LETTER

Conservation Benefits of Marine Reserves are Undiminished Near Coastal Rivers and Cities

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Abstract

Recent assessments of marine reserves have emphasized the importance of socio-economic factors in reserve performance. Debates continue, however, about whether we should avoid or promote the placement of reserves near potentially detrimental forces, including coastal cities or rivers. We performed a global meta-analysis to test whether proximity to major coastal influences affected the ability of marine reserves to enhance the abundance of organisms relative to surrounding areas. A strong effect of reserve performance was evident for a range of trophic groups. Positive effects of reserves were undiminished by proximity to coastal cities or river discharges for the majority of taxonomic groups under conservation. We conclude that reserves placed in coastal areas are likely to protect marine populations to a similar extent as reserves in remote or less-developed locations. Marine reserves in coastal settings can be an important tool to protect species and ecosystems in places threatened by human activities.

Introduction

The rapid growth of human populations in coastal areas is exacerbating pressures on marine ecosystems and the services that they provide (Halpern *et al.* 2008). Prominent impacts include degradation of coastal habitats (Lotze *et al.* 2006), increased flows of terrestrial sediment to coastal waters (Syvitski *et al.* 2005), and overexploitation of fisheries (Jackson *et al.* 2001). Marine reserves have been established worldwide to protect habitats and species from extraction and facilitate recovery of marine ecosystems (Lubchenco *et al.* 2003).

For many no-take marine reserves, positive effects on marine populations have been documented, yet the magnitude of this "reserve effect" is highly variable (Lester *et al.* 2009). Consequently, a central question in spatial conservation planning remains why some reserves perform better than others (Gaines *et al.* 2010). Recently, Edgar *et al.* (2014) demonstrated that successful reserves require a combination of at least four out of five key attributes: they have to be no-take; have high levels of compliance; have been protected for long periods; be large; and be isolated by channels or other geographic features from fished areas. In combination with other recent studies, these findings emphasize the importance of incorporating human-related factors, such as regulations and enforcement, into the evaluation and future design of marine reserves (Pollnac *et al.* 2010; Fox *et al.* 2012; Edgar *et al.* 2014).

In densely populated coastal areas, marine reserves could play an important role in protecting native diversity, which is generally decreasing with increasing

human population densities (Lotze *et al.* 2006). Pollnac *et al.* (2010) found a variable relationship between the density of human populations close to reserves and the biomass of commercially exploited fish species inside reserves relative to control areas. Both positive and negative effects of dense human populations have also been found in other regional studies (Pollnac *et al.* 2000; McClanahan *et al.* 2006) suggesting that positive reserve effects due to fishing restraints might be obscured or overridden by negative effects caused by influences outside reserve boundaries. Besides fishing pressure, the majority of human influences on marine ecosystems are driven by inputs from the land (Halpern *et al.* 2008; Beger *et al.* 2010). Transfer of terrestrial sediments and toxicants by estuarine plumes might diminish positive effects of marine reserves by counteracting fishing controls with greater pollution (Halpern *et al.* 2013). However, rivers also deliver benefits to coastal ecosystems (i.e., stimulating primary production), and many coastal fisheries critically depend on riverine input (Gillson 2011).

Marine reserves are frequently placed in areas with the least potential for commercial uses, such as offshore waters far from land (Pressey & Bottrill 2008; Barr & Possingham 2013). This strategy directs the bulk of conservation investments to remote areas, while species and ecosystems occurring in places close to intense development remain relatively poorly protected (Margules & Pressey 2000). Whether we should continue the practice of avoiding the placement of reserves close to potentially adverse coastal influences—that might diminish their effectiveness—or use reserves as a tool to mitigate disturbances is a matter of active debate (Klein *et al.* 2013, Sale *et al.* 2014).

We tested the effect of proximity to land, urban centers, and river discharges, in combination with reserve characteristics (reserve size, age, substrate, and marine realm) on reserve performance (Figure 1), measured as the abundance of fish, invertebrates, and algae inside relative to outside marine reserves, using a meta-analytic approach. Because reserves near land are closer to human settlements, fishing pressure could potentially be higher (Cinner *et al.* 2013). Fishing effects might be further amplified in areas proximal to large urban centers, resulting in an increased effect size between reserves and control areas. Alternatively, conservation benefits might be reduced near urban centers and/or rivers, where external influences, such as pollution and sediment input, might be larger. Because ecological and biological traits (e.g., behavior, body size, and trophic position) can influence an organism's susceptibility to protection (Claudet *et al.* 2010), we explicitly incorporated the trophic level of organisms in the analysis.
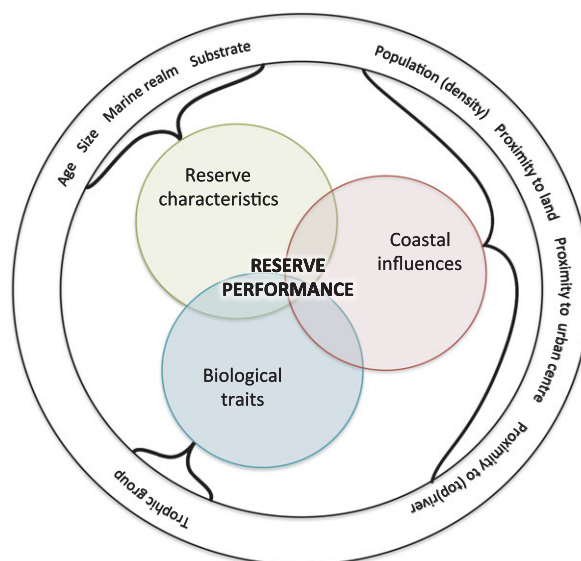

Figure 1 Conceptual diagram representing three major categories of determinants expected to influence the performance of marine reserves. In this study, we have modeled reserve performance (log RR = ln[$Abundance_{Reserve}$/$Abundance_{Control}$]) using the predictors shown in the outer circle of the diagram. Although biomass, size, and species richness were recorded in the database as well, only the abundance data provided sufficient records to run the analysis.

Methods

We compiled a database of peer-reviewed studies that reported biological effects of marine reserves. The ISI Web of Knowledge database was searched using the terms "marine reserve," "marine protected area," "MPA," "marine park," or "no-take reserve." Only studies that measured abundance of fish, invertebrates and/or algae in formally designated marine reserves with a fully protected no-take area were included. Response variables such as biomass and species richness yielded too few observations to facilitate statistical analysis. We included 150 articles, published between 1977 and 2012, reporting on studies from 113 reserves (see Appendix S1). Several reserves were the subject of more than one article, and some studies examined multiple reserves, resulting in a total of 190 unique reserve-article combinations.

The considerable variation in the design of marine reserve studies might itself affect the strength of reserve effects reported. Our database comprised articles that reported abundance either in one site inside and outside of the reserve ($n = 40$), in multiple sites inside and outside of the reserve ($n = 103$), or before and after the reserve was established ($n = 7$). For studies that included multiple measurements over time, we used data only from the most recent observation, thus reflecting the effects of

the longest duration of protection. We tested the sensitivity of our results to variation in the robustness of sampling designs of the original studies (see Appendix S2), but found no significant effects. We, therefore, weighed all studies equally in subsequent analyses, irrespective of design.

For each reserve, estimates for 11 predictor variables were compiled (Table 1). Variables that measured the effect of coastal influences were: (1) proximity to land (defined as the distance from the edge of the reserve to the nearest major landmass with a surface area larger than 5,000 km^2); (2) proximity to the nearest urban center with a population larger than 50,000 people/inhabitants (a criterion selected to include only substantial urban areas); (3) proximity to the mouth of the nearest river with a mean annual discharge > 250,000 Ml per year; and (4) proximity to the mouth of the nearest river classified as top 200 rivers based on the annual river-mouth flow rate by Dai & Trenberth (2002). These distances were measured as the shortest distance over water in Google Earth. For proximity to rivers, we used a maximum of 500 km for top 200 rivers and 40 km for remaining rivers, as riverine influence was not expected to extend beyond these limits (Devlin & Brodie 2005). We also included the population density and total population size of the nearest urban center, extracted from national government reports on population estimates. To account for possible influences of biogeography, we included the marine realm in which the reserve is located according to the classification of the marine ecoregions of the world by Spalding *et al.* (2007). Data on the size of the no-take area were extracted directly from the original article or, if not reported, from the MPA Global online database (Wood 2007). We included the water depth at which data were collected for each study, but found no significant effect, and therefore excluded this factor from the analysis. We also included the main benthic substrate at the sampling sites and the age of the reserve, calculated as the number of years between implementation of the reserve and the final year in which the study was conducted. Collinearity between the predictors was low ($r \leq 0.36$) and hence all were retained in the analysis.

Quantitative data on fish and invertebrate abundance and algal cover were extracted from text, figures, and tables. Adult fish were categorized into six major trophic groups based on family, except for the families Pomacentridae, Holocentridae, and Hexagrammidae, for which classification was based on species, as these families display large interspecific differences in feeding behavior. Trophic groups followed the classification of Paddack *et al.* (2009): (1) piscivores consume living fish, <10% invertebrates/plants/algae/detritus; (2) invertivores consume benthic-associated invertebrates, <10% fish/algae/plants/detritus; (3) other carnivores consume both invertebrates and fish, <10% algae/plants/detritus; (4) omnivores consume both animal and plant matter, >10% of both; (5) herbivores consume plant matter, <10% animal matter; and (6) planktivores consume macro- and microzooplankton, including larval fish. Invertebrates were categorized as carnivorous, omnivorous, herbivorous, or filter/suspension feeding, and all algae were classified into a single group.

Data analysis

We calculated the log response ratio ($\log RR = \ln\left(\frac{Abundance_{Reserve}}{Abudance_{Control}}\right)$) for each record. This metric is commonly used in meta-analyses of experimental data (Hedges *et al.* 1999). The ratio results in a value of zero if there is no effect of the reserves (i.e., abundances inside and outside the reserve, or before and after the establishment of the reserve, are equal), a positive value if the reserve supports greater abundance, and negative if abundances are lower in reserves. The database comprised a total of 1,416 log RR values, of which 227 records (16% of total dataset) had an abundance of zero in either the reserve or control areas for which computation of response ratios was impossible. To be able to use these data in a calculation, we substituted the zeroes with a 1,000th of the minimum value recorded among all data contributing to the numerator or denominator, respectively.

We explored the relationship between the log RR and the 11 predictor variables using boosted regression trees (BRTs). This is an additive regression tree model that fits an ensemble of simple regression trees to optimize predictive accuracy (Elith *et al.* 2008). To minimize a bias towards studies or reserves with a large number of data points, we averaged the log RR per study per reserve for each trophic group. The BRT analysis was run with reserve performance as a binary outcome (0 where log RR ≤ 0, indicating a lack of response or negative response to protection, and 1 otherwise, indicating a positive response). The accuracy of BRT models can be measured using the area under the receiver operating characteristic (ROC), for which a value >0.5 indicates that the model prediction is better than could be expected by chance. The ROC value of our BRT model was 0.77.

Because the BRT results are not probabilistic, the significance of the predictor variables was tested using a generalized linear mixed model (GLMM) with a forward stepwise approach. The initial GLMM started with the most important predictor, as identified by the BRT analysis,

Table 1 Overview of predictor variables used to evaluate abundance of fish, invertebrates, and algae inside no-take marine reserves versus fished control areas

Predictor	Type	Values
Trophic group	Categorical, 11 values	Fish: piscivores, carnivores, invertivores, omnivores, herbivores, planktivores; Invertebrates: carnivores, omnivores, herbivores, filter feeders; Algae
Reserve size (km^2)	Continuous	Min: 0.006, Max: 900.4, Average $\pm$ SD: 70.7 $\pm$ 170.1
Reserve age (years)	Continuous	Min: 0, Max: 53, Average $\pm$ SD: 14.8 $\pm$ 10.9
Marine realm	Categorical, eight values	Temperate Northern Pacific, Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Temperate Southern Africa, Western Indo-Pacific, Central Indo-Pacific, Temperate Australasia
Main substrate	Categorical, three values	Coral reef, rocky reef or soft sediment
Proximity to urban center (km)	Continuous	Min: 0, Max: 1,133, Average $\pm$ SD: 117.3 $\pm$ 199.0
Population density per km^2	Continuous	Min: 11.3, Max: 10,000, Average $\pm$ SD: 1,457 $\pm$ 1,516
Total population	Continuous	Min: 49,675, Max: 6,041,830, Average $\pm$ SD: 566,166 $\pm$ 1,016,213
Proximity to river (km)	Continuous	Min: 0, Max: 40, Average $\pm$ SD: 31.4 $\pm$ 12.7
Proximity to top 200 rivers (km)	Continuous	Min: 17, Max: 500, Average $\pm$ SD: 429.4 $\pm$ 128.9
Proximity to landmass (km)	Continuous	Min: 0, Max: 780, Average $\pm$ SD: 58.7 $\pm$ 130.8

with reserve modeled as a random factor to control for repeated observations within individual reserves. We then added further candidate predictor variables one at a time, along with their interactions, in the order of importance suggested by the BRT. Significance of predictor variables was assessed using standard likelihood ratio tests for linear mixed-effects modeling (Zuur *et al.* 2007). We also ran the GLMM separately for each trophic group in which case we tested each predictor individually. This was done because trophic group could not be removed from the initial model due to its significance (see Results). As a result, the replication of other predictors within each trophic group might have been too low to detect additional significant effects.

Results

Organism abundance was greater inside marine reserves compared to control areas, regardless of proximity to coastal influences. Based on our meta-analysis, log response ratios (abundance inside vs. outside reserves – log RRs) for reserves close to urban centers or rivers were statistically indistinguishable from those of more remotely located reserves.

Trophic group had the largest contribution (38.5%) of all predictors to the fit of the model in the BRT analysis (Figure 2) followed by proximity to urban center (11.9%), marine realm (11.8%), and reserve size (10.0%). Other predictors contributed less than 10%. However, only trophic group proved to be a significant predictor of the log RR (GLMM, $P < 0.001$), with none of the other predictors, including proximity to urban

center, significantly enhancing model fit ($P > 0.247$). Trophic groups exhibited a large variety of responses to protection, with positive reserve effects for most fish groups (piscivores, carnivores, invertivores, and herbivores), and omnivores and filter feeders among the invertebrates (Figure 2A). The fitted function for proximity to urban center offered no support for the predictive hypothesis that reserves close to urban centers have smaller responses compared with reserves further away (Figure 2B). The fitted function for marine realm suggested that marine reserves in the Tropical Atlantic, Temperate South Africa, and in the Western Indo-Pacific were less effective than elsewhere, although this predictor did not contribute significantly to GLMM fit (Figure 2C).

Running the GLMM for each trophic group separately verified the BRT results, showing that proximity to coastal predictors did not influence reserve performance. Only three out of 11 trophic groups showed a significant effect of proximity to urban center, while the other coastal predictors (population density, total population, and proximity to land and rivers) had no significant effect on any group (Table 2). For piscivores, the beneficial reserve effect became larger nearer to urban centers (GLMM coefficient $\pm$ se $= -0.58 \pm 0.27$), whereas for invertivores and herbivorous invertebrates it became smaller (GLMM coefficients $\pm$ se $= 0.49 \pm 0.23$ and 0.97 ± 0.34, respectively). Log RRs for abundance of herbivorous invertebrates was significantly affected by marine realm and main substrate (stronger positive responses in the Central Indo-Pacific, Temperate North Pacific and Temperate South Africa, and rocky reefs and soft sediments). Filter-feeding invertebrates showed more positive responses to reserves in older reserves.
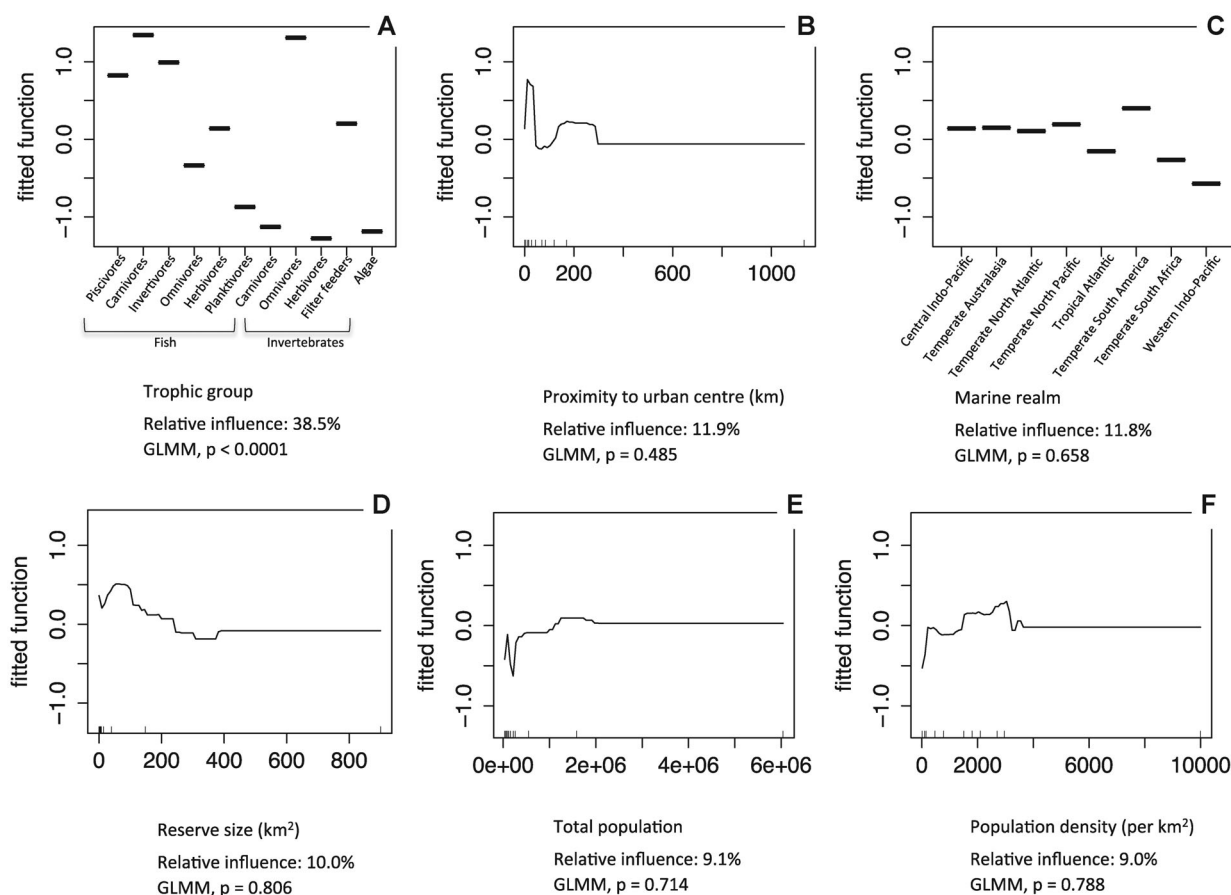
Figure 2 Partial dependence plots of the six most influential predictors according to the BRT analysis. The fitted function visualizes the effect of each predictor variable while controlling for the average effect of all other variables in the model. Positive fitted functions indicate a positive protection effect, thus higher abundances inside reserves compared to control areas, and negative fitted functions suggest a negative reserve effect. The relative contribution of each predictor is given in percentages under the plots.

Discussion

Marine reserves in coastal areas are likely to be more heavily exposed to disturbances that they cannot readily mitigate (e.g., pollution and flooding) than are reserves further offshore, or in less-developed locations. Expectations are thus that reserves closer to urban centers and rivers would perform more poorly in terms of conservation outcomes. By contrast, our global meta-analysis shows that coastal reserves appear equally effective at enhancing or protecting abundances of organisms than their less-impacted counterparts; contrasts in abundances between protected and fished areas were similar irrespective of whether a reserve was located close to either coastal cities or riverine input.

Despite the widespread acknowledgement of the importance of ecosystem protection, the practice of conservation planning still faces a difficult trade-off between the

ecological benefits and socio-economic costs of potential reserves (Klein *et al.* 2013, Sale *et al.* 2014) resulting in the frequent placement of reserves in "residual" areas that are least used by other activities (Pressey & Bottrill 2008). Gradients of marine biodiversity in relation to proximity to land, rivers, and cities are common, as a result of natural variability and anthropogenic influences (e.g., Stevens and Connolly 2004, Coll *et al.* 2012). High biodiversity nevertheless occurs quite commonly in areas adjacent to human impacts (Tittensor *et al.* 2010). Our results suggest that we should not avoid placing reserves in coastal areas, even though these areas can be subjected to disproportionally high risks and disturbances.

The importance of incorporating human-related factors in reserve performance evaluations has been emphasized in recent studies (Pollnac *et al.* 2010; Weeks *et al.* 2010; Klein *et al.* 2013). Pollnac *et al.* (2010) showed that fish biomass inside reserves can be either positively or

Table 2 Results of a generalized linear mixed model (GLMM) that tested the effect of several predictors on reserve performance, for all trophic groups together, and each trophic group separately. For each predictor, the relative influence – as indicated by the boosted regression tree (BRT) analysis – is given in the second column. Bold values indicate a significant effect of a predictor in the GLMM

Predictor	Relative influence (BRT)	GLMM with all trophic groups n = 1416	Fish						Invertebrates				
			Piscivores n = 233	Carnivores n = 59	Invertivores n = 508	Omnivores n = 111	Herbivores n = 166	Planktivores n = 69	Carnivores n = 9	Omnivores n = 38	Herbivores n = 103	Filter feeders n = 50	Algae n = 70
Trophic group	38.5%	**<0.001**											
Proximity to urban center	11.9%	0.485	**0.032**	0.681	**0.030**	0.338	0.978	0.965	0.149	0.660	**0.009**	0.195	0.552
Marine realm	11.8%	0.658	0.217	0.603	0.894	0.374	0.680	0.115	0.188	0.974	**0.044**	0.177	0.179
Reserve size	10.0%	0.806	0.646	0.335	0.791	0.271	0.271	0.766	0.330	0.475	0.911	0.758	0.895
Total population	9.1%	0.714	0.722	0.921	0.400	0.930	0.661	0.737	0.354	0.376	0.692	0.658	0.739
Population density	9.0%	0.788	0.208	0.242	0.737	0.803	0.774	0.841	0.112	0.052	0.684	0.324	0.372
Reserve age	3.3%	0.408	0.193	0.115	0.586	0.645	0.417	0.825	0.358	0.088	0.053	**0.026**	0.356
Proximity to landmass	2.5%	0.247	0.603	0.959	0.702	0.177	0.972	0.987	0.253	0.866	0.261	0.518	0.095
Proximity to river	2.0%	0.575	0.486	0.684	0.460	0.139	0.233	0.660	0.176	0.769	0.484	0.416	0.133
Proximity to top 200 river	1.7%	0.695	0.364	0.912	0.998	0.447	0.477	0.690	0.214	0.933	0.559	0.674	0.866
Main substrate	0.3%	0.305	0.108	0.614	0.990	0.490	0.224	0.058	0.570	0.906	**0.036**	0.668	0.930

negatively affected by human population density and compliance, depending on the region in which the reserve is situated. We also showed variability in responses related to the marine realm in which reserves are located, affirming the importance of locality for the success of reserves. However, on a global basis, organism abundance inside marine reserves was not negatively impacted by human population densities or proximity to rivers and, additionally, for most trophic groups no relationship was found with proximity to urban centers. Although our analyses were limited to fully no-take reserves, and less-restrictive reserve types may elicit different responses to coastal influences, placing marine reserves in areas close to where humans live can foster a greater awareness of biodiversity and other ecological values (Dalton 2005; Ballantine 2014). This might increase the appreciation and success of reserves and provide an essential link between the social and ecological environment (Jentoft *et al.* 2007).

Unfortunately, we cannot uncritically assume that people comply with reserve regulations, and the level of compliance might have a strong impact on reserve performance (Pollnac *et al.* 2010). Efficient enforcement is a key feature of successful reserves (Edgar *et al.* 2014), and several studies have now demonstrated greater effects on fish biomass and ecosystem health where infringement rates are lower (Pollnac *et al.* 2010; Daw *et al.* 2011). Compliance has been reported to be greater when reserves were in sight of nearby villages in Indonesia and Papua New Guinea (McClanahan *et al.* 2006), but whether similar effects exist near urban centers has not been established yet. Given the scale of our study and the number of reserves analyzed, it was impracticable to obtain compliance data for all reserves in a uniform way, precluding the inclusion of compliance as a predictor.

Different responses of fish and invertebrates to protection result from differences in life history traits, which influence their susceptibility to impacts such as fishing (Claudet *et al.* 2010). Fishing effort might be more intense near coastal cities in some areas (Stewart *et al.* 2010), potentially increasing the effect size between reserves and control areas. Our analysis showed that the positive effect on piscivore abundance in reserves relative to control areas was larger near urban centers. Conversely, larger benefits were seen farther from urban centers for invertivores and herbivorous invertebrates. Although reserves are typically not designed solely for particular species, taxa that are strongly affected by fishing, which includes most piscivores, might benefit the most from areas that are closed to fishing (Micheli *et al.* 2004). An increased abundance of fish of higher trophic levels within reserves can subsequently lead to a decrease of lower trophic levels or nontargeted species through top–down control

(Shears & Babcock 2002; Mumby *et al.* 2012). Additionally, land-based human activities can increase sedimentation and pollution of coastal waters (Syvitski *et al.* 2005; Halpern *et al.* 2013), mostly affecting benthic organisms, such as invertivorous fish and herbivorous invertebrates like sea urchins (Airoldi 2003).

This is the first global analysis of marine reserve performance that incorporates proximity to major coastal influences. We found that marine reserves close to coastal cities or rivers are equally effective in protecting marine organisms as reserves sited farther from these potential impacts. Placing reserves close to where humans interact with the marine environment might benefit society by enabling more effective social engagement in conservation (Dalton 2005). Impacts outside reserve boundaries should, however, not be ignored, and management to reduce negative external influences are likely to enhance the long-term success of reserves (Alvarez-Romero *et al.* 2011).

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix S1. Map and list of marine reserves included in this study, located in different marine realms as classified by Spalding *et al.* (2007).

Appendix S2. Description of diagnostic tests to analyze the impact of study design.

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