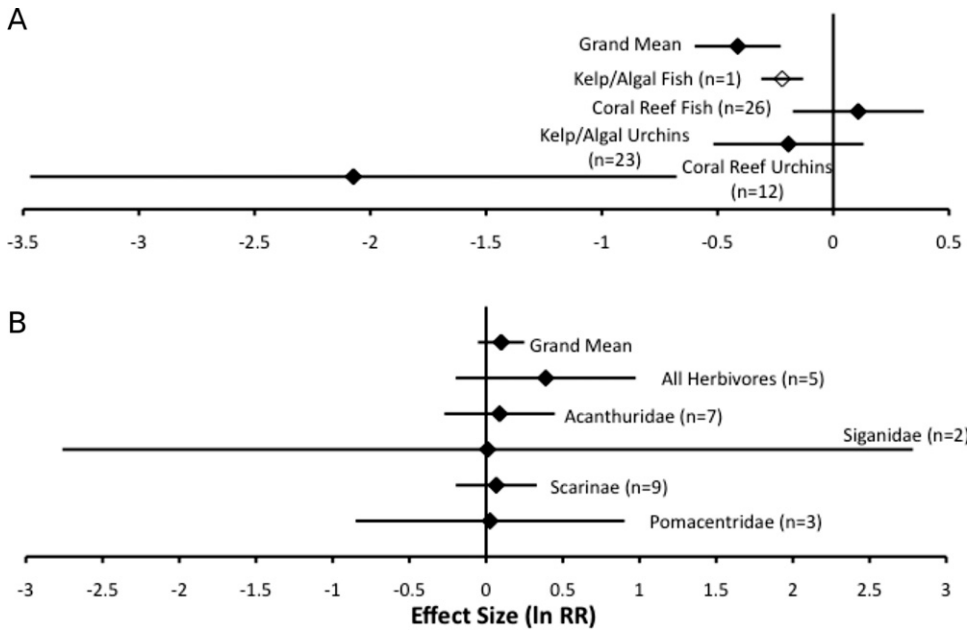

Fig. 5. Mean effect sizes and 95% confidence intervals for (A) coral reef fish, kelp/algal urchins and coral reef urchins (n.b. $n = 1$ for Kelp/algal fish effect size; excluded from group analysis) and (B) for individual herbivorous coral reef fish families and for instances when coral reef fish herbivores were grouped together (All Herbivores).

fish families changed their abundance significantly (Fig. 5(b); $p > 0.05$), which is consistent with the result for overall coral reef fish (Fig. 5(a)).

3.5. Trophic cascades

Next, we examined the correlation between herbivore density and algal coverage within individual MPAs. Within the database, 13 articles, representing 16 MPAs (14 coral reef, 2 kelp/algal), contained suitable information on both primary producers and herbivores from the same MPA, at the same time point. Effect size of herbivores was evenly spread along the *X*-axis (Fig. 6, 7 positive and 9 negative) but was significantly lower than zero (grand mean $= -0.7395$, 95% CI $[-1.3023, -0.1768]$), whereas effect size of primary producers (*Y*-axis on Fig. 6) was not significantly different to zero (grand mean $= -0.0366$, 95% CI $[-0.5593, 0.4861]$; 6 positive, 10 negative). A significant negative relationship was found for all evaluations between primary producers and herbivores when both were reported (Fig. 6; $R^2 = 0.32$, $p = 0.02$), that is, higher populations of herbivores correlated with lower cover of primary producers. Sixty-seven percent ($n = 6$) of evaluations of coral reef MPAs reporting both primary producers and herbivorous fish populations showed decreased macroalgal coverage with increased herbivorous fish density. The correlation for coral reef fish and primary producer coverage observed in Fig. 6 (solid black line) was also significant and negative ($R^2 = 0.7$, $p = 0.04$). Conversely, when coral reef urchins and primary producers were reported ($n = 8$), 38% of MPAs showed lower macroalgae and urchin populations and none showed increases to both groups. This relationship, however, was not significant (Fig. 6, $R^2 = 0.31$, $p = 0.15$).

4. Discussion

Meta-analytical results for overall primary producer groups showed differing trends according to habitat type. MPAs showed lower macroalgal cover than fished areas on coral reefs, but there was no significant difference between MPAs and fished sites in kelp/algal habitats. Coral reef MPAs showed lower herbivore densities than fished sites, but MPAs again had no detectable effect in kelp/algal habitats. Debate continues as to the generality of trophic cascade effects within protected area networks, and how recovery trajectories may vary, even within the same types of habitats (Babcock et al., 2010; Taylor et al., 2011; Huijbers et al., 2014; McClanahan, 2014). In many kelp/algal systems, predator populations recover within MPAs and place pressure on urchin populations (Shears and Babcock, 2002; Micheli et al., 2005; Pederson and Johnson, 2007); while in coral reef habitats, herbivores are protected from fishing and recover, grazing down algal biomass (Mumby et al., 2006; Hughes et al., 2007a; Mumby et al., 2007; Game et al., 2009). Examining MPAs where both herbivores and macroalgae were recorded clarified this result, where higher populations of coral reef herbivorous fishes result in significantly lower macroalgal cover (Fig. 5). Conversely, urchin populations within MPAs were significantly lower in coral reef habitats. Overall, the high variability in our results agrees with many previous studies, where community response to MPAs is strongly

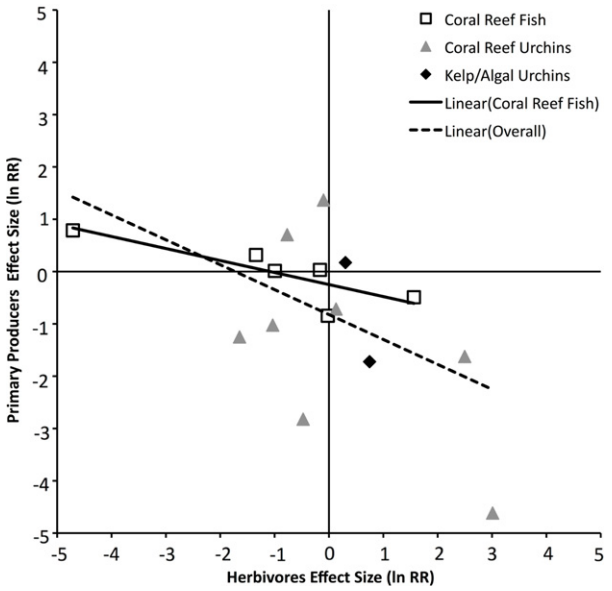

Fig. 6. Plot of primary producers ln RR (*Y*-axis) against herbivore ln RR (*X*-axis) in articles where both are included, categorised by herbivore type. Lines of best fit correspond to coral reef fish (solid line) and overall trends (dashed line). The relationship for coral reef urchins was not significant. Note that negative values indicate lower levels of the given group within MPAs, and vice versa for positive values.

variable, not only between trophic groups, but also within them to the level of species (Micheli et al., 2004b; Lester et al., 2009; Smith et al., 2014).

The high proportion of studies that directly assessed the effectiveness of MPAs (88%) increased confidence in our dataset. Such studies are more likely to have selected control sites outside the MPA that are representative of the habitats found within MPAs and are less likely to contain biases in control site selection or inherent differences in habitat structure (as discussed by Gell and Roberts, 2003). The average age of included MPAs (at 11.97 years) was a positive indication of global MPA continuity and longevity in light of recent studies that have highlighted MPA age as crucial in food web and habitat alterations (Claudet et al., 2008; Vandeperre et al., 2011; Edgar et al., 2014). Our literature searches indicated a dearth of studies investigating macroalgal coverage in kelp/algal MPAs. As a result of the low number of included studies for kelp/algal macroalgal coverage ($n = 5$), effect size variance was quite large (Fig. 4(a)), resulting in reduced statistical power for assessing the capacity for MPAs to elicit changes in macroalgae in rocky habitats. This result stresses the importance of surveying whole communities when assessing MPA efficacy and suggests that further investigations into herbivorous fish populations in temperate regions may assist in uncovering complex trophic interactions in kelp/algal habitats. Finally, the identification of herbivorous species and trophic groups should be presented more explicitly in the literature to avoid grouping of nominally herbivorous species within other groups (e.g. *Sarpa salpa* with sparids).

The absence of significant publication bias for both primary producer and herbivore evaluations gives confidence that the analyses conducted are true indicators of MPA effects. Publication bias analysis has been unusual in previous MPA-related meta-analyses (see Molloy et al., 2008, 2009; Poore et al., 2012, for examples of its previous use), but is important in establishing that meta-analytical outcomes are unaffected by the effects of preferential publication of significant results and associations with pro- or anti-conservation bias.

Predatory fish groups that specifically target echinoids, especially the balistids, sparids, labrids, haemulids and lethrinids, are primary fishing targets in many regions (Pauly, 1998; Kellner et al., 2010). Our results might suggest that larger predatory fish populations in MPAs result in increased fish predation on echinoids, irrespective of benthic habitat (similar to the results found by McClanahan 1995b; Johansson et al., 2010). Given that coral reef MPAs contained significantly lower urchin populations, we suggest that such dynamics might be common on coral reefs. In this case, the identification and associated protection of key echinoid predators, be it from MPAs or other fisheries methods (fishing restrictions etc.), appear crucial to the recovery of habitats on coral reef (e.g. Babcock et al., 2010; McClanahan, 2014). This highlights the need for location and habitat-specific management and MPA design practices, especially relating to how populations are likely to recover in response to the removal of fishing. The recovery of benthic habitats towards unimpacted states may be reliant on the recovery of influential groups of grazers and predators; thus, identifying and actively managing such groups should be an integral component of MPA design (e.g. McClanahan, 1995b; Clemente et al., 2010).

Results of analyses where both primary producers and herbivores were included for an individual reserve reflected our hypothesised top-down trends (Fig. 6). Here the significant negative relationship found between primary producer cover and herbivore abundance agrees with the herbivore–primary producer component of the top-down restructuring hypothesis, where higher herbivore density leads to lower primary producer coverage (Guidetti, 2006; Mumby et al., 2006). Analyses of

both primary producers and herbivores on coral reefs more clearly supported the effects of top-down cascades, where 10 out of 14 studies showed negative primary producer coverage, four of which were matched with negative urchin evaluations and three matched with positive herbivorous fish evaluations. Lower total herbivore density within coral reef MPAs (Fig. 4(b) is primarily driven by significant reductions in urchin density (Fig. 5(a)), whilst primary producer coverage still decreased within this habitat (Fig. 4(a)). This exemplifies the complex relationships that occur within MPAs, as reductions in algal cover are not necessarily caused by increased herbivorous fish density (see Fig. 5(a)). It is likely that combined meta-analyses from multiple locations, such as this, cannot pick up the complex relationships that occur within a regional, or even site context on coral reefs. Conversely, in kelp/algal habitats, decreases in echinoid populations have been found to permit the re-establishment of habitat-forming algae (e.g. Leleu et al., 2012; Sangil et al., 2012), however, this effect was not statistically significant in our study. Given that the majority of studies investigating kelp/algal herbivores reported urchin abundances, the lack of fish herbivores for kelp/algal habitats in this dataset is likely to be indicative of their impact overall in this habitat and of their level and quality of reporting.

This dataset highlights the complexities of population alterations within MPAs. In addition to traditional trophic cascade alterations, MPAs elicit changes in other areas, which are likely to influence population recovery dynamics. For example, human-related removal of macroalgae, especially large Fucoids, is extensive within some regions of the world, with key examples being study of protection effects on the harvested kelp species *Durvillaea* (Castilla and Bustamante, 1989) and degradation of the Black Sea following the overharvesting of *Phyllophora* (Zaitzev and Mamaev, 1997). Although an important process in some locations, none of the included studies in the meta-analysis database referred to human removal of macroalgae. Interactions between coral and algal populations are also an important consideration when evaluating habitat outcomes in coral reef MPAs (Done, 1992; McCook et al., 2001; Box and Mumby, 2007; Korzen et al., 2011). Reduced phase shift feedback processes, such as a limited capacity for coral community recovery due to permanently large macroalgal coverage in spite of increases in herbivore abundance, have been reported in the Caribbean (Williams and Polunin, 2001). Additionally, dense stands of foliose macroalgal have been found to restrict browsing on the Great Barrier Reef (Hoey and Bellwood, 2011). Given the strong evidence in this study for reduction in primary producer coverage following MPA implementation on coral reefs, such feedbacks may not necessarily be the norm on a global scale.

The results of this study emphasise that MPAs may have a range of effects on trophic structures, including either restoring imbalances under some scenarios (circa macroalgae and urchins on coral reefs) or more surprising and counterproductive given habitat goals (macroalgae in kelp/algal habitats). Increases in higher consumer density cause extensive alterations throughout food webs, which alter habitat structure (Bruno and O'Connor, 2005; Mumby et al., 2007; Babcock et al., 2010). However, not all of our results were unequivocally favourable for habitat and trophic relationship restoration in MPAs. Consequently, our results highlight the complex nature of marine trophodynamics and the associated risks of inferring results across habitat or system boundaries.

Although analyses of primary producer and herbivore populations are common, further analyses of the driving process of this relationship, herbivory, are necessary. Measuring grazing rates within and outside of protected areas lessens doubt about direct relationships between primary producers and herbivores, as opposed to presenting count data and percent coverage as almost independent measures. Quantifying processes, such as herbivory, predation and competition, in addition to count data, have the potential to lend significant support to existing MPA evaluation techniques. Despite recent advances in such areas (Mumby and Harborne, 2010; McClanahan and Karnauskas, 2011; Olds et al., 2012), the continuation of such studies is important in investigating direct interactions between primary producers and herbivores, in the context of MPA implementation to qualify the results found here.

Acknowledgements

We thank C. Henderson, P. Maxwell, A. Olds and I. Tibbetts for constructive comments on the manuscript. The study was supported in part by the Australian Rivers Institute at Griffith University. The comments of three anonymous reviewers greatly improved the quality and focus of the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.10.005.

References

Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L., Williamson, D.H., 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28, 339–351.

Anderson, R.J., Bolton, J.J., Stegenga, H., 2009. Using the biogeographical distribution and diversity of seaweed species to test the efficacy of marine protected areas in the warm-temperate Agulhas Marine Province, South Africa. Diversity and Distrib. 15, 1017–1027.

Babcock, R.C., Shears, N.T., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., 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, 18256–18261.

Ballantine, W.J., Langlois, T.J., 2008. Marine reserves: The need for systems. Hydrobiologia 606, 35–44.

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2005. What determines the strength of a trophic cascade? Ecology 86, 528–537.

Box, S., Mumby, P.J., 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Mar. Ecol. Prog. Ser. 342, 139–149.
Bruno, J.F., O'Connor, M.I., 2005. Cascading effects of predator diversity and omnivory in a marine food web. Ecol. Lett. 8, 1048–1056.
Castilla, J.C., Bustamante, R.H., 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile, effects on *Durvillaea antarctica* (Phaeophyta, Durvilleales). Mar. Ecol. Prog. Ser. 50, 203–214.
Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-Ruzafa, Á., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.-M., Dimech, M., Falcón, J.M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P.J., Stobart, B., Vandeperre, F., Valle, C., Planes, S., 2008. Marine reserves: size and age do matter. Ecol. Lett. 11, 481–489.
Clemente, S., Carlos Hernandez, J., Rodriguez, A., Brito, A., 2010. Identifying keystone predators and the importance of preserving functional diversity in sublittoral rocky-bottom areas. Mar. Ecol. Prog. Ser. 413, 55–67.
Coleman, M.A., Chambers, J., Knott, N.A., Malcolm, H.A., Harasti, D., Jordan, A., Kelaher, B.P., 2011. Connectivity within and among a network of temperate marine reserves. PLoS One 6, e20168.
Done, T.J., 1992. Phase-shifts in coral reef communities and their ecological significance. Hydrobiologia 247, 121–132.
Duffy, J.E., 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecol. Lett. 6, 680–687.
Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Forsterra, G., Galvan, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220.
Fulton, C.J., Depczynski, M., Holmes, T.H., Noble, M.M., Radford, B., Wernberg, T., Wilson, S.K., 2014. Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem. Limnol. Oceanogr. 59, 156–166.
Game, E.T., Bode, M., McDonald-Madden, E., Grantham, H.S., Possingham, H.P., 2009. Dynamic marine protected areas can improve the resilience of coral reef systems. Ecol. Lett. 12, 1336–1345.
Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol. Evolut. 18, 448–455.
Graham, N.A.J., Ainsworth, T.D., Baird, A.H., Ban, N.C., Bay, L.K., Cinner, J.E., De Freitas, D.M., Diaz-Pulido, G., Dornelas, M., Dunn, S.R., Fidelman, P.I.J., Foret, S.C.G.T., Kool, J.T., Mallela, J., Penin, L., Pratchett, M.S., Williamson, D.H., 2011. From microbes to people- tracable benefits of no-take areas for coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 49, 117–148.
Guidetti, P., 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. Ecol. Appl. 16, 963–976.
Hedges, L.V., 1982. Estimation of effect size from a series of independent experiments. Psychol. Bull. 92, 490–499.
Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.
Hillebrand, H., 2002. Top-down versus bottom-up control of autotrophic biomass - a meta-analysis on experiments with periphyton. JNABS 21, 349–369.
Hoey, A.S., Bellwood, D.R., 2011. Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? Ecol. Lett. 14, 267–273.
Hughes, T.P., Bellwood, D.R., Folke, C.S., McCook, L.J., Pandolfi, J.M., 2007. No-take areas, herbivory and coral reef resilience. Trends in Ecology & Evolution 22, 1–3.
Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. 17, 360–365.
Huijbers, C.M., Connolly, R.M., Pitt, K.A., Schoeman, D.S., Schlacher, T.A., Burfeind, D.D., Steele, C., Olds, A.D., Maxwell, P.S., Babcock, R.C., Rissik, D., 2014. Conservation benefits of marine reserves are undiminished near coastal rivers and cities. Conserv. Lett., n/a–n/a..
Johansson, C.L., Bellwood, D.R., Depczynski, M., 2010. Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia. Mar. Ecol. Prog. Ser. 414, 65–74.
Kelleher, G., 1999. Guidelines for Marine Protected Areas. IUCN, Gland, Switzerland.
Kellner, J.B., Litvin, S.Y., Hastings, A., Micheli, F., Mumby, P.J., 2010. Disentangling trophic interactions inside a Caribbean marine reserve. Ecol. Appl. 20, 1979–1992.
Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A., Holt, R.D., 2005. Trophic cascades across ecosystems. Nature 437, 880–883.
Korzen, L., Israel, A., Abelson, A., 2011. Grazing effects of fish versus sea urchins on turf algae and coral recruits: possible implications for coral reef resilience and restoration. J. Marine Biol. 1–8.
Leleu, K., Remy-Zephir, B., Grace, R., Costello, M.J., 2012. Mapping habitats in a marine reserve showed how a 30-year trophic cascade altered ecosystem structure. Biol. Cons. 155, 193–201.
Leslie, H.M., 2005. A synthesis of marine conservation planning approaches. Conserv. Biol. 19, 1701–1713.
Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airame, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology-Progress Series 384, 33–46.
Madin, E.M.P., Gaines, S.D., Madin, J.S., Warner, R.R., 2010. Fishing indirectly structures macroalgal assemblages by altering herbivore behavior. Amer. Nat. 176, 785–801.
Maliao, R.J., White, A.T., Maypa, A.P., Turingan, R.G., 2009. Trajectories and magnitude of change in coral reef fish populations in Philippine marine reserves: a meta-analysis. Coral Reefs 28, 809–822.
McClanahan, T.R., 1995. A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. Ecol. Model. 80, 1–19.
McClanahan, T.R., 1995a. Fish predators and scavengers of the sea-urchin Echinometra mathaei in Kenyan coral reef marine parks. Environ. Biol. Fishes 43, 187–193.
McClanahan, T.R., 2014. Recovery of functional groups and trophic relationships in tropical fisheries closures. Mar. Ecol. Prog. Ser. 497, 13–23.
McClanahan, T., Karnauskas, M., 2011. Relationships between benthic cover, current strength, herbivory, and a fisheries closure in Glovers Reef Atoll, Belize. Coral Reefs 30, 9–19.
McClanahan, T., Polunin, N., Done, T., 2002. Ecological states and the resilience of coral reefs. Conserv. Ecol. 6, 18.
McCook, L.J., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19, 400–417.
Micheli, F., Amarasekare, P., Bascompte, J., Gerber, L.R., 2004. Including species interactions in the design and evaluation of marine reserves: Some insights from a predator–prey model. Bull. Mar. Sci. 74, 653–669.
Micheli, F., Benedetti-Cecchi, L., Gambaccini, S., Bertocci, I., Borsini, C., Osio, G.C., Romano, F., 2005. Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. Ecol. Monograph 75, 81–102.
Micheli, F., Halpern, B.S., Botsford, L.W., Warner, R.R., 2004. Trajectories and correlates of community change in no-take marine reserves. Ecol. Appl. 14, 1709–1723.
Molloy, P.P., McLean, I.B., Cote, I.M., 2009. Effects of marine reserve age on fish populations: a global meta-analysis. J. Appl. Ecol. 46, 743–751.
Molloy, P.P., Reynolds, J.D., Gage, M.J.G., Mosqueira, I., Côté, I.M., 2008. Links between sex change and fish densities in marine protected areas. Biol. Cons. 141, 187–197.
Mumby, P.J., 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol. Appl. 16, 747–769.
Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., Holmes, K.E., Mendes, J.M., Broad, K., Sanchirico, J.N., Buch, K., Box, S., Stoffle, R.W., Gill, A.B., 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311, 98–101.
Mumby, P.J., Harborne, A.R., 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS One 5, e8657.
Mumby, P.J., Harborne, A.R., Williams, J., Kappel, C.V., Brumbaugh, D.R., Micheli, F., Holmes, K.E., Dahlgren, C.P., Paris, C.B., Blackwell, P.G., 2007. Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences of the United States of America 104, 8362–8367.
Mumby, P.J., Steneck, R.S., Edwards, A.J., Ferrari, R., Coleman, R., Harborne, A.R., Gibson, J.P., 2012. Fishing down a Caribbean food web relaxes trophic cascades. Mar. Ecol. Prog. Ser. 445, 13–24.
Olds, A.D., Connolly, R.M., Pitt, K.A., Maxwell, P.S., 2012. Habitat connectivity improves reserve performance. Conserv. Lett. 5, 56–63.

O'Leary, J.K., McClanahan, T.R., 2010. Trophic cascades result in large-scale coralline algae loss through differential grazer effects. Ecology 91, 3584–3597.
Osenberg, C.W., Schmitt, R.J., Holbrook, S.J., Abusaba, K.E., Flegal, A.R., 1994. Detection of environmental impacts-natural variability, effect size, and power analysis. Ecol. Appl. 4, 16–30.
Pauly, D., 1998. Fishing down marine food webs. Science 279, 860–863.
Payton, M.E., Miller, A.E., Raun, W.R., 2000. Testing statistical hypotheses using standard error bars and confidence intervals. Commun. Soil Sci. Plant Anal. 31, 547–551.
Pederson, H.G., Johnson, C.R., 2007. Growth and age structure of sea urchins (Heliocidaris erythrogramma) in complex barrens and native macroalgal beds in eastern Tasmania. ICES J. Mar. Sci. 65, 1–11.
Poore, A.G., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V., Reynolds, P.L., Sotka, E.E., Stachowicz, J.J., Taylor, R.B., Vanderklift, M.A., Duffy, J.E., 2012. Global patterns in the impact of marine herbivores on benthic primary producers. Ecol. Lett. 15, 912–922.
Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. Trends in Ecology & Evolution 22, 583–592.
Pullin, A.S., Stewart, G.B., 2006. Guidelines for systematic review in conservation and environmental management. Conserv. Biol. 20, 1647–1656.
Rosenberg, M.S., Adams, D.C., Gurevitch, J., 1999. Metawin: Statistical software for Meta-Analysis. Version 2.0. Sinauer Associates, Sunderland, Massachusetts.
Salomon, A.K., Gaichas, S.K., Shears, N.T., Smith, J.E., Madin, E.M., Gaines, S.D., 2010. Key features and context-dependence of fishery-induced trophic cascades. Conserv. Biol. 24, 382–394.
Sangil, C., Clemente, S., Martín-García, L., Hernández, J.C., 2012, No-take areas as an effective tool to restore urchin barrens on subtropical rocky reefs. Estuarine, Coastal and Shelf Science.
Shears, N., Babcock, R., 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132, 131–142.
Shears, N.T., Smith, F., Babcock, R.C., Duffy, C.A.J., Villouta, E., 2008. Evaluation of biogeographic classification schemes for conservation planning: application to New Zealand's coastal environment. Conserv. Biol. 22, 467–481.
Shurin, J.B., Borer, E.T., Anderson, K., Blanchette, C.A., Brioitman, B., Cooper, S.D., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecol. Lett..
Smith, A.N.H., Anderson, M.J., Millar, R.B., Willis, T.J., 2014. Effects of marine reserves in the context of spatial and temporal variation: an analysis using Bayesian zero-inflated mixed models. Mar. Ecol. Prog. Ser. 499, 203–216.
Steneck, R.S., Paris, C.B., Arnold, S.N., Ablan-Lagman, M.C., Alcala, A.C., Butler, M.J., McCook, L.J., Russ, G.R., Sale, P.F., 2009. Thinking and managing outside the box: Coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. Coral Reefs 28, 367–378.
Stevens, T., 2002. Rigor and representativeness in marine protected area design. Coastal Management 30, 237–248.
Taylor, R.B., Morrison, M.A., Shears, N.T., 2011. Establishing baselines for recovery in a marine reserve (Poor Knights Islands, New Zealand) using local ecological knowledge. Biol. Cons. 144, 3038–3046.
Thomsen, M.S., Wernberg, T., Engelen, A.H., Tuya, F., Vanderklift, M.A., Holmer, M., McGlathery, K.J., Arenas, F., Kotta, J., Silliman, B.R., 2012. A meta-analysis of seaweed impacts on seagrasses: generalities and knowledge gaps. PLoS One 7, e28595.
Underwood, A.J., 1991. Beyond BACI - Experimental designs for detecting environmental impacts on temporal variations in natural populations. Aust. J. Marine Freshwater Res. 42, 569–587.
Valentine, J.F., Heck, K.J., 2005. Perspective review of the impacts of overfishing on coral reef food web linkages. Coral Reefs 24, 209–213.
Vandeperre, F., Higgins, R.M., Sanchez-Meca, J., Maynou, F., Goni, R., Martin-Sosa, P., Perez-Ruzafa, A., Afonso, P., Bertocci, I., Crec'hriou, R., D'Anna, G., Dimech, M., Dorta, C., Esparza, O., Falcon, J.M., Forcada, A., Guala, I., Le Direach, L., Marcos, C., Ojeda-Martinez, C., Pipitone, C., Schembri, P.J., Stelzenmuller, V., Stobart, B., Santos, R.S., 2011. Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. Fish Fish. 12, 412–426.
Williams, I., Polunin, N., 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19, 358–366.
Zaitzev, Y.P., Mamaev, V., 1997, Biological Diversity in the Black Sea: A study of change and Decline, United Nations, New York.