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LETTER

Reserve Sizes Needed to Protect Coral Reef Fishes

Nils C. Krueck[1,2], Christelle Legrand[2], Gabby N. Ahmadia[3], Estradivari[4], Alison Green[5], Geoffrey P. Jones[6], Cynthia Riginos[2], Eric A. Treml[7], & Peter J. Mumby[1,2]

[1] Marine Spatial Ecology Lab and Australian Research Council Centre of Excellence for Coral Reef Studies, The University of Queensland, St Lucia Campus, Brisbane, Queensland 4072, Australia
[2] School of Biological Sciences, The University of Queensland, St Lucia Campus, Brisbane, Queensland 4072, Australia
[3] Oceans Program, World Wildlife Fund United States, 1250 24th Street, Washington, DC 20037–1193, USA
[4] World Wildlife Fund Indonesia, Graha Simatupang Tower, Jalan Letjen TB Simatupang, Jakarta 12540, Indonesia
[5] The Nature Conservancy, 245 Riverside Drive, West End, Queensland 4101, Australia
[6] Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia
[7] School of BioSciences, The University of Melbourne, Melbourne, Victoria 3010, Australia

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Correspondence
Nils C. Krueck or Peter J. Mumby, Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia Campus, Brisbane, Queensland 4072. Tel.: +61 (7) 33651671; Fax: +61 (7) 33651655.
Email: nils.krueck@uqconnect.edu.au or p.j.mumby@uq.edu.au

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Abstract

Marine reserves are a commonly applied conservation tool, but their size is often chosen based on considerations of socioeconomic rather than ecological impact. Here, we use a simple individual-based model together with the latest empirical information on home ranges, densities and schooling behaviour in 66 coral reef fishes to quantify the conservation effectiveness of various reserve sizes. We find that standard reserves with a diameter of 1–2 km can achieve partial protection (≥50% of the maximum number of individuals) of 56% of all simulated species. Partial protection of the most important fishery species, and of species with diverse functional roles, required 2–10 km wide reserves. Full protection of nearly all simulated species required 100 km wide reserves. Linear regressions based on the mean home range and density, and even just the maximum length, of fish species approximated these results reliably, and can therefore be used to support locally effective decision making.

Introduction

Coral reefs around the world are threatened by multiple anthropogenic stressors, including local fishing activities as well as global climate change (Hughes *et al.* 2003). Unsustainable and destructive fishing alone can culminate in the collapse not only of fisheries but entire coral reef ecosystems (Jackson *et al.* 2001). However, fishery impacts can be tackled locally by limiting the use of certain fishing methods in marine protected areas (MPAs), and by prohibiting any type of fishing inside strict no-take marine reserves (see Dudley 2008 for definitions). Specifically to help protect coral reefs, most of which are situated in developing countries with low fisheries management capacity (Mora *et al.* 2009), marine reserves are seen as a feasible and critical conservation tool (White *et al.* 2014).

Following the rapid global implementation of marine reserves since 1992 (the Rio "Earth Summit"), numerous studies have analyzed reserve functioning, identifying important social, economic, and ecological drivers of conservation effectiveness (Lester *et al.* 2009; Mora & Sale 2011; Edgar *et al.* 2014). In addition to good governance with effective leadership, it is now clear that marine reserves are most likely to protect fish populations if they are sufficiently large, persistent, and enforced (Edgar *et al.* 2014). Yet, management decisions on the location and size of reserves tend to be driven by considerations of socioeconomic impact rather than conservation effectiveness (Margules & Pressey 2000),

specifically if a lack of knowledge on the abundance and movements of local fishery species precludes effective decision making (Sale *et al.* 2005). If reserves are too small, they can fail to ensure species conservation, simply because the abundance of fishes is not uniform and because the movements of fishes might extend beyond reserve boundaries so that they can still be fished (Moffitt *et al.* 2009; Gaines *et al.* 2010).

Over recent years, data on the densities and, critically, the movements of coral reef fishes have become increasingly available. These data show that many small species, including damselfishes, butterflyfishes, and angelfishes, have daily home ranges that are restricted to 500 m or less (Kramer & Chapman 1999; Green *et al.* 2015). Many larger species are more wide-ranging (up to 10 km), but extensive movements appear to be limited to some emperors, snappers, jacks, reef sharks, and seasonally migrating groupers (10–100 km) as well as large sharks and tunas (100s–1,000s km; Green *et al.* 2015). Information on coral reef fish movements has previously been used to make predictions about the conservation effectiveness of reserves, including species-specific guidelines on minimum reserve sizes (Kramer & Chapman 1999; Green *et al.* 2015). However, guidelines do not specify the consequences of alternative conservation decisions (Green *et al.* 2015), which would support stakeholder engagement and decision making. Here, we use a combination of empirical data on the density, schooling behavior, and home range of a representative selection of coral reef fishes in order to specify the relationship between reserve size and conservation effectiveness. We measure conservation effectiveness by using a simple spatial model to determine numbers of individual fish a given reserve can be expected to protect, and we analyze these numbers with respect to locally expected population sizes, the fishery value, and functional role of simulated species. We then derive linear regression coefficients that can be used by conservation planners to approximate our results and support locally effective conservation decisions.

Methods

Data collection

Movement data were compiled by accessing a recent review (Green *et al.* 2015). All coral reef fishes with data classified as "home range" were initially included. We then used fish surveys from lightly fished areas in the Solomon Islands (Pacific) and from MPAs in Belize (Caribbean) to add data on density and schooling behavior to matching species in our list ($n = 38$ from the Solomon Islands, $n = 18$ from Belize). Fish surveys using a very similar methodology for 10 other species in our list were identified by literature review, yielding a total of 66 species with robust and comparable data on home range, density, and schooling behavior. Additional information on the geographic distribution, maximum length, fishery value, habitat, and diet of this final set of species was downloaded from Fishbase (Froese & Pauly 2016; see Supporting Information Methods, Table S1 and Figure S1 for details).

Modeling procedure

To quantify the relationship between reserve size and conservation effectiveness, we developed a simple spatial model. The model sampled our empirical data set in order to capture natural variability in both the number and home range of individual fish encountered in hypothetical reserves. All simulations used a one-dimensional modeling environment at a resolution of 1 m, implicitly assuming that home ranges are circular.

All simulations were started by firstly determining the size of the seascape in which a reserve was enforced (e.g., 1 km). The model then implemented multiple, hypothetical fish surveys ($n = 100$ replicates per reserve size and species). These hypothetical surveys determined the number and distribution of fish present in the reserve. In the next step, the model assigned home range values to each fish (or group of fish), assuming that their previously assigned locations represent the centers of their home ranges, and that movements are thus confined to $0.5 \times$ the assigned home range value on either side of the assigned location. In the final step, the model then calculated whether the movements of individuals exceeded reserve boundaries. Conservatively, we assumed that this situation would lead to eventual mortality from fishing. That is, only individuals whose entire home range was contained within reserve boundaries were assumed to be protected. A more detailed description of the modeling procedure is given in the Supporting Information Methods.

Metrics of conservation effectiveness

Conservation effectiveness was calculated as the mean number of protected individuals per species across 100 replicate simulations for each reserve size between 100 m and 100 km. In combination with complementary data, such as total reserve coverage across species ranges, this metric is suitable for population viability analyses. Here, we focused on analyzing a more intuitive and localized metric by normalizing predictions of protected individuals based on the maximum number of individuals a given reserve could be expected to protect. For example, a mean density of 0.005 ± 0.005 fish/m^2 implies that

a 1 km wide reserve can be expected to provide for the protection of maximally 5 (±5) individuals. We assumed that "full" local protection was achieved if model predictions equaled or exceeded 95% of this expected maximum. Thus, if on average at least $0.95 \times 5 = 4.75$ individuals were predicted to be protected, a reserve size of 1 km was assumed to provide for full protection. "Partial" protection was assumed if fewer than 95% but at least 50% of the expected maximum number of individuals was predicted to be protected.

Data analysis

Relationships between mean home ranges, mean densities, and maximum lengths of fishes were visualized in scatter plots and characterized by calculating Pearson's correlation coefficient. Least-square linear regressions were used to determine how well these primary data alone could be used to approximate simulation-based results (see Supporting Information Methods for details). Maximum lengths of all species in an existing coral reef fish community in Kimbe Bay, Papua New Guinea (Table S2), were used as an example to apply resulting regression coefficients in order to quantify the conservation effectiveness of various reserve sizes. A link to download reserve design software that performs such calculations of reserve size conservation effectiveness based on regression coefficients for mean home ranges, mean densities, and maximum fish lengths will soon be available at www.marinespatialecologylab.org.

Practical application of model predictions

Assuming that fish are equally likely to move in any direction, our one-dimensional simulations represent the conservation effectiveness of the minimum diameter of a real (two-dimensional) reserve. However, conservation planners are more likely to apply model predictions in support of decisions on reserve sizes in one specific direction. A recent example of this is our own experience with the designation of no-take reserves in Indonesia. Most coral reefs in our study areas were fringing reefs, which extend along the coastline. While reef fishes might then have a potentially extensive home range in alongshore direction, their movements across a depth gradient in offshore direction are restricted by the extent of available reef habitat (from lagoons to reef slopes and any offshore reef patches). In consequence, we used predictions of conservation effectiveness to quantify the consequences of alternative decisions on reserve sizes in alongshore direction, while suitable reserve sizes in offshore direction were assessed based on local reef geomorphology.

Results

Relationships between the home range, density, and length of simulated fish species followed our general expectations. That is, home ranges and lengths were strongly positively correlated while densities and lengths were negatively correlated. The relationship between home ranges and densities was not clear (Figure S2).

Predicted numbers of protected individuals were highly variable (Table S3), corresponding, for example, to >2,000 individuals of butterflyfishes and not a single individual of some parrotfishes in a 1 km^2 reserve. Small reserves that are only 400 m wide, such as commonly found in the Philippines, achieved the partial protection of only 17% of all simulated species (i.e., ≥50% of the expected number of resident individuals moved within reserve boundaries). Most of these species were of comparatively low fishery value. Not surprisingly, larger reserves achieved higher protection levels for more species. For example, a 2 km wide reserve (global median) ensured the partial protection of 56% of all species, including several of high fishery value (Figures 1A and 2A). A reserve size of 10 km was required to achieve the partial protection of almost all species (94%).

Full protection, which we assumed if ≥95% of the expected number of resident individuals moved exclusively inside reserve boundaries, required much larger reserves than partial protection. With a global median diameter of 2 km, for example, standard reserves can be expected to achieve the full protection of only 2% of all simulated species. And, even much larger reserves with a diameter of 10 km must be expected to protect only 35% of all species fully, merely starting to include species of high fishery value (Figures 1B and 2C).

Across all modeling scenarios, we found that the number of partially protected species increased most rapidly up to a reserve size of 2 km. However, reserve sizes >2 km were needed to avoid underrepresenting certain functional groups (Figure 2B), which are groups of species assigned based on ecological role, such as feeding mode, rather than phylogeny (Table S1). Small reserves underrepresented primarily piscivores (including groupers, snappers, trevallies, and sharks), while 10 km wide reserves achieved the partial protection of almost all species and, thus, functional diversity. Full protection of nearly all species required a 100 km wide reserve (Figure 2D).

Conservation effectiveness predicted based on multiple linear regressions provided a close match to these outcomes based on explicit simulations ($R^2 \geq 0.81$, $P < 0.0001$, see Table 1). In general, data on the mean home range of fishes alone allowed for a robust estimate of reserve sizes required to achieve variable protection levels

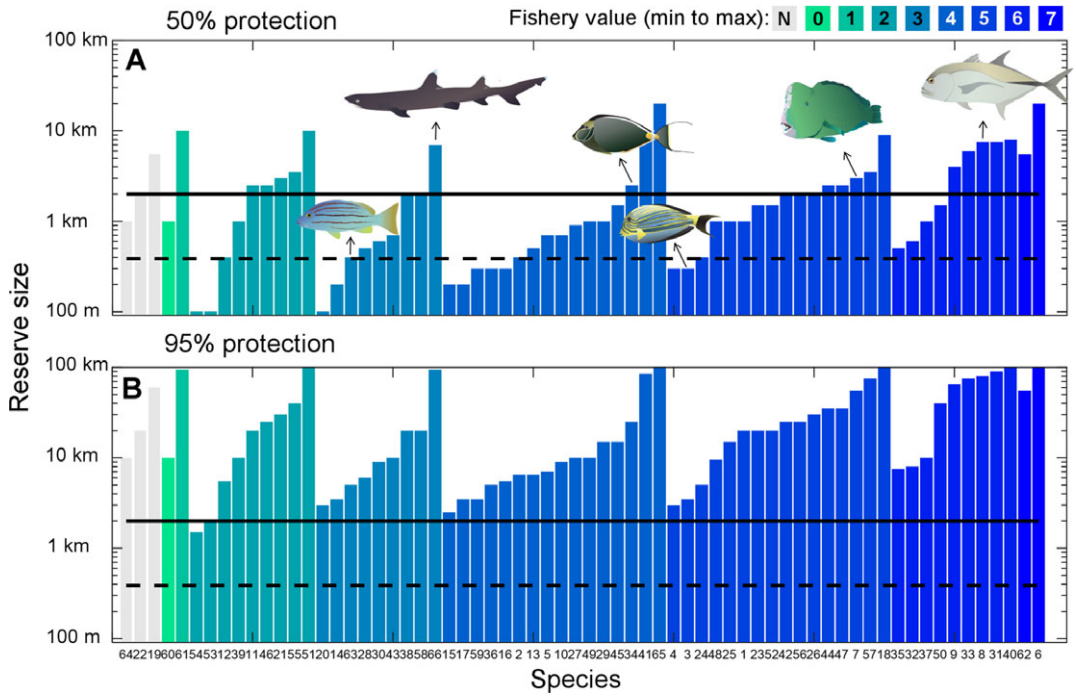

Figure 1 Reserve sizes needed to protect simulated coral reef fishes. Two alternative levels of protection are considered: (A) partial protection (≥50% of the expected maximum number of individuals) and (B) full protection (≥95% of the expected maximum number of individuals). Bars represent individual species ($n = 66$) and are color-coded to highlight differences in fishery value. Reference lines in plots denote the estimated median diameter of no-take reserves in the Philippines (dashed, 387 m) and worldwide (solid, 2 km; see Supporting Information Methods). Small numbers below bars reference individual species as listed in Table S1. N, not defined.

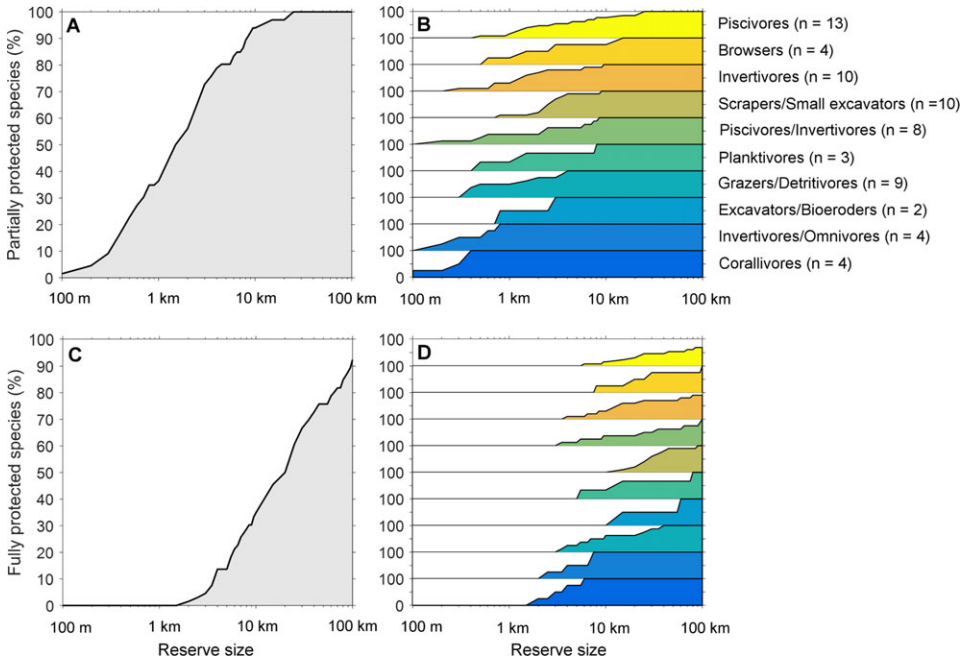

Figure 2 Percentages of species protected in reserves of increasing size. Results refer to "partial" protection (≥50% of the expected maximum number of individuals; A, B) and "full" protection (≥95% of the expected maximum number of individuals; C, D). Unequal proportions of colors in B and D highlight variation in the representation of functional groups. Functional groups are ordered based on reserve sizes needed to achieve maximum protection. Corallivores, for example, was the easiest group to protect, while piscivores required the largest reserves to achieve a given protection level.

Table 1 Summary of multiple linear regressions fitted to simulation-based predictions of effective reserve sizes

Protection level	R^2	Intercept	b1 (home range)	b2 (density)	b3 (home range × density)
50%	0.811	−1.879 (−3.978; 0.221)	1.174 (0.843; 1.505)	−1.153 (−1.510; −0.795)	0.128 (0.072; 0.183)
75%	0.832	−0.828 (−2.722; 1.066)	1.155 (0.856; 1.454)	−1.118 (−1.441; −0.796)	0.126 (0.076; 0.176)
95%	0.808	1.637 (−0.246; 3.519)	1.032 (0.728; 1.336)	−1.033 (−1.356; −0.712)	0.114 (0.062; 0.165)

All regressions were highly significant ($P < 0.0001$), explaining at least 81% of the variation in simulation-based predictions. Mean home range was always a highly significant predictor ($P \leq 1.2 \times 10^{-7}$), yielding close fits to simulated reserve sizes also in univariate regressions (see Supporting Information). Mean density was also a significant predictor ($P \leq 6.4 \times 10^{-5}$), but primarily when home ranges were small, resulting in a significant interaction term ($P \leq 9.1 \times 10^{-4}$). Values in brackets specify lower and upper 95% confidence intervals.

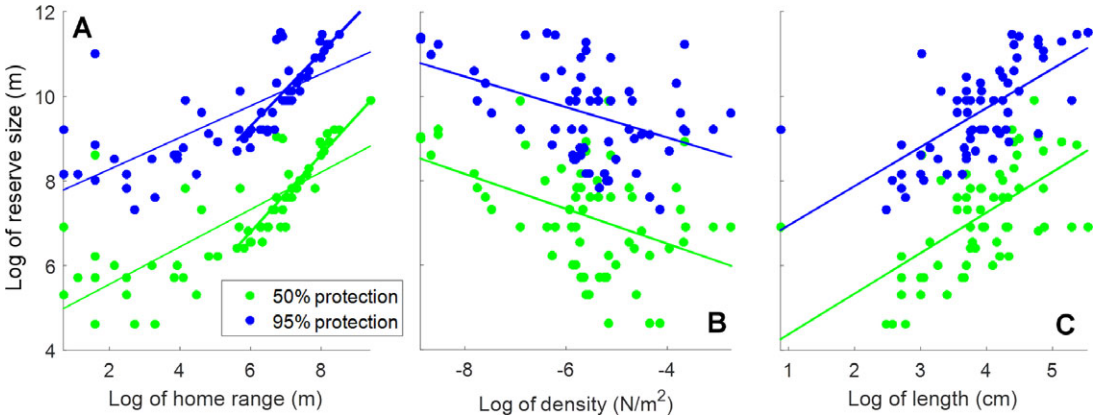

Figure 3 Relationship between predictors used for linear regressions and the simulated reserve sizes required for "partial" (green) and "full" (blue) protection of coral reef fishes. Mean home range (A) and density (B) were used in multiple regressions to predict simulated reserve sizes. More readily available estimates of maximum fish lengths (C) were used in univariate regressions to predict simulated reserve sizes. Mean home ranges >200 m were the single most important predictor (see thick regression line in A and Table S5). See Tables 1 and 2 and Supporting Information for details.

(Figure 3A). However, specifically when home ranges were small (<200 m) and densities highly variable (common for the many aggregating coral reef fish species), or if territoriality was assumed to minimize direct interactions among conspecifics, then density was an important predictor of conservation effectiveness (Figure 3B).

A close match between simulation- and regression-based predictions was achieved also by using maximum fish lengths as the single predictor (R^2 = 0.38–0.45; Table 2, Figure 3C). Length-based predictions were on average 1.4 (±1.2 SD) times higher than predictions based on the multivariate model. For partial protection, deviations in reserve size predictions were unlikely to exceed 1 km (Figure S3B), but deviations in predictions for full protection were more substantial (Figure S3C).

In our applied example, reserve sizes predicted to protect the coral reef fish community in Kimbe Bay, Papua New Guinea, yielded results similar to those based on explicit simulations. Reserve sizes of 2–10 km achieved the partial protection of almost the entire fish community, while full protection of most species, representing the complete functional or size-frequency spectrum, required >10 km wide reserves (Figure 4).

Table 2 Summary of univariate linear regressions based on maximum fish lengths fitted to simulation-based predictions of effective reserve sizes

Protection level	R^2	Intercept	b (fish length)
50%	0.384	3.418 (2.196; 4.640)	0.960 (0.655; 1.262)
75%	0.426	4.189 (3.061; 5.318)	0.966 (0.686; 1.246)
95%	0.447	6.026 (4.978; 7.075)	0.925 (0.659; 1.191)

Maximum fish length was a significant predictor across all protection levels ($P < 0.0001$), explaining at least 38% of the variation in simulation-based predictions (Figure 3C). Values in brackets specify lower and upper 95% confidence intervals.

Discussion

Marine reserves are increasingly used to help conserve functional coral reef ecosystems, specifically where the capacity to regulate human activities by other means is limited (White *et al.* 2014). Knowledge of the relationship between reserve size and conservation effectiveness is a fundamental requirement for decision makers to achieve this objective (Edgar *et al.* 2014). Here, we quantified the protection of coral reef fishes in reserves of various sizes, providing generic formulas that can easily be applied by

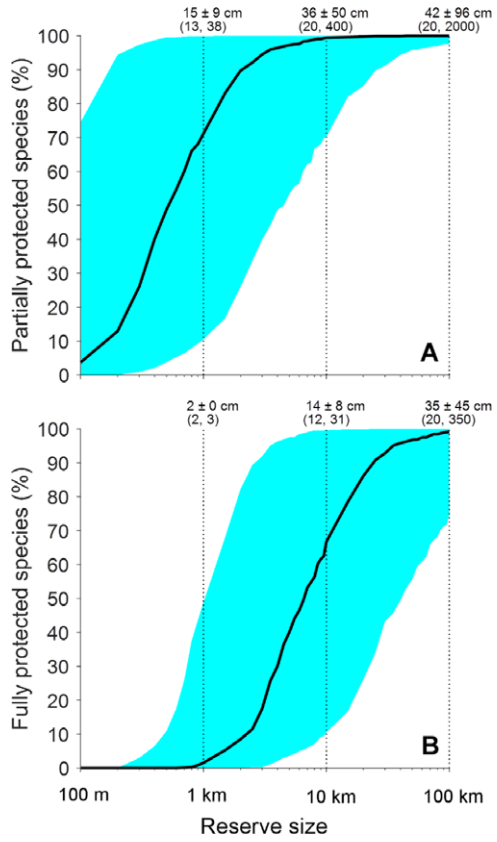

Figure 4 Percentage of the coral reef fish community in Kimbe Bay, Papua New Guinea, predicted to be protected in reserves of increasing size. Predictions are based on maximum fish lengths, approximating simulated reserve sizes required to achieve "partial" (50%; A) and "full" (95%; B) protection (see Table 2 and Supporting Information Methods for details). Light blue areas highlight 95% confidence limits. Numbers above dotted lines specify the size composition of protected fish communities, giving means ± SDs and in brackets medians and maximum lengths. Across all species, mean length was 42 ± 96 cm (20, 2,000).

conservation planners in order to support locally effective decision making. Importantly, this will be possible even if no data on the movements and densities of resident fish species are available.

Our study suggests that most coral reef fishes are at least partially protected in standard reserves around the world. However, our findings raise concerns that currently implemented reserves are biased toward the protection of small species of comparatively low fishery value. Reserves in the Philippines are an example of this potential bias, with diameters generally less than 1 km. Despite this, and even though underlying reasons are unclear, empirical data have shown that reserves in the Philippines function to restore the biomass of fishery species (e.g. Russ *et al.* 2004). Even minor increases in the diameter of reserves up to about 10 km should nevertheless help to increase both the number and functional representation of species experiencing increasing levels of protection.

Clearly, decisions on the size of reserves are based not only on considerations of conservation effectiveness but also of socioeconomic impact (Margules & Pressey 2000). For example, the short-term fishery impacts of large reserves might be overly burdensome (Brown *et al.* 2014; Ovando *et al.* 2016). It is also possible that decision makers seek to enforce small reserves, because they are expected to benefit fisheries by allowing for higher exports of adults and larvae to fished areas than large reserves (Kramer & Chapman 1999; Hastings & Botsford 2003; Gaines *et al.* 2010). In some cases, this fisheries management objective will compromise effective fish population recovery and species conservation in reserves (Moffitt *et al.* 2009). However, in coral reef fishes, current knowledge suggests that the scales of larval dispersal far exceed those of adult home ranges, including species that are large and important for fisheries (Almany *et al.* 2007; Harrison *et al.* 2012; Green *et al.* 2015; Jones 2015; Williamson *et al.* 2016; Almany *et al.* 2017). This novel insight suggests that trade-offs in decisions on reserve sizes to support biodiversity conservation versus fisheries management might often be negligible. Even a 10 km wide reserve, for example, which is likely to protect many coral reef fishes very effectively, is likely to allow for sufficient export of locally produced larvae to benefit adjacent fishing grounds (Krueck *et al.* 2017).

Most previously published recommendations of reserves sizes are close to or higher than 10 km (Metcalfe *et al.* 2015). Estimates of larval dispersal distances, for example, led to reserve size recommendations between 4 and 20 km in order to ensure that enough larvae are locally retained (Palumbi 2003; Shanks 2009; Shanks *et al.* 2003). Intuitively, the protection of adults might require even larger reserves, specifically if species are highly mobile (Palumbi 2004; Kaiser 2005). However, minimum recommended reserve sizes based on "rule of thumb" guidelines for the protection of adult coral reef fishes rarely exceed a few kilometers (Green *et al.* 2015). These "rule of thumb" guidelines assume that the diameter of a reserve should be larger than twice the mean home range of any focal species it aims to protect (Green *et al.* 2015). Applying this rule is likely to support the partial protection of many species, but our results suggest that full protection will require reserve diameters that are 28 ± 23 (mean ± SD) times higher than the mean home ranges of resident species. Earlier work on this relationship between home ranges and reserve sizes revealed higher conservation effectiveness (Kramer & Chapman 1999), but did not capture substantial natural variation in both home ranges and densities of individual fishes.

Notable uncertainties underlying the recommendations of reserve sizes in this and other studies include our current lack of understanding of the long-term movements of most fish species (Green *et al.* 2015). Moreover, even reserves that are larger than necessary to protect resident populations could fail to conserve species, if they do not cover an overall sufficient proportion of the meta-population (Botsford *et al.* 2001). Importantly, the meta-population includes all life history stages and critical habitats, such as nursery areas and spawning grounds. Multiple additional ecological criteria also need to be taken into account alongside decisions on the appropriate size and total coverage of reserves to ensure effective species conservation (Roberts *et al.* 2003; Green *et al.* 2015).

In addition to these considerations, one of the major uncertainties about the conservation effects of marine reserves is their impact on ecological interactions among multiple species. Our model did not capture such interactions, primarily because we would not have been able to parameterize them meaningfully. Nevertheless, our results provide support of ecosystem-based management by specifying the maximum level of functional representation a reserve of a given size can be expected to achieve. If species interactions generate trophic cascades (Mumby *et al.* 2012), then this will benefit some and disadvantage other species. However, specifically where reserves are needed to protect species under threat from heavy overfishing, species interaction strengths will tend to be weak (Bascompte *et al.* 2005). Both predators and their prey might then be able to recover (Micheli, Amarasekare *et al.* 2004).

Empirical data on the conservation effects of reserves suggest that declines in numbers or biomass relative to prereserve conditions are uncommon, affecting about 20% of all species (Micheli, Halpern *et al.* 2004). The vast majority of species across taxonomic and functional groups worldwide has been found to increase in both density and biomass within reserve boundaries (Halpern 2003; Lester *et al.* 2009). Interestingly, the relative magnitude of these positive effects does not generally scale with the size of reserves (Halpern 2003; Lester *et al.* 2009). Potential explanations of this counterintuitive observation include that important drivers of reserve impacts, such as the duration since reserve establishment, fisher compliance and relative fishing pressure, were not considered. Another potential explanation is that fishes actively avoid the exposure to fishing mortality. But, perhaps most importantly, most reviews of reserve impacts have not been able to focus on studies explicitly designed to test the effect of reserve area or size, which might yield fundamentally different outcomes (Lester *et al.* 2009).

Along with a better empirical understanding of reserve size impacts, our work should be extended by developing a modeling approach that incorporates additional complexity and data. An important advancement of this study is the move from population- to individual-based assessments (Codling 2008) that capture our combined empirical understanding of natural variability in the density, schooling behavior, and home range movements of coral reef fishes. However, some defensible but conservative assumptions should be relaxed in future studies, including: (1) that individual home ranges are temporally stable and (2) that all individuals whose home ranges extend beyond reserve boundaries will eventually be fished. More complex modeling approaches could allow for simulating how joint decisions on reserve size, placement and total coverage interact to influence the behavior of both fishers and fishes. Behavioral changes might involve not only locally variable levels of fisher compliance and fishing pressure, but also contracted, relocated, or extended home ranges (see e.g. Abesamis & Russ 2005).

A recent meta-analysis of the effectiveness of reserves highlights that reserve size is one of the five key drivers of conservation success (Edgar *et al.* 2014). Thus, a precautionary approach to species protection and fisheries management demands explicit consideration of the ecological implications of decisions on reserve size. Our findings and regression-based coefficients allow reserve design practitioners to do so by quantifying the protection (and likely spillover) of locally important species under various alternative reserve size scenarios. Comparative illustrations of outcomes can highlight steep increases as well as plateaus in predicted reserve size effectiveness, which provided highly regarded decision support for recent reserve network designs in Indonesia that some of us were involved in.

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Supporting Information

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

Figure S1: Histograms of the primary data for 66 coral reef fish species used for simulations in this study.

Figure S2: Relationships between the home range, density, and maximum body length in 66 coral reef fishes.

Figure S3: Reserve sizes predicted based on multivariate versus univariate regression models.

Table S1: The data set used for simulations in this study (Excel)

Table S2: Taxonomic information and maximum length of coral reef fish species recorded in Kimbe Bay, Papua New Guinea (Excel)

Table S3: Mean number of protected individuals for all simulated species and reserve sizes (Excel)

Table S4: Mean percentage of expected maximum protection for all simulated species and reserve sizes (Excel)

Table S5: Summary of univariate linear regressions based on mean home ranges >200 m fitted to simulation-based predictions of effective reserve sizes. Mean home ranges >200 m were the single most important predictor across all protection levels ($P < 0.0001$), explaining at least 64% of the variation in simulation-based reserve size predictions (Figure 3A). Values in brackets specify lower and upper 95% confidence intervals. For species with home ranges ≤200 m, reserve sizes of 1, 2, and 5 km can be estimated to protect 50%, 75%, and 95% of all individuals, respectively (Figure 3A).

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