

LETTER

A Genuine Win-Win: Resolving the “Conserve or Catch” Conflict in Marine Reserve Network Design

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Abstract

To support fishing communities, reserves should ensure the persistence of meta-populations while boosting fisheries yield. However, so far their design from the onset has rarely considered both objectives simultaneously. Here we overcome this barrier in designing a network of reserves for the Caribbean spiny lobster, a species with long larval duration for which local management is considered pointless because the benefits of protection are believed to be accrued elsewhere. Our reserve design approach uses spatially explicit population models and considers ontogenetic migration, larval and adult movement. We show that yield and persistence are negatively related, but that both objectives can be maximized simultaneously during planning. Importantly, we also show that local efforts to manage spiny lobster, the most economically valuable marine resource in the Caribbean, can result in locally accrued benefits, overcoming a major barrier to investing effort in the appropriate management of this species.

Introduction

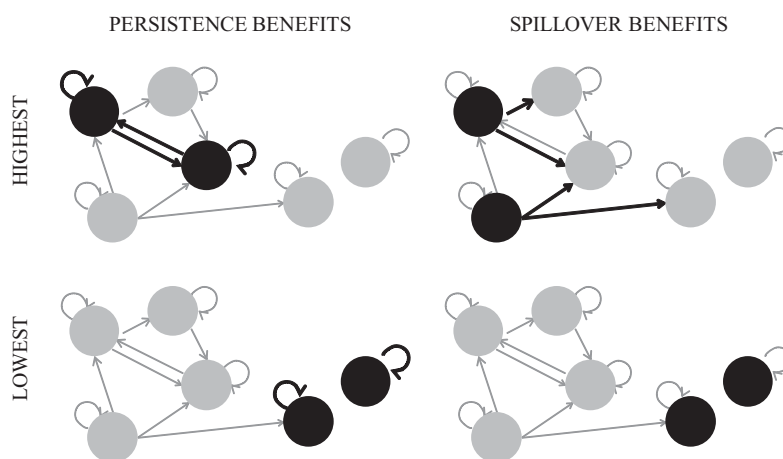
No-take marine reserves have been implemented worldwide as a conservation and fisheries management strategy to prevent and/or recover from overfishing (Gaines *et al.* 2010). Closing areas to fishing allows exploited populations to rebuild, ensuring their continued availability for future generations of resource users (Roberts *et al.* 2001).

The notion of marine reserves as a fisheries management tool is dependent on two mechanisms: persistence and spillover. For a population to continue to exist in the future, it needs to replace itself, which is called population persistence (Hastings & Botsford 2006). In spatially structured marine populations, persistence within a patch is dependent both on endogenous offspring that remain in that patch and exogenous offspring that arrive from

other patches. Consequently, reserves in sites with higher retention and stronger connections to other reserves will have higher persistence (Figure 1, left). However, larger benefits for fisheries will be obtained when maximizing spillover, or the movement of larvae and adults from reserves to fishing grounds (Figure 1, right). Although persistence and spillover are both dependent on connectivity patterns, a reserve network that maximizes either one of these objectives will frequently not be the best design to maximize the other (Hastings & Botsford 2003; Lester *et al.* 2013; Figure 1, top).

The awareness that marine resources are being depleted and appropriate reserve networks are needed to avoid ecological collapse or even boost fisheries has mobilized a large amount of research. Recently published approaches range from using heuristic guidelines on reserve size and spacing (e.g., Green *et al.* 2014), which use

Figure 1 Competing designs for a network of two reserves with the highest (upper panels) and lowest (lower panels) persistence and spillover. Reserves are depicted in black, fishing grounds in grey. Arrows indicate the direction of export of larvae and/or adults. Black arrows highlight the relevant connections to assess either persistence or spillover. The optimal design is highly dependent on the particular connectivity patterns. In this example, the worst configuration for either persistence or spillover is the same, namely protecting poorly connected sites. However, the network that allows the highest persistence protects sites that export mostly to one another, but the network that allows the highest spillover protects sites that export mostly to fished sites. An optimal reserve design for fisheries management must balance these conflicting objectives.



the amount of area protected as a proxy for persistence; maximizing connectivity among units (e.g., Beger *et al.* 2015), which does not take persistence or yield explicitly into account; including site-level metrics of connectivity (e.g., Schill *et al.* 2015), tackling only some aspects of persistence; or maximizing fisheries yield and equilibrium biomass as a proxy for persistence (e.g., Rassweiler *et al.* 2014; Brown *et al.* 2015). To our knowledge, only one example has focused on finding an optimal balance between yield and conservation benefits in 135 patches along the Californian coast (Rassweiler *et al.* 2014).

Robust methods do exist that can simultaneously quantify both objectives, that is ensure the long-term sustainability of the resource and benefit fisheries nearby, within a given reserve network. Spatially explicit population models take into consideration the configuration of networks and the effects of larval (Kaplan *et al.* 2006) and adult (Moffitt *et al.* 2009) movement to quantify persistence and fisheries benefit. However, the models are so computationally intensive that they have only been used to provide *post hoc* assessments of established reserve networks (e.g., Moffitt *et al.* 2009) or to select among a handful of competing network configurations chosen using differing criteria (White *et al.* 2013). Despite their promise, this tool has not to date been used to design optimal reserve networks from the outset within a real-world system.

Here we apply spatially explicit population models to the extant Honduran marine spatial planning process in order to identify a reserve network configuration that will accomplish both objectives at once. Our reserve design considers issues of ontogenetic migration, larval and adult movement, and uses detailed spatial information on habitats and connectivity among patches. We focused on the spiny lobster, *Panulirus argus*, which is not only

the most economically valuable marine fishery in the Caribbean (Cochrane & Chakalall 2001) but is also a considerable management and modeling challenge as its larvae can spend up to 9 months in a pelagic stage before settling (Goldstein *et al.* 2008). We show that yield and persistence display direct trade-offs, so both objectives need to be considered at the same time when planning. In addition, contrary to what was previously thought (e.g., Kough *et al.* 2013), a reserve network for this long-dispersing species can be beneficial at a country level, which is encouraging news for conservationists and resource managers.

Methods

Spatially explicit population modeling approach

We used the dispersal per recruit model to assess the persistence and yield of reserve networks with dispersing larvae and adults (Grüss *et al.* 2011). From an initial number of settlers, the recursive population model quantifies the number of recruits, adults, and eggs produced within each patch, and then uses the larval connectivity matrix to link the production of eggs at one location to settlement at another until reaching equilibrium (Kaplan *et al.* 2006, Figure 2). The method also accounts for the movement of adults, which makes them available to fishing outside reserves therefore decreasing persistence but increasing yield (Kramer & Chapman 1999). The different processes involved in the model are outlined in Figure 2 and explained in detail in the Supporting Information.

Persistence and yield

For studying the effects of spatial management on spiny lobster populations, the population model calculates two

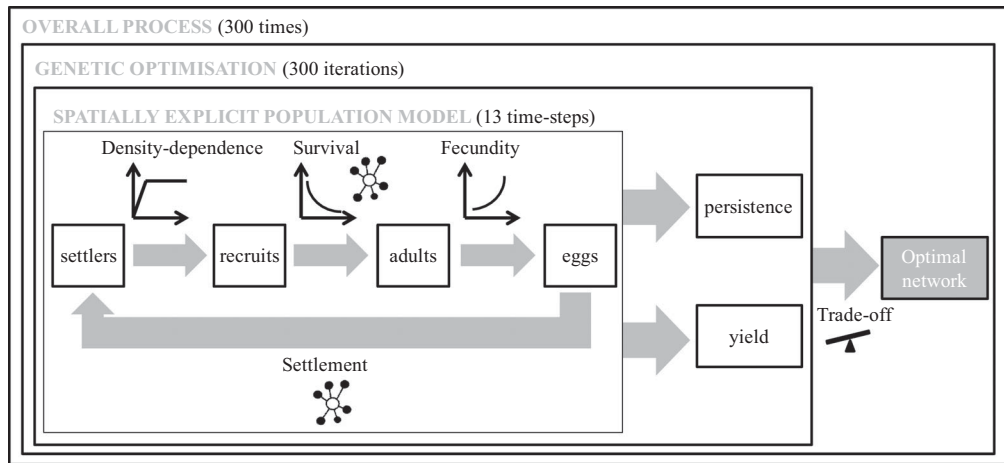


Figure 2 Summary of the modeling approach. For each potential reserve network, a spatially explicit population model encompassing the processes of density-dependent survival of settlers (hockey-stick function with slope at the origin calculated using a critical Fraction of Natural Eggs per Recruit of 0.2 and the correction suggested by White (2010)), adult survival incorporating both natural and fishing mortality that accounts for exposure due to adult movement (Goodyear 1993), fecundity (given by known fecundity at length relationship including multiple broods) and larval settlement, was run for 13 time-steps to calculate persistence and yield. A genetic optimization algorithm was run for 300 iterations to identify network configurations that optimize both persistence and yield, subject to the condition that at least one reserve has values of Fraction of Natural Eggs per Recruit above threshold. The whole process was repeated 300 times and the best solution was chosen.

indices of the fishery's state that are independent of the stock-recruitment relationship: eggs per recruit (EPR) and yield per recruit (YPR). EPR is the number of eggs an average recruit produces over its lifetime (Goodyear 1993). Values of EPR were then used to calculate the Fraction of Natural Eggs per Recruit (FNEPR). This metric is the ratio of the fished (EPR) to the unfished (NEPR) reproductive potential and it is a measure of the impact of fishing on the potential productivity of the population.

For fished populations to persist, successive generations must replace each other, increasing the value of FNEPR. Generally, values of FNEPR are compared against threshold levels, with 20% being recommended for spiny lobsters (SEDAR 2005). Persistence was summarized using two metrics (1) Per_d , a dichotomous metric indicating the existence of at least one reserve with FNEPR values above threshold; and (2) Per_c , a continuous metric given by the sum of FNEPR values inside reserves. Although it has been shown that a meta-population is likely to collapse if there is not at least one population with FNEPR values above threshold (e.g., Kaplan *et al.* 2006), the sum of FNEPR is a measure of larval settlement within the network commonly used for the assessment of persistence in a spatially realistic setting which allows better comparisons of competing reserve networks at similar values of Per_d .

YPR is the effect of fishing on yield, expressed in terms of the yield an average individual provides to the fishery

over its lifetime. YPR was calculated using the Beverton and Holt equation (Sparre & Venema 1998). Yield was summarized as the total yield in the region (e.g., Kaplan *et al.* 2006).

To run the model, fishing mortality (F) outside reserves was assumed uniform ($F = 0.4$) and reserves were considered to be effective ($F = 0$). Initial recruitment levels were set to 1, and the model was run using 13 time-steps, which were sufficient to reach equilibrium (Supporting Information). Sensitivity analyses were carried out to assess the effects of model parameters on the results, showing that the choice of a near-optimal reserve network is insensitive to the values used (Supporting Information). The implementation of the dispersal per recruit model was heavily reliant on the functions of the *R* package ConnMatTools (Andrello 2014).

Trade-offs

A near-optimal network of reserves was identified as the one that would maximize conservation (Per_c) and fisheries (*Yield*) benefits. We consider near-optimal solutions given that the solution does not necessarily represent the global optima, which might be intractable in many real-world problems using heuristic algorithms (Pressey *et al.* 1996). Our near-optimal solution reflects the point where the rate of improvement of the objective function decreases considerably (Supporting Information).

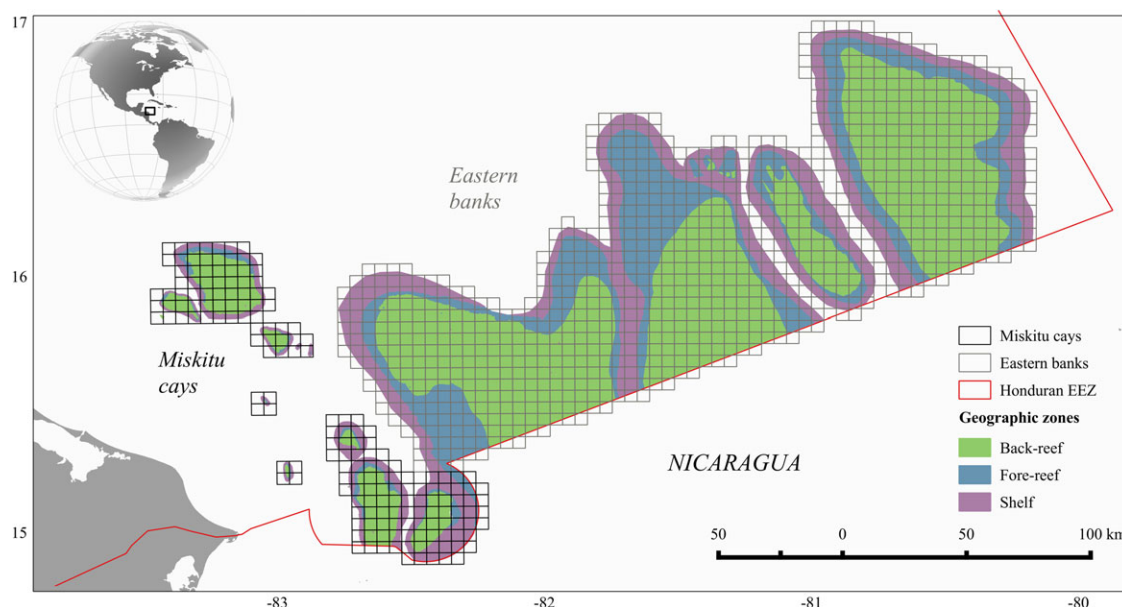


Figure 3 Map of the study area. Area of interest in Honduras, geographic zones and the 1,211 management units of 25 km² in the area distributed along almost 25,000 km² of shallow habitats in the Miskitu cays and the Eastern banks, where the Honduran government requires the protection of 20% of shallow consolidated habitats in a stratified way.

To that end we first calculated the minimum and maximum possible values for Per_c and $Yield$ by running 100 optimizations for each value (i.e., four separate analyses). Then, for each network configuration, we used these ranges to normalize Per_c and $Yield$ values, and finally quantify our objective function (OF) as the square root of the sum of squared differences between the normalized values and the ideal optimum of 1. The OF weights both objectives equally and ranges between 0 and $\sqrt{2}$ (1.4142), with lower values being more desirable. Networks with populations that would collapse ($Per_d = 0$) were penalized and assigned a value of $\sqrt{2}$.

Optimization

A genetic algorithm (Moilanen *et al.* 2009) was used to identify the network configuration that optimizes yield and persistence. The optimization was based on the method kofnGA in the R package of the same name, a genetic algorithm for subset selection that minimizes a user-defined objective function for that subset (Wolters 2015). Each run was carried out 300 iterations, and the whole process was repeated 300 times (details on the method and sensitivity analyses in Supporting Information). The genetic algorithm was run as an array in Hydra, the Smithsonian Institution High Performance Cluster (SI/HPC). Each of the 300 runs took about 512Mb of

memory and one day of computing time. Hydra was able to complete all runs in less than 2 days.

Case study

Eastern Honduras holds 93% of the shallow consolidated habitats and 92% of industrial fishing effort in the country with spiny lobster being the most important fishery in terms of effort (Chollett *et al.* 2016) and profits (FAO 2015). The country-wide governmental target in Honduras is to fully protect 20% of habitats from fishing, the only use in the area (Figure 3).

For species such as spiny lobsters that undertake ontogenetic migration, reserves succeed only if established in each of the habitats used at different stages: (1) lagoonal and back-reef areas where lobsters recruit and juveniles forage, (2) fore-reefs which adults inhabit, and (3) deeper regions where adults reproduce. Reserves were placed only if all three zones needed for spiny lobster were within reach. This is, management units were considered in the analyses only if at least 5 km² of each zone was available within 100 km² of continuous habitat. Four datasets were produced as inputs for this study: (1) a map of geographic zones classified from Landsat satellite imagery; (2) a 3-year larval connectivity matrix encompassing the entire Caribbean basin with a spatial resolution 18 times that of previous datasets (Kough *et al.* 2013); (3) an

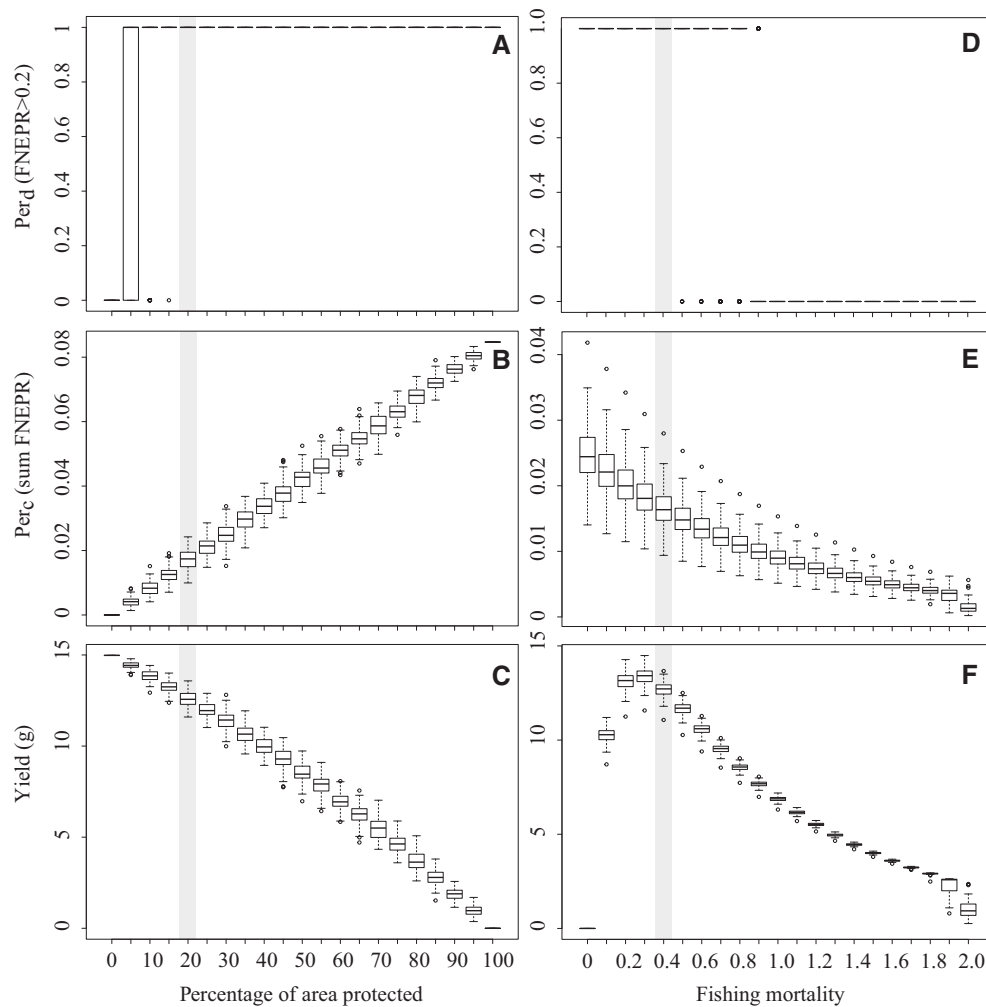


Figure 4 Influence of area protected and fishing mortality on persistence and yield. Changes in Per_d (A, D), average Per_c per management unit inside reserves (B, E) and average yield per management unit outside reserves (C, F) at different values of area protected (A, B, C) and fishing mortality (D, E, F). Variability indicates the range of outcomes after running the population model in 100 reserve networks. In boxplots, lines represent the median, boxes the 25th and 75th percentiles and whiskers the extremes of the data (median \pm 1.5 * interquartile range). Yield indicates the average yield (g) an individual lobster contributes to the fishery over its lifetime. Grey bars indicate the percentage of area protected (20%) and level of fishing mortality (0.4) used in subsequent analyses.

adult connectivity matrix considering daily and nomadic movements for lobster; and (4) a synthesis of published population parameters for spiny lobster. All datasets are described in the Supporting Information.

Before identifying the best network configuration for the study area, we assessed the three following questions related to the general approach. (1) Can the management for spiny lobsters at country level produce conservation benefits?; (2) Will management be effective if fishing intensity increases? (3) What is the nature of the trade-offs between yield and persistence? To assess these questions, we ran the population model for 100 reserve networks randomly distributed over the management units while

varying two parameters, the proportion of area protected (from 0 to 100% at 5% intervals) and fishing mortality (F , from 0 to 2 at 0.1 intervals).

Results

Can the management for spiny lobsters at country level produce conservation benefits?

Both metrics of persistence (Per_d and Per_c) increase with increasing amount of area protected in Honduras (Figure 4A, B). Populations always collapse ($Per_d = 0$) under no protection and reserve networks never collapse

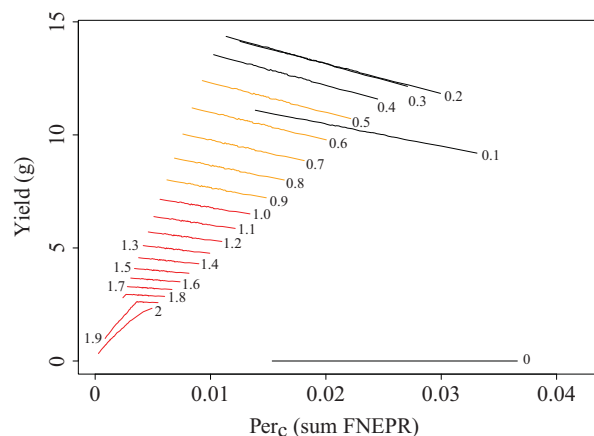


Figure 5 Trade-offs between yield and persistence when protecting 20% of the region. Trade-offs between yield and Per_c for 100 random reserve networks at different values of fishing mortality between 0 and 2 (annotated in the figure). Yield and persistence are expressed per management unit. Colors indicate differences in Per_d : black indicates when none of the networks collapse (i.e., there is always at least one reserve with FNEPR > 0.2), red indicates when all networks collapse, yellow indicates when results are mixed.

when protecting at least 20% of the area (Figure 4A). Serendipitously, this 20% cut-off coincides with the governmental target of protection imposed in the country. Yield decreases almost linearly with increasing amount of area protected, as fewer areas are available to fishing (Figure 4C).

Will management be effective if fishing intensity increases?

When protecting 20% of the region, both metrics of persistence decrease with fishing pressure (Figure 4D, E). Population collapse is possible if $F \geq 0.5$, and it always occurs if $F \geq 1$ (Figure 4D). The relationship between fishing mortality and yield is more complex (Figure 4F). Yield increases with fishing mortality up to a maximum around values of F of 0.3, after which populations are not able to replenish themselves and yield decreases steadily with further increases in fishing.

What is the nature of the trade-offs between yield and persistence?

Interestingly, the nature of the trade-off between yield and Per_c (Figure 5) varies with the level of fishing mortality when protecting 20% of the region. At low values of F , these variables show direct trade-offs, and reserve networks that increase yield result in a proportional decrease of persistence and vice versa. At high values of F , the relationship becomes less steep, and at very high values of F

(bottom left of Figure 5) the relationship is inverted, with high yield obtained in networks that also provide high persistence.

Near-optimal network configuration

The genetic algorithm found solutions with varied spatial configurations that achieved similarly high levels of yield and persistence, indicating that there are many viable spatial options for achieving both goals. Although there is large variability among results, some locations are key and are always selected by the algorithm (Figure 6A). The near-optimal solution is presented in Figure 6B.

Discussion

By leveraging advances in cluster computing and bio-physical modeling, we were able to design a reserve network to sustain the fishery of a demographically complex and commercially important species at a country level.

Successfully managing spiny lobster fisheries at a country level is possible. Our results show that populations always collapse when no protection is in place and that reserves located in Honduras can directly benefit the lobster populations of the country itself. This result challenges the perception that because of their long larval pelagic duration, spiny lobster populations are unmanageable or necessarily require international cooperation for effective management (Kough *et al.* 2013), overcoming a major barrier to investing local effort in the management of this marine species. The relative importance of within-country versus international management would be dependent on country-level patterns of population persistence, which must be assessed to identify which strategy is most likely to be effective.

The proposed network of reserves protecting 20% of the fishable area might not be enough to avoid the collapse of the resource in the face of increasing fishing effort. Therefore, the long-term benefits of the proposed network of reserves are contingent on complementary management strategies that regulate fishing effort (Roberts 1997).

Yield and persistence show direct negative trade-offs, therefore both variables need to be considered explicitly and simultaneously when planning for fisheries and conservation benefits. Rassweiler *et al.* (2014) found similar results when planning in California. An interesting contribution of our research, however, is that the nature of this trade-off can change if the resource is on the verge of collapse. Recent marine spatial planning attempts that maximize only one benefit at a time (e.g., Schill *et al.* 2015) might produce perverse outcomes.

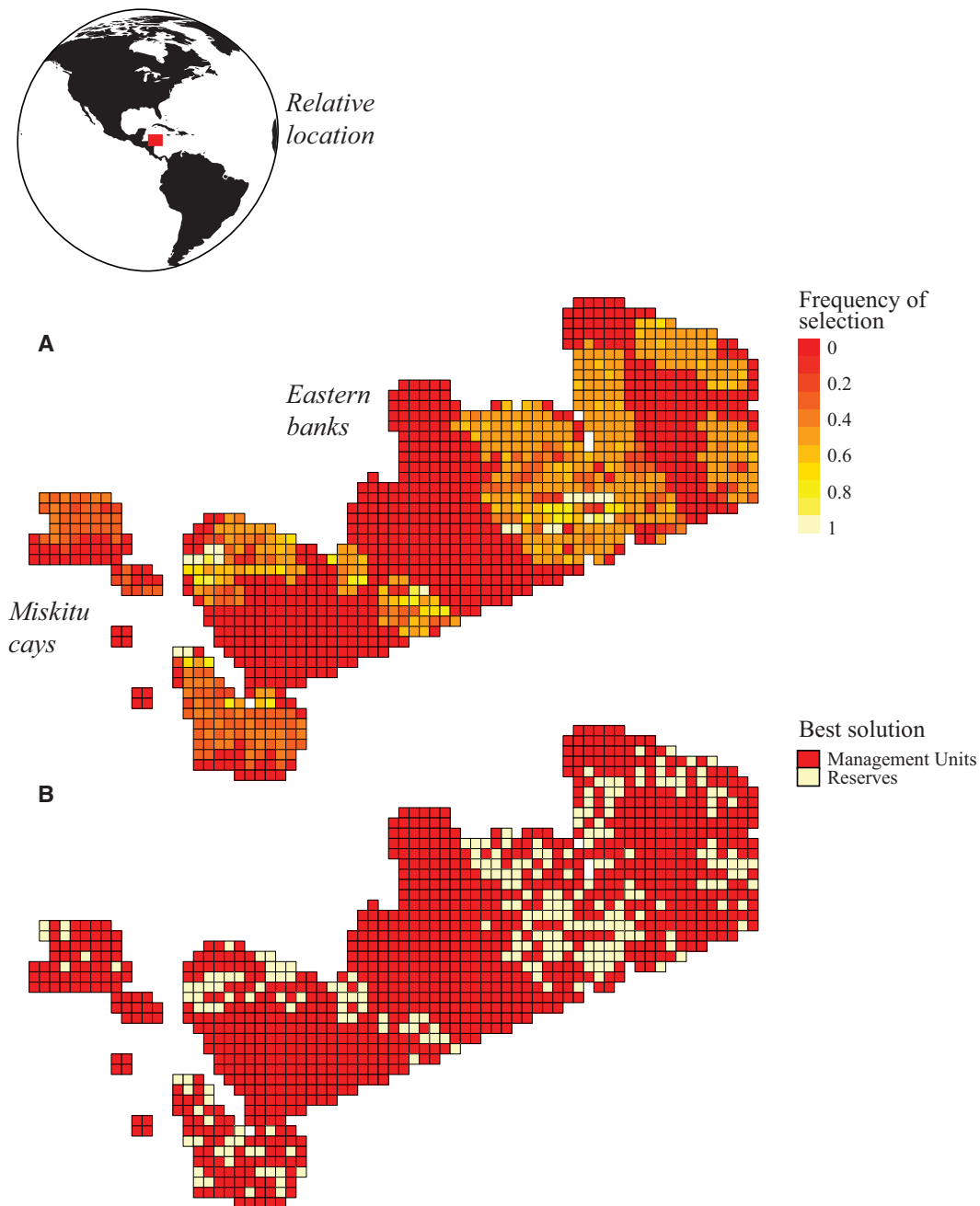


Figure 6 Selecting reserve networks in Honduras. Frequency of selection of 300 solutions (A); and best solution (B).

The approach presented here is transferable to other species and regions (as long as population parameters and connectivity data are available), and can be extended to consider more complex case studies that trade off multiple objectives (by modifying the objective function). Presently, marine spatial planning is dominated by the use of a decision support tool (Marxan: Ball & Possingham 2000) that requires the use of static information on

connectivity (Beger *et al.* 2010). It has been shown that incorporating connectivity information in static planning is suboptimal in the sense that it does not capture conservation benefits or persistence of all species under all settings (Costello *et al.* 2010; White *et al.* 2014; Brown *et al.* 2015). We hope that by showing it is possible to explicitly include population persistence during planning, we will promote the use of more comprehensive approaches in

future efforts for designing reserve networks when benefiting fisheries is the main objective of the design.

The knowledge that local management actions can accrue benefits within the country is a powerful motivation for the development of a network of reserves and new policies in Honduras. Currently, local stakeholders are pushing for a change in socially and ecologically unsustainable methods of fishing (based on dangerous scuba diving: Harborne *et al.* 2001). The establishment of a network of reserves, linked to the development of artisanal skin-dive fisheries and the setting up of artificial shelters in fishing grounds that receive spillover (Baine & Side 2003) would facilitate the transition towards better ways of fishing. Within a broader regional context, the knowledge that reserve networks can promote the sustainability of the resource could complement the management of spiny lobster from traditional tools based on seasonal bans and size restrictions (Seijo 2007) with the inclusion of networks of reserves encompassing the entire Mesoamerican region, a process that is currently underway and to which the authors are contributing.

This study uses existing tools combined with new information and technology to provide a spatial conservation support tool with direct application for the key fisheries in the Caribbean. Our approach has overcome two research barriers, showing that marine reserves can be designed from scratch to provide both, short-term fisheries income and long-term sustainability of the fisheries resources, and that marine reserve networks can promote the sustainability of spiny lobster. We anticipate these methods can support effective fisheries management and policy formation in other regions.

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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:

1. Spatially explicit population model: Detail.
2. Spatially explicit population model: Sensitivity analyses.
3. Genetic optimisation: Detail.
4. Genetic optimisation: Sensitivity analyses.
5. Data sources: Map of zones.
6. Data sources: Larval connectivity matrix.
7. Data sources: Adult connectivity matrix.
8. Data sources: Lobster parameters.

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