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Review paper

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

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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.

Contents

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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