Gravity of human impacts mediates coral reef conservation gains

Joshua Cinner, Eva Maire, Cindy Huchery, M. Aaron Macneil, Graham Graham, Camilo Mora, Tim McClanahan, Michel Barnes, John Kittinger, Christina Hicks, et al.

To cite this version:


HAL Id: hal-01824520
https://hal.umontpellier.fr/hal-01824520

Submitted on 27 Oct 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L’archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution 4.0 International License
Gravity of human impacts mediates coral reef conservation gains

Joshua E. Cinner|a, Eva Maire|b, Cindy Huchery|b, M. Aaron MacNeil|b, Nicholas A. J. Graham|ab, Camilo Mora|c, Tim R. McClanahan|a, Michele L. Barnes|ab, John N. Kittinger|d, Christina C. Hicks|ab, Stephanie D’Agata|ab, Andrew S. Hoey|a, Georgina G. Gurney|a, David Feary|b, Ivor D. Williams|a, Michel Kulbicki|a, Laurent Vigliola|a, Laurent Wantiez|a, Graham J. Edgar|d, Rick D. Stuart-Smith|a, Stuart A. Sandin|a, Alison Green|, Marah J. Hardt|d, Maria Beger|d, Alan M. Friedlander|a, Shaun K. Wilson|y, Eran Brokovich|a, Andrew J. Brooks|a, Juan J. Cruz-Motta|a, David J. Booth|c, Pascale Chabanet|d, Charlotte Gough|e, Mark Tupper|f, Sebastian C. A. Ferse|g, U. Rashid Sumailah|h, Shinta Parredo|a, and David Mouillot|a,b

*Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia; |bMarine Biodiversity Exploration and Conservation, UMR Institut de Recherche pour le Développement-UMR Institut Français de Recherche pour l’Exploitation de la Mer 9190, University of Montpellier, 34095 Montpellier Cedex, France; |cAustralian Institute of Marine Science, Townsville, QLD 4810, Australia; |dDepartment of Biology, Dalhousie University, Halifax, NS B3J 1S5, Canada; |eCarnegie Endowment Centre, Lancaster University, LA1 4YQ Lancaster, United Kingdom; |fDepartment of Geography, University of Hawaii at Manoa, Honolulu, HI 96822; |gGlobal Marine Program, Wildlife Conservation Society, Bronx, NY 10460; |hDepartment of Botany, University of Hawaii at Manoa, Honolulu, HI 96822; |iCenter for Oceans, Conservation International, Honolulu, HI 96823; |jCenter for Biodiversity Outcomes, Julie Ann Wrigley Global Institute of Sustainability, Life Sciences Center, Arizona State University, Tempe, AZ 85281; |kLaboratoire d’Excellence LABEX CORAIL, UMR-Institut de Recherche pour le Développement-UR-CNRS ENTROPE, BP A5, 98848 Nouméa Cedex, New Caledonia; |lSchool of Life Sciences, University of Nottingham, NG7 2RD Nottingham, United Kingdom; |mCoral Reef Ecosystems Program, NOAA Pacific Islands Fisheries Science Center, Honolulu, HI 96818; |nUMR Entropie, Labex Corail, Institut de Recherche pour le Développement, Université de Perpignan, 66000 Perpignan, France; |oEA4243 LIVE, University of New Caledonia, BPRA 98851 Noumea cedex, New Caledonia; |pInstitute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia; |qScripps Institution of Oceanography, University of California, La Jolla, CA 92093; |rThe Nature Conservancy, Brisbane, QLD 4011, Australia; |sFuture of Fish, Bethesda, MD 20814; |tAustralian Research Council Centre of Excellence for Environmental Decisions, Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, QLD 4074, Australia; |uSchool of Biology, Faculty of Biological Sciences, University of Leeds, LS2 9JT Leeds, United Kingdom; |vFisheries Ecology Research Laboratory, Department of Biology, University of Hawaii, Honolulu, HI 96822; |wPristine Seas Program, National Geographic Society, Washington, DC 20036-4688; |xDepartment of Parks and Wildlife, Kensington, Perth, WA 6151, Australia; |yOceans Institute, University of Western Australia, Crawley, WA 6009, Australia; |zThe Israel Society of Ecology and Environmental Sciences, 6773323 Tel Aviv, Israel; |{Marine Science Institute, University of California, Santa Barbara, CA 93106-6150; |}Department of Ciencias Marinas, Recinto Universitario de Mayaguez, Universidad de Puerto Rico, Mayaguez 00680, Puerto Rico; ||School of Life Sciences, University of Technology Sydney, NSW 2007, Australia; |{|UMR ENTROPE, Laboratoire d’Excellence LABEX CORAIL, Institut de Recherche pour le Développement, CS 41095, 79495 Sainte Clotilde La Réunion (RF); |}Omnibus Business Centre, Blue Ventures Conservation, N 9DP London, United Kingdom; |}Advanced Centre for Coastal and Ocean Research and Development, University of Trinidad and Tobago, Chaguaramas, Trinidad and Tobago, W.I; |{Leibniz Centre for Tropical Marine Research, D-28359 Bremen, Germany; and |{Fisheries Economics Research Unit, Institute for the Oceans and Fisheries and Liu Institute for Global Studies, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

Edited by David M. Karl, University of Hawaii, Honolulu, HI, and approved May 15, 2018 (received for review May 17, 2017)

Coral reefs provide ecosystem goods and services for millions of people in the tropics, but reef conditions are declining worldwide. Effective solutions to the crisis facing coral reefs depend in part on understanding the context under which different types of conservation benefits can be maximized. Our global analysis of nearly 1,800 tropical reefs reveals how the intensity of human impacts in the surrounding seascape, measured as a function of human population size and accessibility to reefs (“gravity”), diminishes the effectiveness of marine reserves at sustaining reef fish biomass and the presence of top predators, even where compliance with reserve rules is high. Critically, fish biomass in high-compliance marine reserves located where human impacts were low sustained top predators. Fish biomass inside marine reserves declined along a gradient of human impacts in surrounding areas; however, reserves located where human impacts were moderate had the greatest difference in fish biomass compared with openly fished areas. Reserves in low-human-impact areas are required for sustaining ecological functions like high-order predation, but reserves in high-impact areas can provide substantial conservation gains in fish biomass.

Significance

Marine reserves that prohibit fishing are a critical tool for sustaining coral reef ecosystems, yet it remains unclear how human impacts in surrounding areas affect the capacity of marine reserves to deliver key conservation benefits. Our global study found that only marine reserves in areas of low human impact consistently sustained top predators. Fish biomass inside marine reserves declined along a gradient of human impacts in surrounding areas; however, reserves located where human impacts are moderate had the greatest difference in fish biomass compared with openly fished areas. Reserves in low-human-impact areas are required for sustaining ecological functions like high-order predation, but reserves in high-impact areas can provide substantial conservation gains in fish biomass.


The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

Data deposition: A gridded global gravity data layer is freely available at dx.doi.org/10.4225/28/5a0e7b1bc30e.

To whom correspondence should be addressed. Email: Joshua.Cinner@jcu.edu.au.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1708001115/-/DCSupplemental.

The world’s coral reefs are rapidly degrading (1–3), which is diminishing ecological functioning and potentially affecting the well-being of the millions of people with reef-dependent livelihoods (4). Global climate change and local human impacts (such as fishing) are pervasive drivers of reef degradation (1, 5). In

marine reserves | fisheries | coral reefs | social-ecological | socioeconomic
response to this “coral reef crisis,” governments around the world have developed a number of reef conservation initiatives (1, 6, 7). Our focus here is on the efficacy of management tools that limit or prohibit fishing. Management efforts that reduce fishing mortality should help to sustain reef ecosystems by increasing the abundance, mean body size, and diversity of fishes that perform critical ecological functions (8–10). In practice, however, outcomes from these reef-management tools have been mixed (5, 11–13).

A number of studies have examined the social, institutional, and environmental conditions that enable reef management to achieve key ecological outcomes, such as sustaining fish biomass (5, 14, 15), coral cover (16), or the presence of top predators (17). These studies often emphasize the role of: (i) types of key management strategies in use, such as marine reserves where fishing is prohibited, or areas where fishing gears and/or effort are restricted to reduce fishing mortality (8, 18); (ii) levels of compliance with management (12, 19, 20); (iii) the design characteristics of these management initiatives, for example the size and age of reserves, and whether they are placed in remote versus populated areas (11, 21); and (iv) the role of social drivers, such as markets, socioeconomic development, and human demographics that shape people’s relationship with nature (14, 22).

In addition to examining when key ecological conditions are sustained, it is also crucial to understand the context under which conservation gains can be maximized (23, 24). By conservation gains, we are referring to the difference in a conservation outcome (e.g., the amount of fish biomass) when some form of management (i.e., a marine reserve or fishery restriction) is implemented relative to unmanaged areas. These conservation gains can be beneficial for both people and ecosystems. For example, increased fish biomass inside marine reserves is not only related to a range of ecosystem characteristics of these management initiatives, for example the size and age of reserves, and whether they are placed in remote versus populated areas (11, 21); and (iv) the role of social drivers, such as markets, socioeconomic development, and human demographics that shape people’s relationship with nature (14, 22).

In addition to examining when key ecological conditions are sustained, it is also crucial to understand the context under which conservation gains can be maximized (23, 24). By conservation gains, we are referring to the difference in a conservation outcome (e.g., the amount of fish biomass) when some form of management (i.e., a marine reserve or fishery restriction) is implemented relative to unmanaged areas. These conservation gains can be beneficial for both people and ecosystems. For example, increased fish biomass inside marine reserves is not only related to a range of ecosystem characteristics of these management initiatives, for example the size and age of reserves, and whether they are placed in remote versus populated areas (11, 21); and (iv) the role of social drivers, such as markets, socioeconomic development, and human demographics that shape people’s relationship with nature (14, 22).

In addition to examining when key ecological conditions are sustained, it is also crucial to understand the context under which conservation gains can be maximized (23, 24). By conservation gains, we are referring to the difference in a conservation outcome (e.g., the amount of fish biomass) when some form of management (i.e., a marine reserve or fishery restriction) is implemented relative to unmanaged areas. These conservation gains can be beneficial for both people and ecosystems. For example, increased fish biomass inside marine reserves is not only related to a range of ecosystem characteristics of these management initiatives, for example the size and age of reserves, and whether they are placed in remote versus populated areas (11, 21); and (iv) the role of social drivers, such as markets, socioeconomic development, and human demographics that shape people’s relationship with nature (14, 22).

In addition to examining when key ecological conditions are sustained, it is also crucial to understand the context under which conservation gains can be maximized (23, 24). By conservation gains, we are referring to the difference in a conservation outcome (e.g., the amount of fish biomass) when some form of management (i.e., a marine reserve or fishery restriction) is implemented relative to unmanaged areas. These conservation gains can be beneficial for both people and ecosystems. For example, increased fish biomass inside marine reserves is not only related to a range of ecosystem characteristics of these management initiatives, for example the size and age of reserves, and whether they are placed in remote versus populated areas (11, 21); and (iv) the role of social drivers, such as markets, socioeconomic development, and human demographics that shape people’s relationship with nature (14, 22).
complied with; (ii) restricted fishing, where there are actively enforced restrictions on the types of gears that can be used (e.g., bans on spear guns) or on access (e.g., marine tenure systems that restrict fishing by “outsiders”); or (iii) high-compliance marine reserves, where fishing is effectively prohibited (Materials and Methods). We hypothesized that our ecological indicators would decline with increasing gravity in fished areas, but that marine reserves areas would be less sensitive to gravity. To test our hypotheses, we used general and generalized linear mixed-effects models to predict target fish biomass and the presence of top predators, respectively, at each site based on gravity and management status, while accounting for other key environmental and social conditions thought to influence our ecological outcomes (14) (Materials and Methods). Based on our models, we calculated expected conservation gains along a gravity gradient as the difference between managed sites and openly fished sites.

Our analysis reveals that human gravity was the strongest predictor of fish biomass (Fig. 2 and SI Appendix, Fig. S1). Fish biomass consistently declined along a human gravity gradient, a trend particularly evident at the nation/state scale (Fig. 2 C–E). However, this relationship can vary by management type (Fig. 2 and SI Appendix, Fig. S1). Specifically, we found that biomass in reserves demonstrated a flatter (but still negative) relationship with gravity compared with openly fished and restricted areas (Fig. 2B). In the highest-gravity locations, modeled fish biomass in marine reserves was approximately five times higher than in fished and restricted areas (Fig. 2B). The relationship between reserves and fished areas (Fig. 2B) was due to a strong interaction between gravity and reserve age such that older reserves contributed more to biomass in high-gravity situations than in low-gravity ones (SI Appendix, Fig. S1). This is likely due to fish stocks at high-gravity sites being heavily depleted and requiring decades to recover, whereas low-gravity sites would likely require less time to reach unfished biomass levels (8). Thus, given average reserve age in our sample (15.5 y), biomass in reserves did not decline as rapidly with gravity compared with fished and restricted areas (Fig. 2B).

In the highest-gravity locations, modeled fish biomass in marine reserves was approximately five times higher than in fished areas (270 kg/ha compared with 56 kg/ha) (Fig. 2B). At the reef site scale, there was considerable variability in reef fish biomass, particularly at low gravity (Fig. 2 F–H). For example, at the lowest-gravity locations, biomass levels in reserves spanned more than three orders-of-magnitude (Fig. 2F). Importantly, there was never extremely high biomass encountered in high-gravity locations. Our estimates of target fish biomass into our supplemental analysis, we also examined target fish biomass with the biomass of top predators excluded, which displays a similar trend, but with lower fish biomass in reserves at low gravity compared with when top predators are included (SI Appendix, Fig. S2).

A key finding from our study is that top predators were encountered on only 28% of our reef sites, but as gravity increases, the probability of encountering top predator on tropical coral reefs dropped to almost zero (<0.005), regardless of management (Fig. 3). The probability of encountering top predators was strongly related to gravity and the type of management in place, as well as sampling methodology and area surveyed (Fig. 3 and SI Appendix, Fig. S1). At low gravity, the probability of encountering a top predator was highest in marine reserves (0.59) and lowest in fished areas (0.14), when controlling for sampling and other environmental and social drivers (Fig. 3 and SI Appendix, Fig. S1).

Our study demonstrates the degree to which fish communities inside marine reserves can be affected by human impacts in the broader seascape (Figs. 2 and 3). Critically, high-compliance marine reserves in the lowest-gravity locations tended to support more than four times more fish biomass than the highest-gravity reserves (1,150 vs. 270 kg/ha, respectively) (Fig. 2F). Similarly, the modeled probability of encountering a top predator decreased by more than 100-fold from 0.59 in low-gravity reserves to 0.0046 in the highest-gravity reserves (Fig. 3B). Our study design meant that it was not possible to uncover the mechanisms responsible for this decline of ecological condition indicators within marine reserves along a gravity gradient, but this pattern of depletion is likely related to: (i) human impacts in the surrounding seascape (fishing, pollution, and so forth) affecting ecological processes (recruitment, feeding behavior, and so forth) within reserves (33, 34); (ii) almost every marine reserve is likely to have some degree of poaching, even where compliance is considered high (20, 35) and the cumulative impacts from occasional poaching events is probably higher in high-gravity situations; (iii) the life history of top predators, such as old age of reproduction and small clutch size for some (e.g., sharks), which makes then particularly susceptible to even mild levels of exploitation (36); and (iv) high-gravity marine reserves in our sample possibly being too young or too small to provide substantial conservation gains (11, 37). We conducted a supplementary analysis to further examine this latter potential explanation. Because of collinearity, we could not directly account for reserve size in our model, but conducted a supplemental analysis where we separated reserves into small (<28 km²) and large (Materials and Methods and SI Appendix, Fig. S3). We found that the biomass and probability of encountering top predators was higher in large compared with small reserves, but surprisingly, we found a flatter slope for small compared with large reserves (SI Appendix, Fig. S3). However, there were no large high-compliance reserves in high-gravity areas in our sample, likely due to the social and political difficulties in establishing large reserves near people (38). Because there is little overlap between large and small reserves along the gravity gradient in our sample, we are unable to distinguish the effects of reserve size from those of gravity, but this is an important area for future research. Additionally, we modeled how the relationship between gravity and our ecological outcomes changed with reserve age, comparing outcomes using the average reserve age (15.5 y) to those from reserves nearly twice as old (29 y, which was the third quartile of our global distribution in reserve age). Older reserves were predicted to sustain an additional 180 kg/ha (+66%) of fish biomass at the highest levels of gravity compared with average age reserves. However, the effects of reserve age on the probability of encountering a top predator was less marked: the modeled probability of encountering a top predator in older reserves (29 y) was only 0.01, compared with <0.005 for average age (~15 y) reserves, suggesting that small reserves common in high-gravity situations can support high levels of biomass, but are unlikely to sustain top predators, even when they are mature.

Although absolute fish biomass under all management categories declined with increasing gravity (Fig. 2B), the maximum expected conservation gains (i.e., the difference in biomass between reserves managed) differed by management type along the gravity gradient (Fig. 4). Interestingly, the conservation gains for restricted fishing is highest in low-gravity situations, but rapidly declines as human impacts increase (Fig. 4A) (39). For marine reserves, biomass conservation gains demonstrated a hump-shaped pattern that peaked at very low gravity when predators were included in the biomass estimates (Fig. 4A, solid blue line). When top predators were excluded from biomass estimates, conservation gains peaked at intermediate gravity levels, and were higher in high gravity compared with low gravity (Fig. 4A, dotted blue line). Our results highlight how the expected differences between openly fished and marine reserves change along a gravity gradient, given a range of other social and environmental conditions that are controlled for within our model (SI Appendix, Fig. S1). Thus, differences in these trends are relative to average conditions, and individual reserves may demonstrate larger or smaller biomass build-up over time, which can vary by fish groups or families (e.g., ref. 40).

In an effort to minimize costs to users, many marine reserves, particularly the large ones, tend to be placed in remote locations that experience low human pressure (24, 41). However, critics of marine reserves in remote locations suggest that limited resources could be better spent protecting areas under higher threat that could potentially yield greater conservation gains (23, 24, 42). Our results make explicit the types of benefits—and the limitations—to placing reserves in high versus low human-impact locations. We found that for nontop predator reef fishes,
substantial conservation gains can occur at even the highest-gravity locations but that optimal gains are obtained at moderate gravity (Fig. 4A). Our results also show that low-gravity marine reserves (and to a lesser extent low-gravity fisheries restrictions) are critical to support the presence of top predators (Fig. 3). However, the expected conservation gains for top predators declines rapidly with gravity in both marine reserves and restricted areas (Fig. 4B). Our results illustrate a critical ecological trade-off inherent in the placement of marine reserves: high-gravity reserves can have the substantial conservation gains for fish biomass, yet they are unlikely to support key ecosystem functions like predation, even with high levels of compliance. This highlights the importance of having clear objectives for conservation initiatives and recognizing the trade-offs involved.

Our analysis does not allow us to uncover the mechanisms behind why we might observe the greatest differences in top predators between marine reserves and fished areas in low-gravity locations. A plausible explanation is that top predators, such as sharks, are...
particularly vulnerable to fishing (17) and are exposed to some fishing even in the most remote fished areas, driven by the extremely high price for shark fins [shark fins can fetch US$960/kg in wholesale markets (45), compared with only $43/kg for parrotfish in European supermarkets (46)]. Thus, even small amounts of fishing in remote openly fished areas may be depleting top predators, which creates a large difference between low-gravity–fished areas and marine reserves. This difference may diminish along the gravity because top predators tend to have large home ranges (37), and there were only small reserves in high-gravity locations (SI Appendix, Fig. S3), which may mean that existing high-gravity reserves are not likely big enough to support the large home ranges of many predators (37, 47).

Fig. 3. Model-predicted relationships between human gravity and the probability of encountering top predators under different types of fisheries management. (A) Map of our study sites indicating the presence of top predators. (B) Model-predicted relationships of how the probability of encountering predators declines as gravity increases. Shaded areas represent 95% confidence intervals. The presence of top predators along a gravity gradient under different types of management at the nation/state (C–E) and site (F–H) scale; openly fished (red), restricted (green), and high-compliance marine reserves (blue). Bubble size in C–E reflect the number of reef sites in each nation/state, scaled for each management type (such that the largest bubble in each panel represent the highest number of sites per nation/state for that type of management) (SI Appendix, Table S5). Nation/state name abbreviations for F–H in SI Appendix, Table S5.
Successful conservation also depends on a range of social considerations (48). For example, gear restrictions often have greater support from local fishers (49) and are usually implemented over greater reef areas than marine reserves. We show here that there are conservation gains produced by gear restrictions, although they are low relative to marine reserves (Fig. 4). Thus, in locations where a lack of support makes establishing marine reserves untenable, gear restrictions may still provide incremental gains toward achieving some conservation goals (8), particularly for specific fish groups and families (39).

As a supplemental analysis, we examined the conservation gains for biomass of nontarget species (SI Appendix, Figs. S1D and S4). This supplemental analysis addresses whether the effects of gravity on reef fish communities are from fishing or other impacts, such as sedimentation or pollution. We found very different patterns for nontarget species compared with target species, suggesting the relationship between target fish biomass and gravity (SI Appendix, Fig. S1) is primarily driven by fishing pressure.

Overall, our results demonstrate that the capacity to not only sustain reef fish biomass and the presence of top predators, but also the potential to achieve conservation gains, may be highly dependent on the level of human impact in the surrounding seascape. It is therefore essential to consider the global context of present and future human gravity in coral reef governance. Consequently, we calculated gravity of human impacts for every reef cell globally using a 10° × 10-km grid across the world’s coral reefs (Fig. 5). Critically, the distribution of gravity varies substantially among regions, with the central and eastern Indo-Pacific demonstrating lower-gravity values. Even within a region, there can be substantial variability in gravity values. For example, the Central Indo-Pacific has highly contrasting gravity patterns, with Southeast Asian reefs (Fig. 5A, 3) generally showing extremely high-gravity values while Australian and Melanesian reefs (Fig. 5A, 4) are dominated by relatively low-gravity values.

The ways in which gravity will increase over time, and how the impacts of gravity on reef systems can be reduced, is of substantial concern for coral reef governance. The potential benefits of protecting locations that are currently remote could increase over time as human populations and the accessibility of reefs change (50). Demographic projections of high migration and fertility rates in some countries suggest substantial increases in coastal human populations in developing countries, where the majority of coral reefs are located (5, 51–53). Development projects that address high rates of fertility through improvements in women’s education, empowerment, and the expansion of family-planning opportunities have successfully reduced fertility rates (54, 55). Such initiatives, when partnered with resource management, have the potential to be beneficial to both people and reefs. Demographic changes, such as increased migration in coastal areas, are also expected to be coupled with coastal development and road building that will increase the accessibility of reefs. For example, previously uninhabited areas have become more accessible, as evidenced by China’s recent Belt and Roads Initiative and island-building enterprise in the South China Sea (56–58). Investments in sustainable planning of coastal development and road building could help to minimize unnecessary increases in reef accessibility. Importantly, stressing increases in gravity is only part of the potential solution space: it will also be important to dampen the mechanisms through which gravity operates, such as a given level of gravity can have a lesser impact on reef systems (1). People’s environmental behavior is fundamentally driven by their social norms, tastes, values, practices, and preferences (59), all of which can be altered by policies, media, and other campaigns in ways that could change the local relationship between gravity and reef degradation.

**Gravity Future Directions**

Our gravity index (Materials and Methods and Box 1) makes several key assumptions that could potentially be refined in further applications. First, our application of gravity held friction constant across each specific type of surface (i.e., all paved roads had the same friction value). Future applications of more localized studies could vary travel time to reflect the quality of road networks, topographic barriers to access (such as cliffs), and the availability of technology. Similarly, future applications could also aim to incorporate local information about fishing fleet efficiency. Second, our adaptation of the gravity model (31) is unidirectional, assuming a constant level of attraction from any reef (i.e., gravity varies based on human population size, but not
on the quality or quantity of fish on a specific reef). Reefs with more fish, or higher fish value, could be more attractive and exert a higher pull for exploitation (60). Likewise, societal values and preferences can also make certain fish more or less attractive. Our adaptation of gravity was designed to examine the observed conditions of reefs as a function of potential interactions with markets and local settlements, so our modification of the concept for this application was appropriate. However, future applications wishing to predict where reefs may be most vulnerable might wish to consider incorporating fish biomass or composition (i.e., potential market price of reef fish) in the gravity equation. Third, our database was not designed to look at ecological changes in a single location over time. However, future applications could examine whether ecological recovery in reserves (8) depends on the level of gravity present. To this end, we provide a global dataset of gravity for every reef pixel globally (Materials and Methods).

We demonstrate that human impacts deplete reef fish stocks and how certain types of management can mediate but not eliminate these pressures. In an era of increasing change, the global network of marine reserves may not safeguard reef fish communities from human impacts adequately enough to ensure key ecological functions, such as predation, are sustained. Efforts must be made to both reduce and dampen key drivers of change (1, 61), while maintaining or improving the well-being of reef-dependent people. Importantly, we find evidence that both

---

**Fig. 5.** Distribution of gravity on the world’s coral reefs. (A) Map of gravity calculated for every coral reef in the world ranging from blue (low gravity) to red (high gravity). The four coral reef realms (70) are delineated. Insets highlight gravity for key coral reef regions of the world: (1) Red Sea, (2) Western Indian Ocean, (3) Southeast Asia, (4) Great Barrier Reef of Australia and the South Pacific, (5) Caribbean. For visual effect, gravity values in Inset maps are also given vertical relief, with higher relief indicating higher gravity values. (B) Distribution of gravity values per coral reef realm.
remote and human-surrounded reserves can produce different types of conservation gains. Ultimately, multiple forms of management are needed across the seascape to sustain coral reef fishes and the people who depend upon them.

Materials and Methods

Scales of Data. Our data were organized at three spatial scales: reef site (n = 1,798), reef cluster (n = 734), and nation/state (n = 41).

Reef site is the smallest scale, which had an average of 2.4 surveys (transsects), hereafter referred to as “reef.”

For reef cluster (which had an average of 2.4 ± 2.4 reef sites), we clustered reefs together that were within 4 km of each other, and used the centroid to estimate reef cluster-level social and environmental covariates. To define reef clusters, we first estimated the linear distance between all reef sites, then used a hierarchical analysis with the complete-linkage clustering technique based on the maximum distance between reefs. We set the cut-off at 4 km to select mutually exclusive sites where reefs cannot be more than 4 km. The choice of 4 km was informed by a 3-y study of the spatial movement patterns of artisanal coral reef fishers, corresponding to the highest density of fishing activities on reefs based on GPS-derived effort density maps of artisanal coral reef fishing activities (62).

This clustering analysis was carried out using the R functions “hclust” and “cutree.”

A larger scale in our analysis was “nation/state” (nation, state, or territory, which had an average of 44 ± 59 reef clusters), which are jurisdictions that generally correspond to individual nations (but could also include states, territories, overseas regions), within which sites were nested for analysis.

Targeted fish biomass. Reef fish biomass estimates were based on visual counts in 1,798 reef sites. All surveys used standard belt-transects, distance sampling, or point-counts, and were conducted between 2004 and 2013. Where data from multiple years were available from a single reef site, we included only data from the year closest to 2010. Within each survey area, reef-associated fishes were identified to species level, their abundance counted, and total length (TL) estimated, with the exception of one data provider who measured biomass at the family level. To make estimates of targeted biomass from these transect-level data comparable among studies, we did the following. (i) We retained families that were consistently studied, commonly targeted, and were above a minimum size cut-off. Thus, we retained counts of >10 cm diurnally active, noncryptic reef fish that are resident on the reef (14 families), excluding sharks and semipelagic species (SI Appendix, Table S1). We calculated total biomass of targeted fishes on each reef using standard published species-level length–weight relationship parameters or those available on FishBase (63). When length–weight relationship parameters were not available for a species, we used the parameters for a closely related species or genus. For comparison, we also calculated nontarget fish biomass (SI Appendix, Table S1). (ii) We directly accounted for depth and habitat as covariates in the model (see Environmental Drivers, below). (iii) We accounted for differences among census methods by including the census method (standard belt-transects, distance sampling, or point-counts) as a covariate in the model. (iv) We accounted for differences in sampling area by including total sampling area for each reef (m²) as a covariate in the model.

Top predators. We examined the presence/absence of eight families of fish considered top predators (SI Appendix, Table S1). We considered presence/ absence instead of biomass because biomass was heavily zero inflated.

Gravity. We first developed a gravity index for each of our reef sites where we had in situ ecological data. We gathered data on both population estimates and semipelagic species (i.e., targets for fishing effort, which could have included areas inside marine protected areas that were not necessarily no-take). Or (ii) openly fished: regularly fished without effective restrictions. To determine these classifications, we used the expert opinion of the data providers, and triangulated this with a global database of marine reserve boundaries (66). We also calculated size (median = 113.6 km², mean = 217,516 km², SD = 304,417) and age (median = 9, mean = 15.5 y, SD = 14.5) of the no-take portion of each reserve. Reserve size was strongly related to our measure of gravity and could not be directly included in the analysis. We conducted a supplemental analysis where we stratified data into small (≤ 228 km²) and large (>228 km²) reserves based on a natural break in the data to illustrate: (i) how biomass and the presence of top predators might differ between small and large reserves; and (ii) how large reserves are absent in our sample in high gravity.

Other Social Drivers. To account for the influence of other social drivers that are thought to be related to the condition of reef fish biomass, we also included the following covariates in our model: cell within 500 km of reef site to get the “total gravity” within 500 km. We used the squared distance (or in our case, travel time), which is relatively common in geography and economics, although other exponents can be used (31) (Table S3).

We also developed a gravity index for each 10 × 10 km grid of reef in the world (Box 1), which we provide as an open-access dataset. The procedure to calculate gravity was similar to above with the only difference being in the precision of the location; the former was a single data point (reef site), while the latter was a grid cell (reef cell). For the purpose of the analysis, gravity was log-transformed and standardized.

We also explored various exponents (1–3) and buffer sizes (50, 250, and 500 km) to build nine gravity metrics. The metric providing the best model, so derived effort density maps of artisanal coral reef fishing activities (62). Travel time estimates across a particular surface could be affected by the infrastructure (e.g., road quality) and types of technology used (e.g., types of boats). These types of data were not available at a global scale but could be important modifications in more localized studies.

Gravity computation. To compute gravity, we calculated the population of the cell and divided that by the squared travel time between the reef site and the cell containing values that represent the time required to travel across them (32) (SI Appendix, Table S2). We termed this raster grid a “friction-surface” (with the time required to travel across different types of surfaces analogous to different levels of friction). To develop the friction-surface, we used global datasets of road networks, land cover, and shorelines: Road network data were extracted from the Vector Map Level 0 (VMap0) from the National Imagery and Mapping Agency’s (NIMA) Digital Chart of the World (DCW). We converted vector data from VMap0 to 1 km resolution raster.

Land cover data were extracted from the Global Land Cover 2000 (64).

To define the shorelines, we used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database v2.2.2.

These three friction components (road networks, land cover, and shorelines) were combined into a single friction surface with a Behrmann map projection (an equal area projection). We calculated our cost-distance models in R using the accCost function of the “gdistance” package. The function uses Dijkstra’s algorithm to calculate least-cost distance between two cells (i.e., taking into account the friction of a single friction surface of the landscape (65). Travel time estimates over a particular surface could be affected by the infrastructure (e.g., road quality) and types of technology used (e.g., types of boats). These types of data were not available at a global scale but could be important modifications in more localized studies.

Gravity computation. To compute gravity, we calculated the population of the cell and divided that by the squared travel time between the reef site and the cell containing values that represent the time required to travel across them (32) (SI Appendix, Table S2). We termed this raster grid a “friction-surface” (with the time required to travel across different types of surfaces analogous to different levels of friction). To develop the friction-surface, we used global datasets of road networks, land cover, and shorelines: Road network data were extracted from the Vector Map Level 0 (VMap0) from the National Imagery and Mapping Agency’s (NIMA) Digital Chart of the World (DCW). We converted vector data from VMap0 to 1 km resolution raster.

To define the shorelines, we used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database v2.2.2.

These three friction components (road networks, land cover, and shorelines) were combined into a single friction surface with a Behrmann map projection (an equal area projection). We calculated our cost-distance models in R using the accCost function of the “gdistance” package. The function uses Dijkstra’s algorithm to calculate least-cost distance between two cells (i.e., taking into account the friction of a single friction surface of the landscape (65). Travel time estimates over a particular surface could be affected by the infrastructure (e.g., road quality) and types of technology used (e.g., types of boats). These types of data were not available at a global scale but could be important modifications in more localized studies.

Gravity computation. To compute gravity, we calculated the population of the cell and divided that by the squared travel time between the reef site and the cell containing values that represent the time required to travel across them (32) (SI Appendix, Table S2). We termed this raster grid a “friction-surface” (with the time required to travel across different types of surfaces analogous to different levels of friction). To develop the friction-surface, we used global datasets of road networks, land cover, and shorelines: Road network data were extracted from the Vector Map Level 0 (VMap0) from the National Imagery and Mapping Agency’s (NIMA) Digital Chart of the World (DCW). We converted vector data from VMap0 to 1 km resolution raster.

Land cover data were extracted from the Global Land Cover 2000 (64).

To define the shorelines, we used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database v2.2.2.

These three friction components (road networks, land cover, and shorelines) were combined into a single friction surface with a Behrmann map projection (an equal area projection). We calculated our cost-distance models in R using the accCost function of the “gdistance” package. The function uses Dijkstra’s algorithm to calculate least-cost distance between two cells (i.e., taking into account the friction of a single friction surface of the landscape (65). Travel time estimates over a particular surface could be affected by the infrastructure (e.g., road quality) and types of technology used (e.g., types of boats). These types of data were not available at a global scale but could be important modifications in more localized studies.

Gravity computation. To compute gravity, we calculated the population of the cell and divided that by the squared travel time between the reef site and the cell containing values that represent the time required to travel across them (32) (SI Appendix, Table S2). We termed this raster grid a “friction-surface” (with the time required to travel across different types of surfaces analogous to different levels of friction). To develop the friction-surface, we used global datasets of road networks, land cover, and shorelines: Road network data were extracted from the Vector Map Level 0 (VMap0) from the National Imagery and Mapping Agency’s (NIMA) Digital Chart of the World (DCW). We converted vector data from VMap0 to 1 km resolution raster.

Land cover data were extracted from the Global Land Cover 2000 (64).

To define the shorelines, we used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database v2.2.2.

These three friction components (road networks, land cover, and shorelines) were combined into a single friction surface with a Behrmann map projection (an equal area projection). We calculated our cost-distance models in R using the accCost function of the “gdistance” package. The function uses Dijkstra’s algorithm to calculate least-cost distance between two cells (i.e., taking into account the friction of a single friction surface of the landscape (65). Travel time estimates over a particular surface could be affected by the infrastructure (e.g., road quality) and types of technology used (e.g., types of boats). These types of data were not available at a global scale but could be important modifications in more localized studies.
Environmental Drivers. Depth. The depth of reef surveys was grouped into the following categories:

- 0–4 m
- 5–10 m
- >10 m

We included the following habitat categories. (i) Slope: the reef slope habitat is typically on the ocean side of a reef, where the reef slopes down into deeper water. (ii) Crest: the crest reef habitat is the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (i.e., where the waves break). It is also typified by a change in the angle of the reef from an inclined slope to a horizontal reef flat. (iii) Flat: the reef flat habitat is typically horizontal and extends back from the reef crest for tens to hundreds of meters. (iv) Lagoon/back reef: lagoonal reef habitats are where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind high-cord (e.g., fringing reefs) or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous “lagoon style” reef habitat. Due to minimal representation among our sample, we excluded other less-prevalent habitat types, such as channels and banks. To verify the sites’ habitat information, we used the Millennium Coral Reef Mapping Project hierarchical data (68), Google Earth, and site depth information.

Productivity. We examined ocean productivity for each of our sites in milligrams of C per square meter per day (mg C m−2 d−1) (www.science.oregonstate.edu/ocean.productivity). Using the monthly data for years 2005–2010 (in hfd format), we imported and converted those data into ArcGIS. We then calculated yearly average and finally an average for all these years. We used a 100-km buffer around each of our sites and examined the average productivity within that radius. Note that ocean productivity estimates are less accurate for nearshore environments, but we used the best available data. For the purpose of the analysis, productivity was log-transformed.

Climate stress. We included an index of climate stress for corals, developed by Maina et al. (69), which incorporated 11 different environmental conditions, such as the mean and variability of sea-surface temperature.

Analyses. We first looked for collinearity among our covariates using bivariate correlations and variance inflation factor estimates. This led to the exclusion of several lowly described bivariate effects (but high-correlation among gravity and management (and a combination of gravity and reserve age) for consistency. All continuous covariates were standardized to account for broad differences in reef fish community structure attributable to a number of interlinked depth-related factors. Categories were necessary to standardize methods used by data providers and were determined by preexisting categories used by several data providers. Habitat. We included the following habitat categories. (i) Slope: the reef slope habitat is typically on the ocean side of a reef, where the reef slopes down into deeper water. (ii) Crest: the crest reef habitat is the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (i.e., where the waves break). It is also typified by a change in the angle of the reef from an inclined slope to a horizontal reef flat. (iii) Flat: the reef flat habitat is typically horizontal and extends back from the reef crest for tens to hundreds of meters. (iv) Lagoon/back reef: lagoonal reef habitats are where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind high-cord (e.g., fringing reefs) or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous “lagoon style” reef habitat. Due to minimal representation among our sample, we excluded other less-prevalent habitat types, such as channels and banks. To verify the sites’ habitat information, we used the Millennium Coral Reef Mapping Project hierarchical data (68), Google Earth, and site depth information.

We planned yearly average and finally an average for all these years. We used a 100-km buffer around each of our sites and examined the average productivity within that radius. Note that ocean productivity estimates are less accurate for nearshore environments, but we used the best available data. For the purpose of the analysis, productivity was log-transformed.

Climate stress. We included an index of climate stress for corals, developed by Maina et al. (69), which incorporated 11 different environmental conditions, such as the mean and variability of sea-surface temperature.