



A genuine win-win: resolving the “conserve or catch” conflict in marine reserve network design

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Abstract:	<p>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 optimised 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.</p>

For Peer Review

1 **A genuine win-win: resolving the “conserve or catch” conflict in**
2 **marine reserve network design**

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28 **Abstract**

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

40 **Introduction**

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

45 The notion of marine reserves as a fisheries management tool is dependent on two mechanisms:
46 persistence and spillover. For a population to continue to exist in the future, it needs to replace itself,
47 which is called *population persistence* (Hastings & Botsford 2006). In spatially structured marine
48 populations, persistence within a patch is dependent both on endogenous offspring that remain in that
49 patch and exogenous offspring that arrive from other patches. Consequently, reserves in sites with
50 higher retention and stronger connections to other reserves will have higher persistence (Fig. 1, left).
51 On the other hand, larger benefits for fisheries will be obtained when maximizing *spillover*, or the
52 movement of larvae and adults from reserves to fishing grounds (Fig. 1, right). Although persistence
53 and spillover are both dependent on connectivity patterns, a reserve network that maximises either one
54 of these objectives will frequently not be the best design to maximise the other (Hastings & Botsford
55 2003; Lester et al. 2013, Fig. 1, top).

56 The awareness that marine resources are being depleted and appropriate reserve networks are needed
57 to avoid ecological collapse or even boost fisheries has mobilised a large amount of research.

58 Recently published approaches range from using heuristic guidelines on reserve size and spacing (e.g.
59 Green et al. 2014), which use the amount of area protected as a proxy for persistence; maximising
60 connectivity among units (e.g. Beger et al. 2015), which does not take persistence or yield explicitly
61 into account; including site-level metrics of connectivity (e.g. Schill et al. 2015), tackling only some
62 aspects of persistence; or maximising fisheries yield and equilibrium biomass as a proxy for
63 persistence (e.g. Rassweiler et al. 2014; Brown et al. 2015). To our knowledge, only one example has
64 focused on finding an optimal balance between yield and conservation benefits in 135 patches along
65 the Californian coast (Rassweiler et al. 2014).

66 Robust methods do exist that can simultaneously quantify both objectives, i.e. ensure the long-term
67 sustainability of the resource and benefit fisheries nearby, within a given reserve network. Spatially
68 explicit population models take into consideration the configuration of networks and the effects of
69 larval (Kaplan et al. 2006) and adult (Moffitt et al. 2009) movement to quantify persistence and
70 fisheries benefit. However, the models are so computationally intensive that they have only been used
71 to provide *post hoc* assessments of established reserve networks (e.g. Moffitt et al. 2009) or to select
72 among a handful of competing network configurations chosen using differing criteria (White et al.
73 2013). Despite their promise, this tool has not to date been used to design optimal reserve networks
74 from the outset within a real-world system.

75 Here we apply spatially explicit population models to the extant Honduran marine spatial planning
76 process in order to identify a reserve network configuration that will accomplish both objectives at
77 once. Our reserve design considers issues of ontogenetic migration, larval and adult movement, and
78 uses detailed spatial information on habitats and connectivity among patches. We focused on the
79 spiny lobster, *Panulirus argus*, which is not only the most economically valuable marine fishery in the
80 Caribbean (Cochrane & Chakalall 2001) but is also a considerable management and modelling
81 challenge as its larvae can spend up to 9 months in a pelagic stage before settling (Goldstein et al.
82 2008). We show that yield and persistence display direct trade-offs, so both objectives need to be
83 considered at the same time when planning. Additionally, contrary to what was previously thought
84 (e.g., Kough et al. 2013), a reserve network for this long-dispersing species can be beneficial at a
85 country level, which is encouraging news for conservationists and resource managers.

86

87 **Methods**

88 *Spatially explicit population modelling approach*

89 We used the dispersal per recruit model to assess the persistence and yield of reserve networks with
90 dispersing larvae and adults (Grüss et al. 2011). From an initial number of settlers, the recursive
91 population model quantifies the number of recruits, adults and eggs produced within each patch, and
92 then uses the larval connectivity matrix to link the production of eggs at one location to settlement at
93 another until reaching equilibrium (Kaplan et al. 2006, Fig. 2). The method also accounts for the

94 movement of adults, which makes them available to fishing outside reserves therefore decreasing
95 persistence but increasing yield (Kramer & Chapman 1999). The different processes involved in the
96 model are outlined in Fig. 2 and explained in detail in the Supporting Information.

97

98 *Persistence and yield* - For studying the effects of spatial management on spiny lobster populations
99 the population model calculates two indices of the fishery's state that are independent of the stock-
100 recruitment relationship: eggs per recruit (EPR) and yield per recruit (YPR). EPR is the number of
101 eggs an average recruit produces over its lifetime (Goodyear 1993). Values of EPR were then used to
102 calculate the Fraction of Natural Eggs per Recruit (FNEPR). This metric is the ratio of the fished
103 (EPR) to the unfished (NEPR) reproductive potential and it is a measure of the impact of fishing on
104 the potential productivity of the population.

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

115 YPR is the effect of fishing on yield, expressed in terms of the yield an average individual provides to
116 the fishery over its lifetime. YPR was calculated using the Beverton and Holt equation (Sparre &
117 Venema 1998). Yield was summarised as the total yield in the region (e.g. Kaplan et al. 2006).

118 To run the model, fishing mortality (F) outside reserves was assumed uniform ($F= 0.4$) and reserves
119 were considered to be effective ($F=0$). Initial recruitment levels were set to 1, and the model was run
120 using 13 time-steps, which were sufficient to reach equilibrium (Supporting Information). Sensitivity
121 analyses were carried out to assess the effects of model parameters on the results, showing that the

122 choice of a near-optimal reserve network is insensitive to the values used (Supporting Information).
123 The implementation of the dispersal per recruit model was heavily reliant on the functions of the *R*
124 package ConnMatTools (Andrello 2014).

125 *Trade-offs*

126 A near-optimal network of reserves was identified as the one that would maximise conservation (Per_c)
127 and fisheries ($Yield$) benefits. We consider near-optimal solutions given that the solution does not
128 necessarily represent the global optima, which might be intractable in many real-world problems
129 using heuristic algorithms (Pressey et al. 1996). Our near-optimal solution reflects the point where the
130 rate of improvement of the objective function decreases considerably (Supporting Information). To
131 that end we first calculated the minimum and maximum possible values for Per_c and $Yield$ by running
132 100 optimisations for each value (i.e. 4 separate analyses). Then, for each network configuration, we
133 used these ranges to normalize Per_c and $Yield$ values, and finally quantify our objective function (OF)
134 as the square root of the sum of squared differences between the normalized values and the ideal
135 optimum of 1. The OF weights both objectives equally and ranges between 0 and $\sqrt{2}$ (1.4142), with
136 lower values being more desirable. Networks with populations that would collapse ($Per_d=0$) were
137 penalized and assigned a value of $\sqrt{2}$.

138 *Optimisation*

139 A genetic algorithm (Moilanen et al. 2009) was used to identify the network configuration that
140 optimises yield and persistence. The optimisation was based on the method kofnGA in the *R* package
141 of the same name, a genetic algorithm for subset selection that minimises a user-defined objective
142 function for that subset (Wolters 2015). Each run was carried out 300 iterations, and the whole
143 process was repeated 300 times (details on the method and sensitivity analyses in Supporting
144 Information). The genetic algorithm was run as an array in Hydra, the Smithsonian Institution High
145 Performance Cluster (SI/HPC). Each of the 300 runs took about 512Mb of memory and one day of
146 computing time. Hydra was able to complete all runs in less than two days.

147 *Case study*

148 Eastern Honduras holds 93% of the shallow consolidated habitats and 92% of industrial fishing effort
149 in the country with spiny lobster being the most important fishery in terms of effort (Chollett et al.
150 2016) and profits (FAO 2015). The country-wide governmental target in Honduras is to fully protect
151 20% of habitats from fishing, the only use in the area (Fig. 3).

152 For species such as spiny lobsters that undertake ontogenetic migration, reserves succeed only if
153 established in each of the habitats used at different stages: (1) lagoonal and back-reef areas where
154 lobsters recruit and juveniles forage, (2) fore-reefs which adults inhabit and (3) deeper regions where
155 adults reproduce. Reserves were placed only if all three zones needed for spiny lobster were within
156 reach. This is, management units were considered in the analyses only if at least 5 km² of each zone
157 was available within 100 km² of continuous habitat. Four datasets were produced as inputs for this
158 study: (1) a map of geographic zones classified from Landsat satellite imagery; (2) a three-year larval
159 connectivity matrix encompassing the entire Caribbean basin with a spatial resolution 18 times that of
160 previous datasets (Kough et al. 2013); (3) an adult connectivity matrix considering daily and nomadic
161 movements for lobster; (4) a synthesis of published population parameters for spiny lobster. All
162 datasets are described in the Supporting Information.

163 Before identifying the best network configuration for the study area, we assessed the three following
164 questions related to the general approach. (1) Can the management for spiny lobsters at country level
165 produce conservation benefits; (2) Will management be effective if fishing intensity increases?; (3)
166 What is the nature of the trade-offs between yield and persistence? To assess these questions, we ran
167 the population model for 100 reserve networks randomly distributed over the management units while
168 varying two parameters, the proportion of area protected (from 0 to 100% at 5% intervals) and fishing
169 mortality (F , from 0 to 2 at 0.1 intervals).

170

171 **Results**

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

173 Both metrics of persistence (Per_d and Per_c) increase with increasing amount of area protected in
174 Honduras (Fig. 4A, 4B). Populations always collapse ($Per_d = 0$) under no protection and reserve
175 networks never collapse when protecting at least 20% of the area (Fig. 4A). Serendipitously, this 20%

176 cut-off coincides with the governmental target of protection imposed in the country. Yield decreases
177 almost linearly with increasing amount of area protected, as fewer areas are available to fishing (Fig.
178 4C).

179 *Will management be effective if fishing intensity increases?*

180 When protecting 20% of the region, both metrics of persistence decrease with fishing pressure (Fig.
181 4D, 4E). Population collapse is possible if $F \geq 0.5$, and it always occurs if $F \geq 1$ (Fig. 4D). The
182 relationship between fishing mortality and yield is more complex (Fig. 4F). Yield increases with
183 fishing mortality up to a maximum around values of F of 0.3, after which populations are not able to
184 replenish themselves and yield decreases steadily with further increases in fishing.

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

186 Interestingly, the nature of the trade-off between yield and Per_c (Fig. 5) varies with the level of fishing
187 mortality when protecting 20% of the region. At low values of F these variables show direct trade-
188 offs, and reserve networks that increase yield result in a proportional decrease of persistence and vice
189 versa. At high values of F the relationship becomes less steep, and at very high values of F (bottom
190 left of Fig. 5) the relationship is inverted, with high yield obtained in networks that also provide high
191 persistence.

192 *Near-optimal network configuration*

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

197

198 **Discussion**

199 By leveraging advances in cluster computing and biophysical modelling, we were able to design a
200 reserve network to sustain the fishery of a demographically complex and commercially important
201 species at a country level.

202 Successfully managing spiny lobster fisheries at a country level is possible. Our results show that
203 populations always collapse when no protection is in place and that reserves located in Honduras can

204 directly benefit the lobster populations of the country itself. This result challenges the perception that
205 because of their long larval pelagic duration, spiny lobster populations are unmanageable or
206 necessarily require international cooperation for effective management (Kough et al. 2013),
207 overcoming a major barrier to investing local effort in the management of this marine species. The
208 relative importance of within-country vs. international management would be dependent on country-
209 level patterns of population persistence, which must be assessed to identify which strategy is most
210 likely to be effective.

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

215 Yield and persistence show direct negative trade-offs, therefore both variables need to be considered
216 explicitly and simultaneously when planning for fisheries and conservation benefits. Rassweiler et al.
217 (2014) found similar results when planning in California. An interesting contribution of our research,
218 however, is that the nature of this trade-off can change if the resource is on the verge of collapse.
219 Recent marine spatial planning attempts that maximise only one benefit at a time (e.g. Brown et al.
220 2015; Schill et al. 2015) might produce perverse outcomes.

221 The approach presented here is transferable to other species and regions (as long as population
222 parameters and connectivity data are available), and can be extended to consider more complex case
223 studies that trade off multiple objectives (by modifying the objective function). Presently marine
224 spatial planning is dominated by the use of a decision support tool (Marxan: Ball & Possingham
225 2000) that requires the use of static information on connectivity (Beger et al. 2010). It has been shown
226 that incorporating connectivity information in static planning is sub-optimal in the sense that it does
227 not capture conservation benefits or persistence of all species under all settings (Costello et al. 2010;
228 White et al. 2014; Brown et al. 2015). We hope that by showing it is possible to explicitly include
229 population persistence during planning, we will promote the use of more comprehensive approaches
230 in future efforts for designing reserve networks when benefiting fisheries is the main objective of the
231 design.

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

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

249

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257

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- 340
- 341

342 **Figure Legends**

343

344 Figure 1. Competing designs for a network of two reserves with the highest (upper panels) and lowest
345 (lower panels) persistence and spillover. Reserves are depicted in black, fishing grounds in grey.

346 Arrows indicate the direction of export of larvae and/or adults. Black arrows highlight the relevant
347 connections to assess either persistence or spillover. The optimal design is highly dependent on the
348 particular connectivity patterns. In this example, the worst configuration for either persistence or
349 spillover is the same, namely protecting poorly connected sites. However, the network that allows the
350 highest persistence protects sites that export mostly to one another, but the network that allows the
351 highest spillover protects sites that export mostly to fished sites. An optimal reserve design for
352 fisheries management must balance these conflicting objectives.

353

354 Figure 2. Summary of the modelling approach. For each potential reserve network, a spatially explicit
355 population model encompassing the processes of density-dependent survival of settlers (hockey-stick
356 function with slope at the origin calculated using a critical Fraction of Natural Eggs per Recruit of 0.2
357 and the correction suggested by White (2010)), adult survival incorporating both natural and fishing
358 mortality that accounts for exposure due to adult movement (Goodyear 1993), fecundity (given by
359 known fecundity at length relationship including multiple broods) and larval settlement, was run for
360 13 time-steps to calculate persistence and yield. A genetic optimisation algorithm was run for 300
361 iterations to identify network configurations that optimise both persistence and yield, subject to the
362 condition that at least one reserve has values of Fraction of Natural Eggs per Recruit above threshold.
363 The whole process was repeated 300 times and the best solution was chosen.

364

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

369

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

378

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

385

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

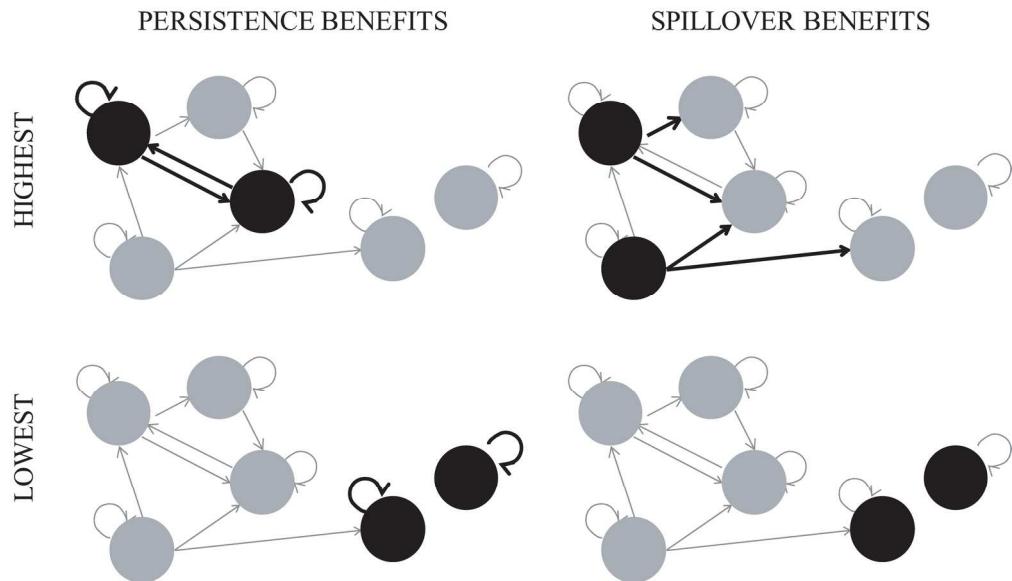


Figure 1. Competing designs for a network of two reserves with the highest (upper panels) and lowest (lower panels) persistence and spillover. Reserves are depicted in black, fishing grounds in grey. Arrows indicate the direction of export of larvae and/or adults. Black arrows highlight the relevant 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.

178x102mm (300 x 300 DPI)

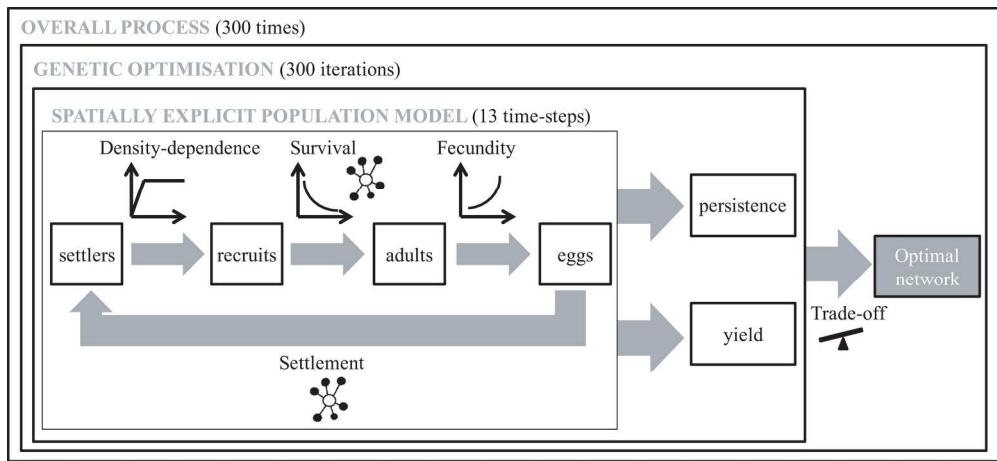


Figure 2. Summary of the modelling approach. For each potential reserve network, a spatially explicit population model encompassing the processes of density-dependent survival of settlers (hockey-stick function with slope at the origin calculated using a critical Fraction of Natural Eggs per Recruit 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 optimisation algorithm was run for 300 iterations to identify network configurations that optimise 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.

197x89mm (300 x 300 DPI)

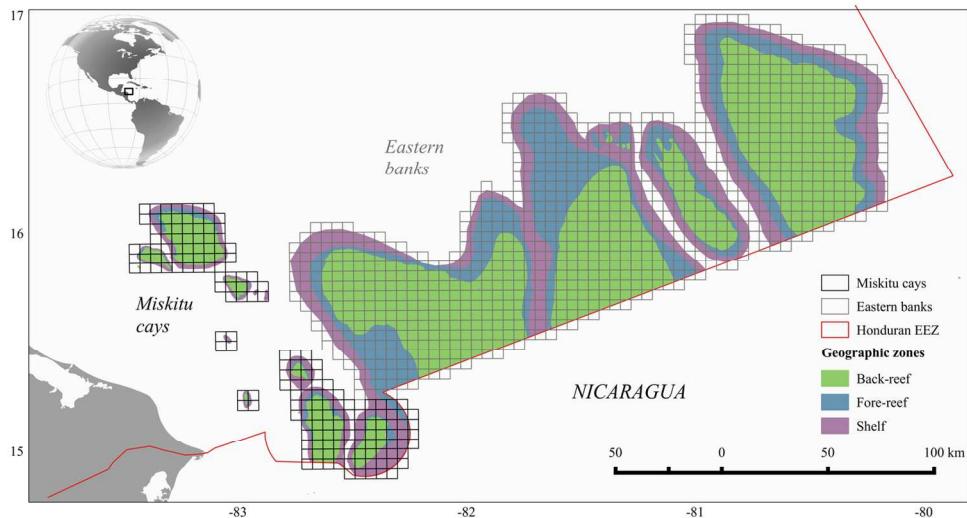


Figure 3. Map of the study area. Area of interest in Honduras, geographic zones and the 1,211 management units of 25 km² in the area distributed along almost 25,000 km² of shallow habitats in the Miskitu cays and the Eastern banks, where the Honduran government requires the protection of 20% of shallow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

Fig. 3
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Review

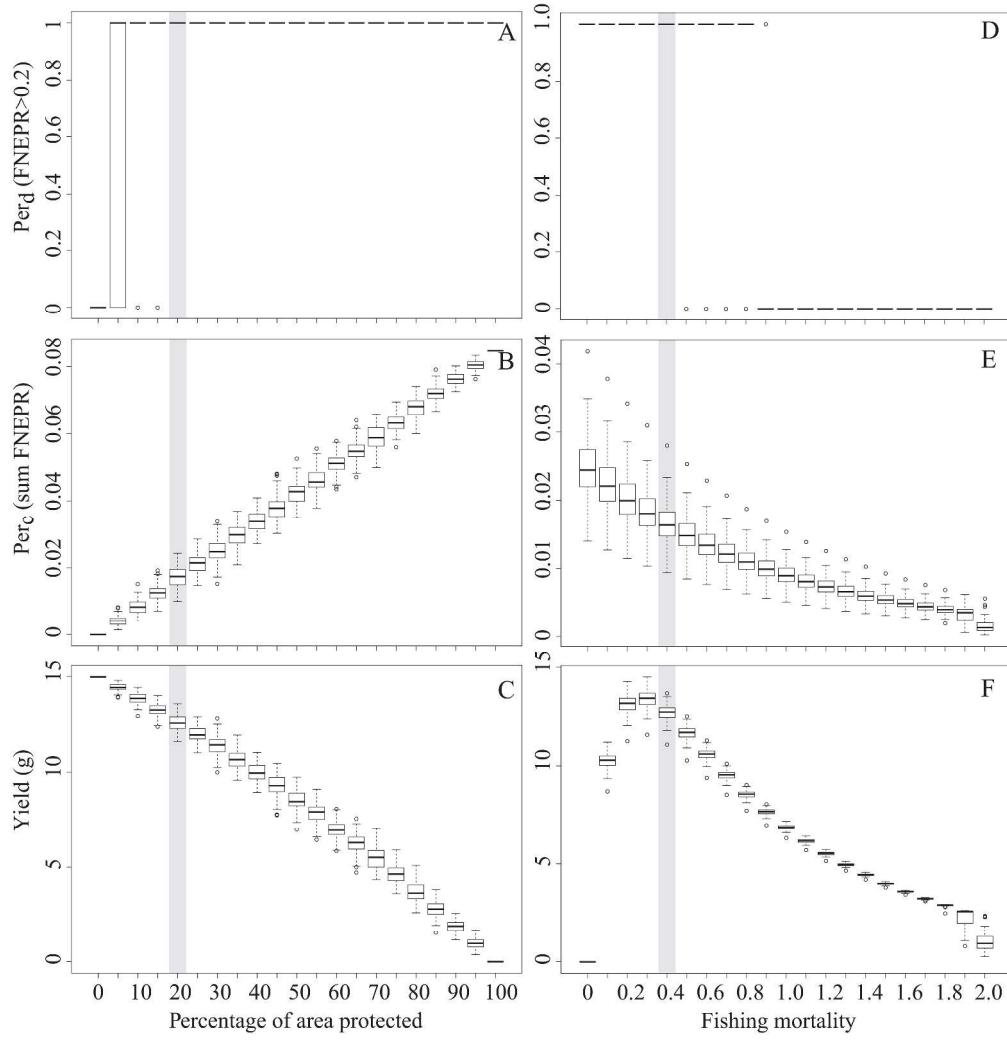


Figure 4. Influence of area protected and fishing mortality on persistence and yield. Changes in Perd (A, D), average Perc per management unit inside reserves (B, E) and average yield per management unit outside reserves (C, F) at different values of area protected (A, B, C) and fishing mortality (D, 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 ($\text{median} \pm 1.5 * \text{interquartile range}$). 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.

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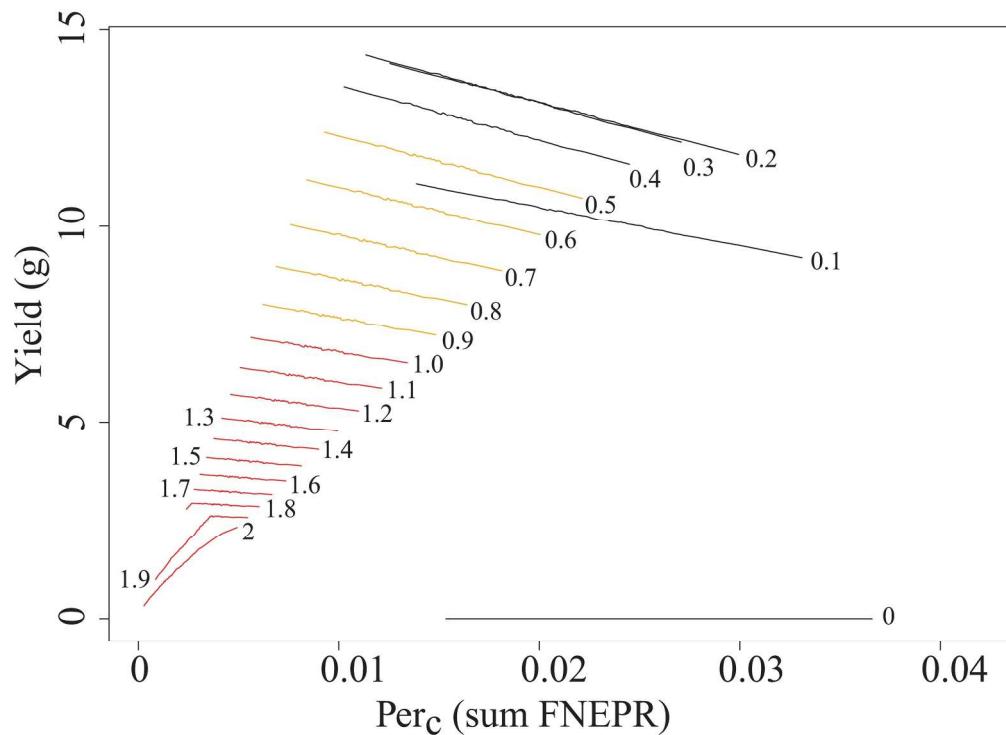


Figure 5. Trade-offs between yield and persistence when protecting 20% of the region. Trade-offs between yield and Perc for 100 random reserve networks at different values of fishing mortality between 0 and 2 (annotated in the figure). Yield and persistence are expressed per management unit. Colours indicate differences in Perd: 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.

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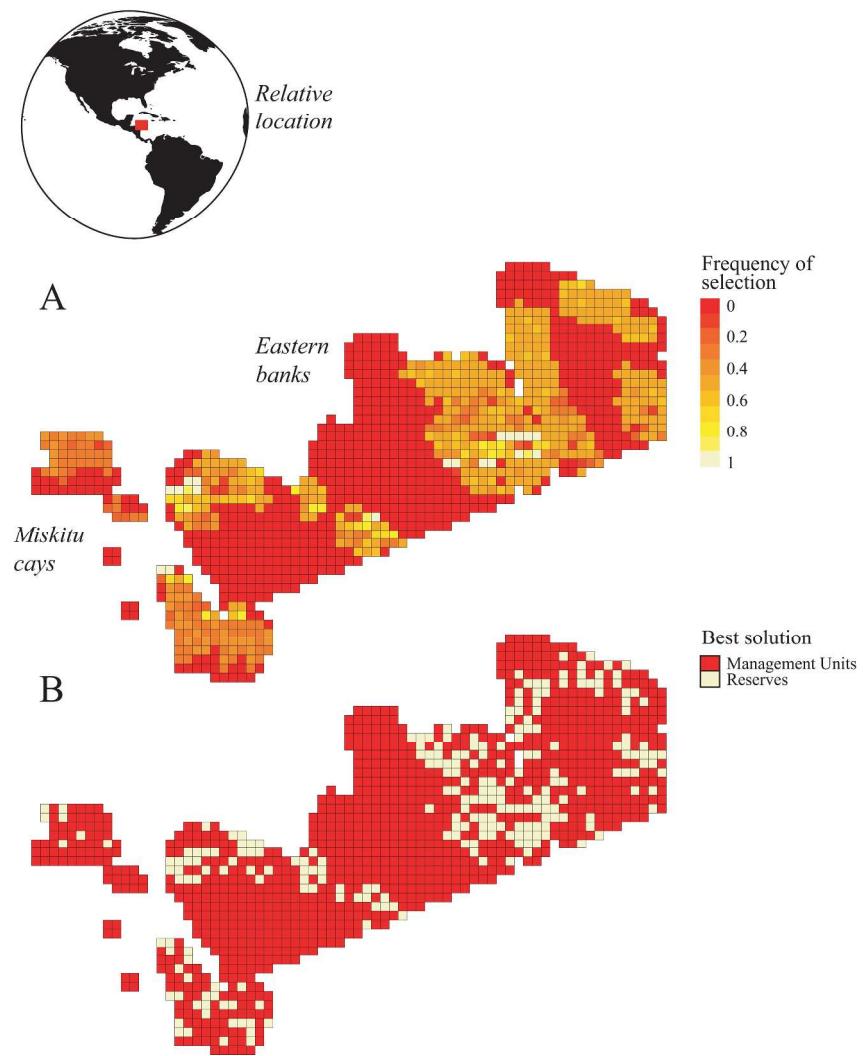


Figure 6. Selecting reserve networks in Honduras. Frequency of selection of 300 solutions (A); and best solution (B).

281x293mm (300 x 300 DPI)

Supporting Information

A genuine win-win: resolving the “conserve or catch” conflict in fisheries reserve network design
Iliana Chollett, Lysel Garavelli, Shay O’Farrell, Laurent Cherubin, Thomas R Matthews, Peter J Mumby,
Stephen J Box

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1. Spatially explicit population model: Detail

In this section we present in detail the different processes involved in the spatially explicit population model introduced in the methods section (Grüss et al. 2011).

Density dependence - To calculate the number of recruits from the number of settlers we used a hockey-stick recruitment function (Barrowman & Myers 2000), which describes appropriately density-dependent recruitment in benthic invertebrates with limited post-settlement habitat (Wahle & Steneck 1991; Kaplan et al. 2006). The slope at the origin of the egg-recruitment curve was calculated using a critical Fraction of Natural Eggs per Recruit (a measure of the impact of fishing on the potential productivity of the stock) of 0.2 (SEDAR 2005) and the correction suggested by White (2010) which accounts for processes spanning the egg-recruit transition that are characteristics of a spatial population.

Survival - Adults are subjected to natural and fishing mortality (Eq. 1). The survival of individuals at different ages (l_a) was calculated using the relationship given by Goodyear (1993, Eq. 1), which incorporates both natural mortality (M) and the instantaneous fishing mortality rate which accounts for exposure due to adult movement (F^*) when individuals are older than the age at first capture (t_c).

$$l_a = \begin{cases} e^{-M} & a < t_c \\ e^{-(M+F^*)} & a \geq t_c \end{cases} \quad \text{Eq. 1}$$

Fecundity - Due to the difficulty of aging lobsters, most population parameters for the species have been calculated using length, particularly the length of the carapace (CL). Therefore, we used known relationships between CL and age a (von Bertalanffy growth, Eq. 2), and between egg production (EP) and CL (Eq. 3), to estimate egg production at a given age. Continuous values were discretised to the mean value for each age category. K , L_∞ and t_0 are the von Bertalanffy parameters for, respectively, growth rate, asymptotic length (mm) and age at which individual would be length 0 (yr). α and β are parameters for the fecundity-at-length relationship.

$$\text{CL}_a = L_\infty(1 - \exp^{-K(a-t_0)}) \quad \text{Eq. 2}$$

$$\text{EP}_a = \alpha \text{CL}_a^\beta \quad \text{Eq. 3}$$

Large spiny lobster females produce several broods per year (Briones-Fourzán, 2014). Therefore, fecundity at age (f_a) was quantified by multiplying the number of eggs by the number of broods produced that year (b , Eq. 4).

$$f_a = \text{EP}_a b \quad \text{Eq. 4}$$

Settlement - Using the fecundity values and the spatially explicit larval connectivity information we were able to estimate the number of settlers arriving at each site in the next time-step (Kaplan et al. 2006).

Persistence and yield - For studying the effects of spatial management on spiny lobster populations the spatially explicit population model calculates two 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, which approximates to the spawning stock biomass per recruit. EPR was calculated by considering fecundity (f_a) and survival (l_a) for all ages using Eq. 5 (Goodyear, 1993).

$$\text{EPR} = \sum l_a f_a \quad \text{Eq. 5}$$

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 (Eq. 6).

$$\text{FNEPR} = \frac{\text{EPR}}{\text{NEPR}} \quad \text{Eq. 6}$$

With NEPR being quantified as in Eq. 5, and survival calculated without the influence of fishing mortality (Eq. 7):

$$l_a = e^{-M} \text{ Eq. 7}$$

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 and Venema, 1998):

$$YPR = W_\infty F e^{-M(t_c-t_r)} \sum_{n=0}^3 [U_n e^{-nK(t_c-t_0)} / (F + M + nK)] \text{ Eq. 8}$$

Where W_∞ is the mean asymptotic weight calculated from L_∞ and the weight-at-length relationship showed in Eq. 9, with t_r as the age at recruitment, with $U=[1,-3,3,-1]$.

$$W_a = \gamma C L_a^\delta \text{ Eq. 9}$$

Trade-offs - An optimal network of reserves was identified as the one that would maximise as much as possible both the benefit to fisheries (i.e. *Yield*) and persistence (i.e. *Per_c*). To that end, we first normalized *Yield* and *Per_c* values using their known minimum and maximum (Eq. 10, 11):

$$nPer_c = \frac{Per_c - minPer_c}{maxPer_c - minPer_c} \text{ Eq. 10}$$

$$nYield = \frac{Yield - minYield}{maxYield - minYield} \text{ Eq. 11}$$

Minimum and maximum persistence and yield values were obtained by running 100 optimisations for each parameter. Dimensionless, normalized values ($nPer_c$ and $nYield$) were then used to build the objective function (OF) that minimises the square root of the sum of squared distances of individual observations from their known optimal, in this case for normalized values, 1 (Eq. 12). The procedure described in Eq. 12 is what Branke et al. (2008) called a global criterion method in L2 or Euclidean norm.

$$OF = \sqrt{(1 - nPer_c)^2 + (1 - nYield)^2} \text{ Eq. 12}$$

This “no-preference” unweighted method was used to find a compromise solution that was as close as possible to optimal (maximum) values of yield and persistence.

2. Spatially explicit population model: Sensitivity analyses

Equilibrium

Simulations were considered to have reached equilibrium if the slopes of the regression lines fit to the 10 most recent normalized (between 0 and 1) values of each state were all less than 0.001 in absolute value (Caswell and Etter 1993). Equilibrium was invariably reached at 11 iterations, both for yield and number of settlers, when assessing 100 networks for 100 time-steps. Therefore, in subsequent analyses, all runs were iterated for 13 time-steps.

Parameters

The influence of each parameter in total yield and persistence (sum of FNEPR within the reserve or Per_c) was tested one at the time. Unless noted, parameters were varied $\pm 10\%$ their default value (Table S8.I). To compare patterns of yield and persistence we ran the spatially explicit population model using the same 100 random reserve networks, each covering 20% of the targeted area. After each model run we quantified:

- (1) The percentage change between average yield and persistence obtained with the default parameter and the alternative.
- (2) The pair-wise dissimilarity (calculated as 1-Pearson correlation coefficient) between the values of yield and persistence obtained with the default parameter and the alternative.

Although comparing absolute values is the most common approach during sensitivity analyses, the second metric is more informative to our aim of identifying parameters that prevent ranking reserve networks in a consistent manner.

All outputs are highly correlated and dissimilarities are very small (Figure S2.1C, D). This indicates that the same networks always have the largest (or the smallest) values for yield and persistence. Therefore, the process of comparing, ranking, and choosing an optimal network is largely insensitive to the population parameters included within the model.

The parameters, however, do influence absolute changes in yield, and to a lesser degree, persistence (Figure S2.1A, B). Fishing mortality (F) has the largest influence on persistence. The critical value of FNEP ($crit_{FNEP}$, or the slope at the origin of the egg-recruitment curve) and one of the parameters of the weight-at-length relationship (Δ) are the most important factors determining yield.

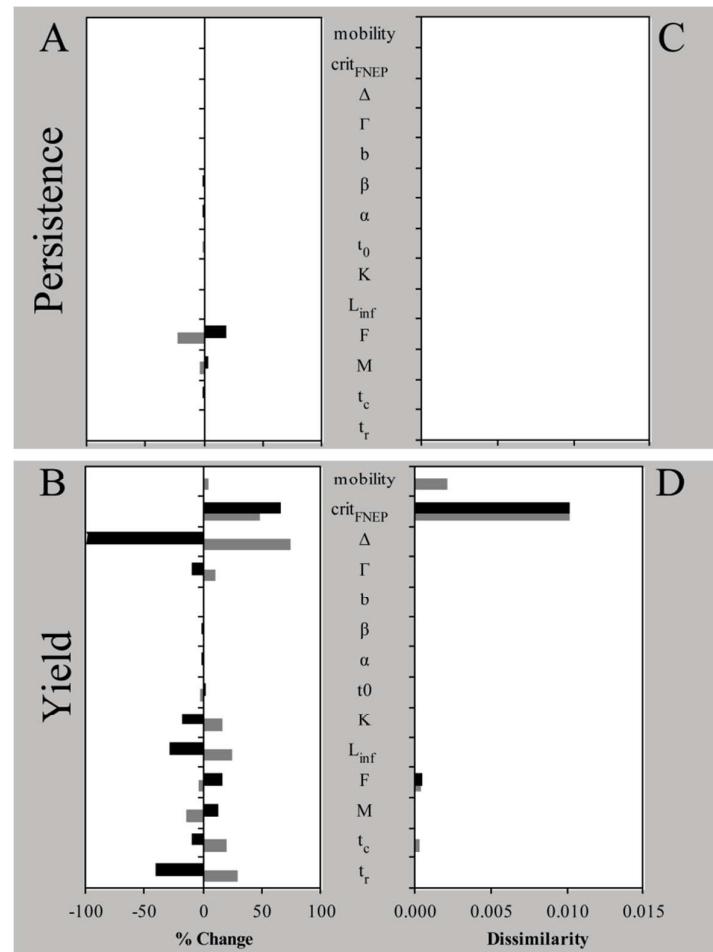


Figure S2.1. Sensitivity of persistence within the reserve and total fisheries yield to model parameters. (A) Percentage change in average persistence; (B) Percentage change in average yield; (C) dissimilarity (1-R) between outputs for persistence; (D) dissimilarity between outputs for yield.

We assessed the parameters listed in Table SIII with two additions: the critical FNEP used to calculate the slope at the origin of the egg-recruitment curve ($\text{crit}_{\text{FNEP}}$), and ‘mobility’, or the effect of including adult spillover in our results, by comparing our default results with the ones obtained assuming sedentary adults. Parameters were assessed considering variation of -10% (grey) and +10% (black) around the default value with the exception of parameters that are known to vary more wildly: t_r (assessed at ages of 1 and 3), t_c (assessed at ages of 1.45, 3.45), F (assessed at values of 0.2, 0.4), b (with 1 or 3 broods), $\text{crit}_{\text{FNEP}}$ (assessed at values of 0.1, 0.3).

3. Genetic optimisation: Detail

The reserve design network problem involves choosing the best subset of k reserves from n candidate sites, which is a combination problem that in our case has 10,261 subsets to choose from. Because the number of possibilities is large enough to make exhaustive search impractical, efficient optimisation was needed to solve our problem. Several optimisation techniques allow searching solutions spaces with multiple local optima, with simulated annealing and genetic algorithms being the most commonly used in spatial planning (Moilanen et al. 2009).

Genetic algorithms are common optimisation techniques that improve a population of possible solutions through generations using principles of evolution such as natural selection, crossover and mutation. In a genetic algorithm an initial population (a set of candidate solutions) is chosen at random, and its fitness is determined by the objective function value. In each generation, a proportion of the population gets to reproduce with a frequency that is proportional to its fitness. During reproduction, two parents (selected at random) are combined in crossover, where a new child is generated containing properties of both parents, with some mutations allowed. In the next step, the new solutions generated by the process of crossover and mutation are included in the next population, their fitness calculated, and then the population of the next generation will be selected from this augmented population. During the process, some solutions with better fitness, called elite, will enter directly in the new generation, while the other will be randomly chosen. This way good solutions with high fitness get to reproduce more frequently.

To apply the genetic optimisation, we used the method *kofnGA*, a genetic algorithm for subset selection that minimizes a user-defined objective function for that subset (Wolters 2015). The method includes five parameters: the initial population size, the tourney size, the mutation probability, the percentage of fit solutions to keep and the number of generations to run (Table S3.I).

Table S3.I. Parameters included in the genetic optimisation process, description, default value used during the runs and implications of changing the value.

Parameter	Description	Value	Implications
<i>popsiz</i>	Initial population size. A set of candidate solutions	200	Larger values tend to improve the diversity of the search with a computational cost
<i>tourney size</i>	Tourney size. The selection of mating pairs is done by tournament selection based on ranks, where two groups of solutions including <i>tourney size</i> of <i>popsiz</i> are selected at random, compared, and a victor is chosen based on ranks	10% <i>popsiz</i>	Smaller values will promote a better search of the solution space while reducing the convergence rate
<i>mutprob</i>	Mutation probability. Crossover between victors occurs by selecting indices of the two parent vectors uniformly at random. Each element has a fixed probability of <i>mutprob</i> of undergoing mutation	0.01	Higher values will promote exploration of the search space while reducing the convergence rate
<i>keepbest</i>	Percentage of fit solutions to keep. New populations are formed by combining the <i>keepbest</i> most fit solutions from the old generation with the new offspring	10% <i>popsiz</i>	Smaller values will promote diversity while reducing the convergence rate
<i>ngen</i>	Number of generations to run. The process is carried out <i>ngen</i> times	300	Larger values will favour equilibrium conditions

4. Genetic optimisation: Sensitivity analyses

Equilibrium

As in section 2, simulations were considered to have reached equilibrium if the slopes of the regression lines fit to the 50 most recent normalized (between 0 and 1) values of the objective function were all less than 0.001 in absolute value (Caswell and Etter 1993). Equilibrium was reached between 64 and 145 iterations when assessing 20 runs for 500 generations. This indicates that the value used for all analyses of 300 generations was sufficient to assess equilibrium conditions in the optimisation process. It is important to note, however, that although in small amounts (the difference between values at generation 500 and 300 had a median of 0.05), the solutions kept improving when increasing the number of generations (Figure S4.1). For future work it would be interesting to compare this and alternative optimisation algorithms (e.g. simulated annealing) in terms of convergence rate and speed, in order to implement the spatially explicit population model using the best optimisation available.

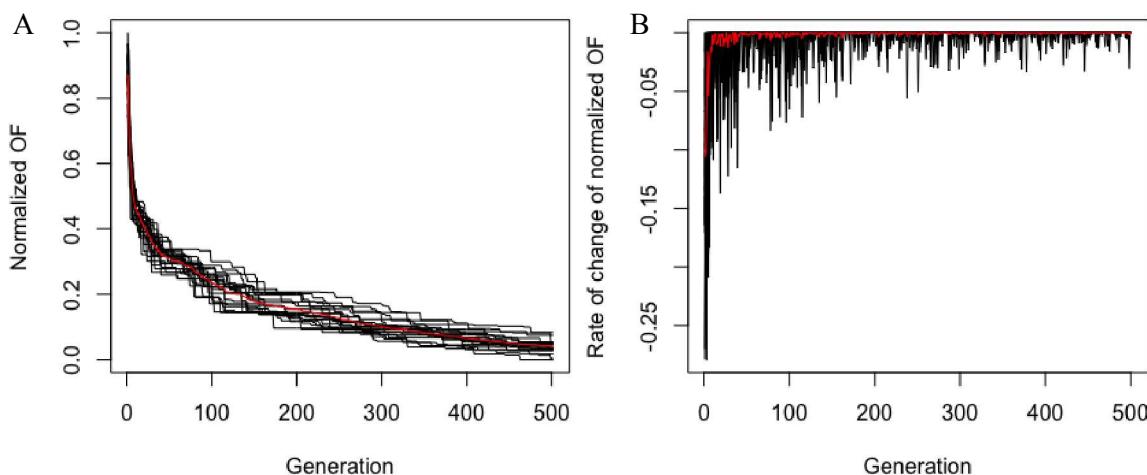


Figure S4.1. Values of (A) normalized Objective Function (*OF*); and (B) rate of change in this value when increasing the number of generations in the optimisation procedure. Black lines indicate each of 20 runs, red line the average of all runs.

Parameters

We used the default values defined by Wolters (2015) within the optimisation framework. To assess the sensitivity of the genetic algorithm to the specific choice of parameter values, the influence of each optimisation parameter in the value of the objective function, normalized persistence and yield was tested one at the time, as in section 2. To compare patterns, we ran the optimisation algorithm 20 times and quantified the percentage change obtained with the default parameter and the alternative. Pair-wise dissimilarities could not be calculated because the optimisation method initiates each run with random conditions.

The results are highly insensitive to the choice of optimisation parameters (Figure S4.2). The objective function (*OF*) is the least sensitive to the choice of parameters, and values of *OF* vary less than 1% when optimisation parameters are changed. Relatively, persistence (Per_c) is the most sensitive variable to the choice of parameters, however, maximum deviations are less than 3% from the baseline. The mutation probability (*mutprob*) and the percentage of fit solutions to keep (*keepbest*) had the largest influence in the results.

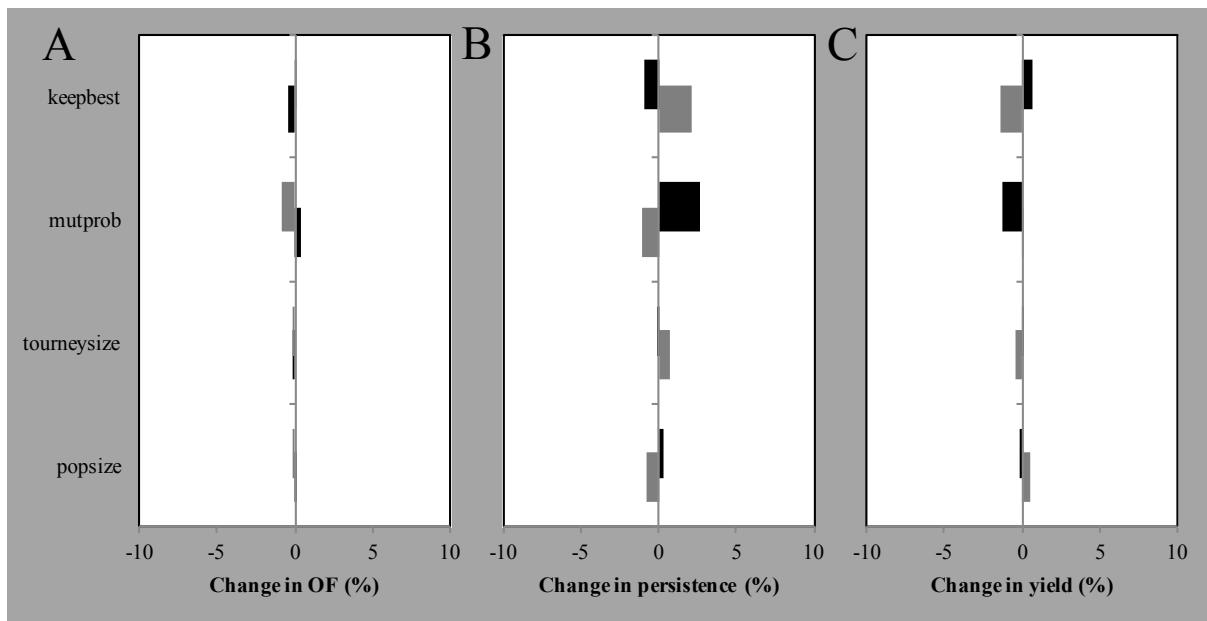


Figure S4.2. Sensitivity of the outputs to optimisation parameters. (A) Percentage change in average value for the objective function; (B) Percentage change in average normalized persistence; (C) Percentage change in average normalized yield. We assessed the parameters listed in Table S3.I. Parameters were assessed considering positive (black) and negative (grey) variation around the default value. *popsizes* (assessed at 100 and 300), *tourneysize* (assessed at 5 and 15%), *mutprob* (assessed at values of 0.001 and 0.05), *keepbest* (assessed at 5 and 15%).

5. Data sources: Map of zones

Shallow areas (above approximately 30 m deep) were mapped for this study using remote sensing imagery. The map of geographic zones was built using Landsat imagery and an object-oriented approach, and has a spatial resolution of 30 m. The map follows a zonation scheme adapted from Zitello et al. (2009) to capture the morphology of reef-rimmed platforms observed in the Miskitu cays and the non-rimmed, flat-topped platforms of the Eastern banks. The map of zones was used to identify (1) lagoon and back-reef areas; (2) fore-reef areas and (3) deep bank areas, relevant to recognize functional seascape units in the region. Although the map remains unvalidated due to logistical difficulties, broad geographic zones are generally identified using Landsat with reasonable accuracy (Andréfouët et al., 2006).

Source imagery

Available Landsat-8 imagery was assessed for cloud cover, suspended sediment load and the general degree to which the submerged habitats could be discerned. The best scenes (Table S5.I) were downloaded and mosaicked using ENVI image processing software. During construction of the mosaic, individual images were colour-balanced and feathered (a technique used to blend the suture lines between adjacent images in a mosaic by running a spatial filter over the seam) across the image boundaries over a distance of 500 m to smooth scene seams. Landsat channels 5-8 were used to mask out emergent areas prior to benthic image classification.

Table S5.I. Landsat-8 imagery used as inputs to the classification

Image ID#	Date of Acquisition	Path	Row
LC80140482014187LGN00	2014-07-06	14	48
LC80140492014187LGN00	2014-07-06	14	49
LC80140502014363LGN00	2014-12-29	14	50
LC80150482014354LGN00	2014-12-20	15	48
LC80150492014354LGN00	2014-12-20	15	49
LC80150482014354LGN00	2014-12-20	15	50
LC80160472014265LGN00	2014-09-22	16	47
LC80160482014265LGN00	2014-09-22	16	48

Methodology

Geographic zones were delineated using an object-oriented approach. In contrast to pixel-based classification methods, object-oriented image analysis segments satellite data into landscape objects that have ecologically-meaningful shapes and classifies the objects across spatial, spectral and textural scales. Object-oriented methods have been shown to yield significant accuracy improvements over traditional pixel-based image analysis techniques (Kelly and Tuxen, 2009; Purkis and Klemas, 2011).

Imagery was first radiometrically and atmospherically corrected using ENVI software to yield units of reflectance at the water surface. A water column correction was not applied in this study as the object-based strategy for mapping is not as confounded as a pixel-based classifier to bathymetric artefacts. This is because object-based mapping utilizes image texture, a property invariant to variable water depth (Purkis et al., 2006). Zones were classified using the software eCognition (v. 9.0, Trimble Inc.) and the multi-resolution segmentation algorithm with a scale parameter of 200. Zone boundaries within each platform were classified through visual identification of platform morphology.

Areas were mapped according to a scheme adapted from Zitello et al. (2009, Figure S5.1) to capture the morphology of reefs in the region characterized by poor development. For the Miskitu Cays, the zone "reef flat" and "back-reef" was added to the Zitello's atoll model to yield seven classes that were sufficient to capture the geographic zones of the platforms (Figure S5.1A). This model may be termed a "reef-rimmed" carbonate platform. Because the Eastern banks display even more depauperate reef development, further modification of the Zitello zones was required. The approach adopted here was to develop a zonation that was independent of the presence of coral reefs and instead keyed on platform morphology. The adapted scheme uses five zone classes (Figure S5.1B) and may be termed as a "flat-topped" carbonate platform. Equivalences between Zitello's (2009) and the zonation schemes developed during the mapping of consolidated areas in eastern Honduras can be found in Table S5.II.

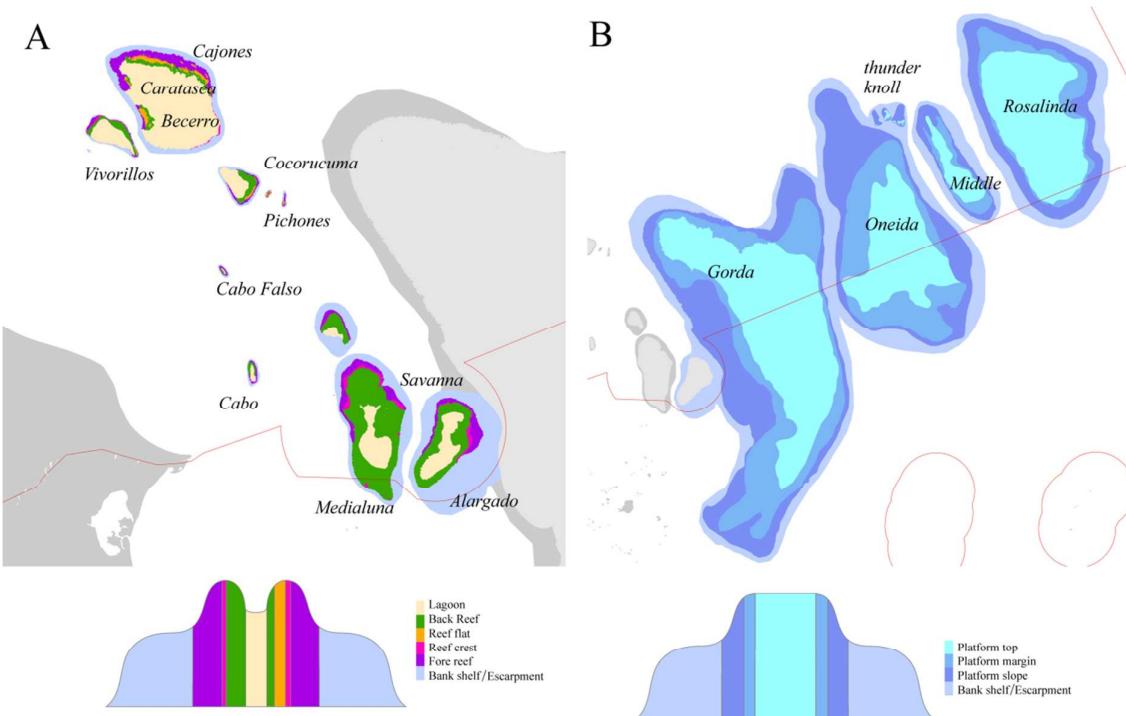


Figure S5.1. Map and zonation schemes developed for the “reef rimmed” morphology of the Miskitu cays (A) and the “flat-topped” morphology of the Eastern banks (B).

Table S5.II. Equivalence matrix between Zitello et al. (2009) zonation scheme for an ‘atoll’ and the ‘reef-rimmed’ and ‘flat-topped’ geomorphology found within the study area.

Atoll: Zonation scheme according to Zitello et al.	Reef-rimmed: Zonation scheme used for the Miskitu cays	Flat-topped: Zonation scheme used for the Eastern banks
Lagoon	Lagoon, Back-reef	Platform top
Reef crest	Reef crest, Reef-flat	Platform margin
Fore-reef	Fore-reef	Platform slope
Bank/Shelf/Escarpment	Bank shelf/Escarpment	Bank shelf/Escarpment

Assessment

The region encompasses a total area of shallow consolidated habitats of 24,947 km² in Honduras, a 33-fold increase in coverage when related to previous global assessments of reef extent which only mapped 750 km² of shallow habitats in this region (Andréfouët et al., 2006). The area can be divided into two geomorphologically distinct regions, the Miskitu cays and the Eastern banks, all atop the Nicaraguan rise.

The Miskitu cays comprise a collection of 49 cays covering just 0.3 km² of land and about 2,844 km² of shallow consolidated habitats within Honduran waters. Shallow areas are distributed along ten reef-rimmed isolated carbonate platforms separated by deep structural lows (Figure S5.1A). The windward (eastern) margins of the platforms host well-developed reef rims, while leeward margins have less vigorous growth, languish in deeper waters and are fully exposed to marine conditions.

The Honduran Eastern banks are large (22,103 km² within Honduran waters), drowned structures atop the Nicaraguan rise (Figure S5.1B). With the exception of the windward margins of Gorda and Rosalinda banks, these flat-topped platforms have depauperated reefs and extensive shallow paved areas ideal habitat for lobster, conch and sea cucumber.

Differences in geographic zonation among the Miskitu cays and the Eastern banks might be related to different development guided by different rates of flooding during the Holocene transgression, a mechanism that has been used to explain divergent morphologies of banks in the Bahamas (Purkis et al., 2014).

6. Data sources: Larval connectivity matrix

A larval connectivity matrix for spiny lobster was produced for this study. The dataset differs of similar ones available for the Caribbean basin (Kough et al., 2013) in spatial resolution and coverage: it represents a 18-fold increase in spatial resolution, and captures more than 24,000 km² habitat areas in our study region that have been overlooked by global databases of reef extent (Andréfouët et al., 2006) and therefore in all previous efforts to assess larval connectivity patterns in the Caribbean.

To model larval dispersal of spiny lobster in the Caribbean region, we developed a biophysical larval dispersal model using the individual-based offline Lagragian tool Ichthyop v3.1 (Lett et al., 2008). The virtual larvae were represented as particles in three dimensions and characterized by their latitude, longitude, and depth at each time step of the model (one hour). A forward-Euler advection was implemented in the model and horizontal diffusion was included following Peliz et al. (2007) with a turbulent dissipation rate of 10–9 m²s⁻³. Using coral reef habitat location from the Millenium Coral Reef Mapping Project (Andréfouët et al., 2006) and fishing grounds locations of lobster in Honduras, 4921 areas representing larval release and larval settlement locations were identified in the Caribbean region. Areas in Honduras were defined as 16 km² square polygons whereas in the rest of the Caribbean release areas were 64 km². Over these areas, 100,000 particles were randomly released from January 2006 to December 2008 in the HYCOM consortium global model (Chassignet et al. 2009). The HYCOM model fields for the intra America Seas region were extracted daily from the global model and converted to match Ichthyop's input format. An ontogenetic vertical migration module was implemented to represent lobster larvae behaviour (Butler et al., 2011) following Callwood (2010). The larval dispersal duration was set to 196 days with 152 days of pre-competency period (Goldstein et al., 2008). Virtual larvae were considered settled when they were located in a settlement area and they were at least 152 days old. Simulations outputs are represented as connectivity matrices with dimensions 4,921x4,921, a vast improvement when related to 261 sites assessed by Kough et al. (2013). Patterns of larval connectivity in the Caribbean are extremely heterogeneous, with median larval dispersal distance ranging from 69 to more than 3,000 km (Figure S6.1).

This Caribbean-wide connectivity matrix was subsetted to extract values for our study area. To this end, we assigned the closest connectivity value to each of our 1211 management units, and represented locations outside our region of interest as one unique additional site that represents the summation of all supplied and received larvae from elsewhere in the Caribbean.

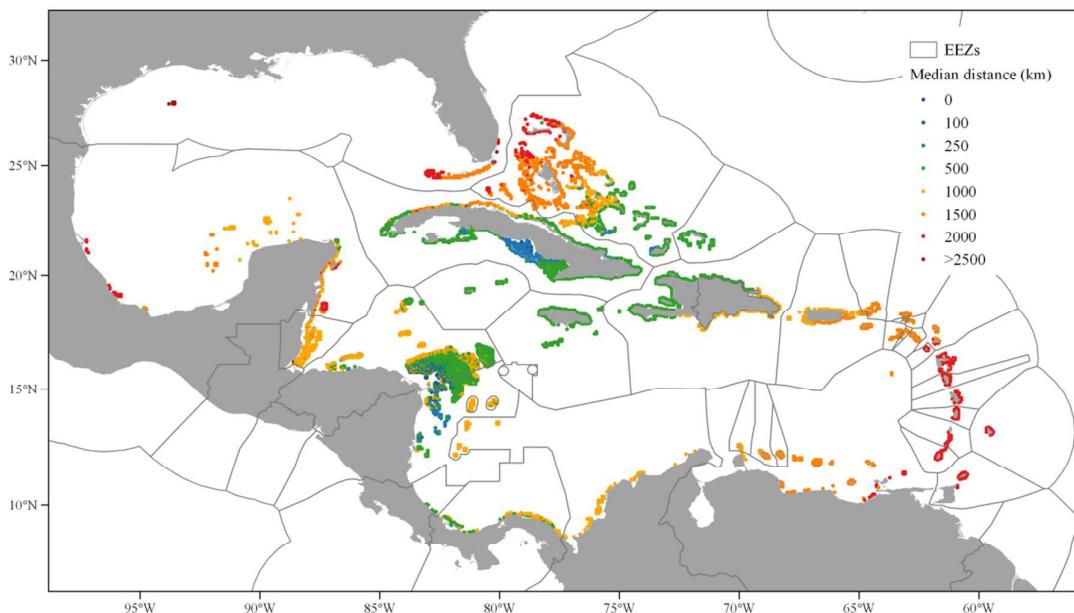


Figure S6.1. Median larval dispersal of spiny lobster in the Caribbean for the period 2006-2008, showing large differences in regional retention across the basin

7. Data sources: Adult connectivity matrix

As a consequence of home ranges mobile species become vulnerable to fishing outside the management unit. To reflect this behaviour, we calculated an exposure matrix, which indicates the probability of occurrence of the species in nearby management units as a function of its home range and the configuration of the habitat. This information was then used to parameterize adult spillover and calculate effective fishing mortality within the spatially explicit population model.

Lobster movement

Random diffusion patterns are generally assumed when exploring the response of fish populations to protection from exploitation by marine reserves (e.g. Grüss et al., 2011; Moffitt et al., 2009). This is not realistic for many species that exhibit complex movement patterns (e.g. homing, migratory, nomadic) and restricted movement through habitat, such as spiny lobster, but also many fishes (e.g. Chapman and Kramer, 2000; Farmer and Ault, 2011).

Panulirus argus participates in daily, seasonal, nomadic and ontogenetic movements (Butler et al., 2007; Herrnkind, 1980). Daily movements (also called homing) are short and random, where lobsters leave shelter to forage for food at night, encompassing about 1 km around dens (Bertelsen and Hornbeck, 2009). Seasonal migratory movements expand several kilometres and have been associated to reproductive activity, when lobster move from shallow inshore areas to deep reefs to spawn. Nomadic, undirected long movements are haphazard, individual and sporadic, and the causes are unclear. They occur with low probability of occurrence (of about 15%) over an area of about 4 km (Bertelsen, 2013). Finally, ontogenetic movements involve changes in habitats from back-reefs to patch-reefs and fore-reefs through the lobster's life cycle.

We considered all types of movement for the design of reserve networks for spiny lobster. Spawning and ontogenetic migrations occur within the seascape units. Daily homing and nomadic movements were modelled explicitly through the inclusion of an adult movement matrix, or exposure matrix, which we describe below.

Exposure matrix

The daily and nomadic movements of lobsters were characterized by an exposure matrix. Exposure E outside the management unit was calculated using the relationship given by Kramer and Chapman (1999, Eq. 1, Figure S7.1) where R is the ratio between the length of the management unit (5 km) and the home range.

$$\begin{aligned} E &= 100(1 - R) \text{ if } R < 0.5 \\ E &= 100\left(\frac{1}{4}R\right) \text{ if } R > 0.5 \end{aligned} \quad \text{Eq. 1}$$

Following this equation, exposure equals 0.05 for daily movement (E_d) and 0.2 for nomadic movement (E_n). While daily movements occur all the time, nomadic movements are rare and occur only about 15% of the time. To calculate total exposure, we corrected exposure values by considering the probability of the specific type of movement to occur, and added them, given that the two forms of movement are independent (Eq. 2, Figure S7.1). This produced a total value of exposure of 0.08.

$$E_t = 1E_d + 0.15E_n \quad \text{Eq. 2}$$

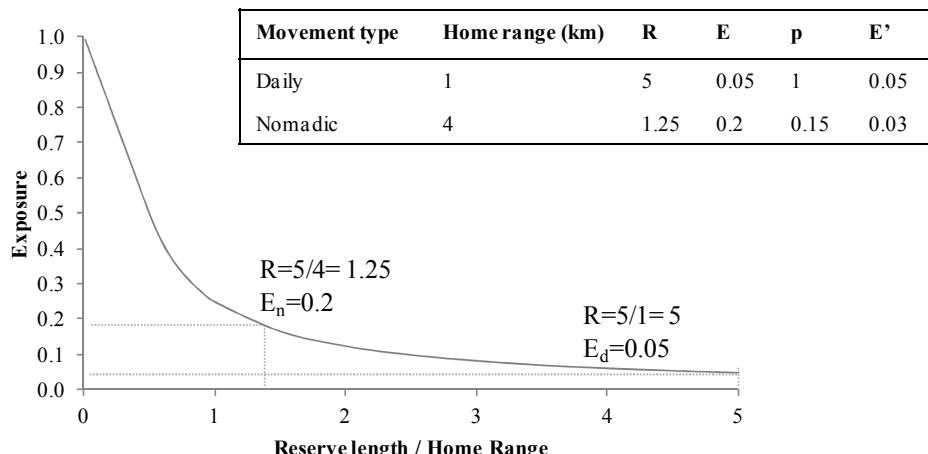


Figure S7.1. Relationship between exposure and R (the ratio between reserve length and home range) according to Kramer and Chapman (1999) and calculation of E and corrected E (E') for daily and nomadic movement.

Lobsters generally remain within the habitat patch, with deeper, sand areas serving as habitat barriers (Acosta, 1999; Freeman et al., 2009), a phenomenon also common in some fishes (Chapman and Kramer, 2000; Farmer and Ault, 2011). This restricted behaviour implies that adult spillover will occur if cells in the Moore neighbourhood present continuous habitat. For simplicity, exposure in each of the E_{ij} 8 neighbour cells was proportional to the amount of contiguous habitat available in the cell i (Eq. 3).

$$E_{ij} = E_t \frac{Area_i}{\sum Area_{neighb}} \quad \text{Eq. 3}$$

Using these constraints, an adult connectivity matrix E_{ij} was calculated, reflecting the probability of an adult from area j to be present in area i . This information was used to calculate effective fishing mortality in each management unit within the spatially explicit population model.

8. Data sources: Lobster parameters

To estimate EPR and YPR we used the parameters described in Table S8.I. Because no population parameters for Honduran spiny lobsters have been compiled, we reviewed values reported for the Caribbean basin and chose typical ones, following, when available, the advice of research groups that have experience in stock assessment in the region: the Food and Agriculture Organization of the United Nations (FAO) and NOAA's South-East Data, Assessment, and Review organization (SEDAR). The review for each parameter can be found below.

The population model included 16 size classes. Individuals become reproductively mature at 2 years, at the same time they become available to the fishery. Fecundity increases with age. Individuals experience a natural mortality rate of 0.34 yr^{-1} throughout their lives and fishing mortality of 0.4 yr^{-1} .

Table S8.I. Parameters used for modelling EPR and YPR for *Panulirus argus*

Parameter	Value	Definition	Reference
a_{\max}	16	Maximum age (year)	Kanciruk 1980
t_r	2	Age at recruitment (year)	Munro 1983
t_c	2.45	Age at first capture (year)	Honduran legislation and morphometric relationship
M	0.34	Instantaneous natural mortality rate	FAO (2001), SEDAR (2010)
F	0.4	Instantaneous fishing mortality rate	SEDAR (2010)
L_∞	183.55	Asymptotic von Bertalanffy length (mm)	Leon et al. 2005
K	0.24	von Bertalanffy growth parameter	Leon et al. 2005
t_0	0.45	Age at which individual would be length 0 for von Bertalanffy (year)	Leon et al. 2005
α	91.88	Parameter of fecundity-at-length relationship	Cox and Bertelsen 1997
β	231212	Parameter of fecundity-at-length relationship	Cox and Bertelsen 1997
b	{1 if $a \leq 3$ 2 if $a > 3$	Number of broods per year	SEDAR 2010
Γ	0.0046	Parameter of weight-at-length relationship	Cruz et al. 1981
Δ	2.630	Parameter of weight-at-length relationship	Cruz et al. 1981

Maximum age (a_{\max})

We considered a maximum age of 16 years, which coincides with values used by SEDAR (2005, 2010) for population modelling of *P. argus* (Kanciruk, 1980).

Age at recruitment (t_r)

We considered an age of 2 years, which corresponds to 60 mm, the recruitment size used by Munro (1983) for *P. argus* and Frisch and Hobbs (2012) for *P. versicolor*.

Age at first capture (t_c)

In Honduras, regulations include a minimum legal size of 5.5 inches (140 mm) of tail length. This corresponds to approximately 70 mm of carapace length (CL) if an average of the morphometric functions considered in Table S8.II is used. As a reference, the minimum legal size for capture in the USA is 76.2 mm CL (SEDAR, 2010). This CL can, in turn, be transformed into age by considering the length-at-age relationship for spiny lobster, resulting in an age of first capture of 2.45 years.

Table S8.II. Length (Lt) to carapace length (CL) relationships published for female lobsters

Reference	Location	Equation	CL for Lt=140
Ivo 1996*	Brazil	CL=0.5432Lt + 0.3442	76.39
Cruz et al. 1981*	Cuba	CL=0.3374Lt -2.3439	44.89
Zetina et al. 1996*	Yucatan, Mexico	CL=0.45Lt -0.06	62.94
Coba-Cetina 1990*	Bahia de la Ascension, Mexico	CL=0.56Lt -1.23	77.17
Gonzalez-Cano 1991*	Quintana Roo, Mexico	CL=0.5687Lt +0.01377	79.63
Wade et al. 1999	Belize	CL=0.433Lt+17.37	77.99
Matthews et al. 2003	Florida	CL=0.56*Lt-5.07	73.33

* References in FAO (2001)

Instantaneous natural mortality rate (M)

We used a constant value of natural mortality of 0.34 year⁻¹ for all ages. This has been used recently by SEDAR (2010), and it falls within the range of 0.3-0.4 year⁻¹ considered as most reliable for the Caribbean basin by FAO (2001) and SEDAR (2010).

Values of natural mortality rate reported in the literature, however, range widely (Table S8.III), with a median of 0.36. Sources of variation could be related to differences in relative abundance of lobster predators in the area as well as the size structure of the particular populations (with smaller lobsters experiencing higher mortality).

Table S8.III. Some natural mortality values reported in the literature for *P. argus* (both sexes).

Reference	M	Location
Ehrhard*	0.36	Bahamas
Ivo 1996*	0.30	Brazil
Gallo et al. 1998*	0.62	Colombia
Buesa 1972*	0.26	Cuba
Cruz et al. 1986a*	0.44	Cuba
Cruz et al. 1981*	0.34	Cuba
Powers and Sutherland 1989*	0.42	Florida, USA
Muller et al. 1997*	0.30	Florida, USA
Haughton 1988*	0.62	Jamaica
Medley and Ninnis 1997*	0.36	Turks and Caicos

* From SEDAR (2005)

Instantaneous fishing mortality rate (F)

Values reported for fishing mortality vary widely for the Caribbean among locations, years and methods, with minimums of 0.15 (SEDAR 2010) and maximum of 1.20 (FAO 2001). Although *F* is defined as the fraction of the average population abundance taken by fishing, and therefore one would expect it to take values less than 1, it can in practice have a value of more than 1 on an annual basis for stocks with a high biological regeneration rate such as lobster. In the USA, *F* values have been relatively constant around 0.21 during the last three years assessed. Here we considered values of 0.4.

Length at age (L_∞ , K, t_0)

Because lobsters lack bony parts they cannot be aged in the same way as bony fish, in which annual increments in the ear-bones or otoliths are commonly used. Although recent efforts to age these crustaceans using other body structures have been underway (Maxwell et al. 2013), the lack of consistency in the relationship between age and length makes difficult to use these results to age lobsters using more novel methods (SEDAR 2010). Therefore length-at-age relationships for lobster are still derived from tag and recapture experiments, even though tagging is difficult for lobster due to their molting habits (SEDAR 2010).

Although there are some criticisms to the use of von Bertalanffy-type functions for lobster because of the discontinuous growth of the species related to its molting habits (Ehrhardt 2008), the limited research on the subject and localized application (only Florida) precludes the consideration of discontinuous growth approaches at this time.

FAO (2001) reviewed numerous parameter values for the application of the von Bertalanffy growth curve for female lobsters (Table S8.IV, Figure S4) and suggested the estimates of Leon et al. (1995) for Cuba as the most reliable, because of its large sample size. Since then, the same authors published updated parameter values, from 39 years of data (1963-2002) and 797,784 lobsters (Leon et al. 2005), and those were the values used here. According to Leon et al. (2005) $K=0.24$, $L_\infty=183.55$ and $t_0=0.45$.

Table S8.IV. von Bertalanffy parameters for female *P. argus*. Parameters used highlighted in bold font

Reference	K	L_∞	t_0	Location
Waugh 1980*	0.23	190	0	Bahamas
Evans 1988*	0.15	192	1	Bermuda
Santos et al. 1964*	0.38	148	0	Brazil
Ivo 1996*	0.236	233	0	Brazil
Gonzalez Cano and Rocha 1995*	0.18	162	0	Brazil
Cruz et al. 1981*	0.31	139	0.08	Cuba SW
Baez et al. 1991*	0.31	209	0	Cuba SW
Phillips et al. 1992*	0.39	171	0	Cuba SW
Leon et al. 1994*	0.24	174	0	Cuba SW
Baez et al. 1994*	0.21	171	0	Cuba SW
Leon et al. 1995*	0.19	155	0.37	Cuba
Clairovin 1980*	0.23	188	0	Martinique
Gonzalez-Cano 1991*	0.22	165	0.86	Mexico, Isla mujeres
Gonzalez-Cano and Rocha 1995*	0.22	146	0	Mexico, Isla mujeres
Arce 1990*	0.3	122	0	Mexico, Isla mujeres
Lozano-Alvarez et al. 1991a*	0.25	215	0	Mexico, Bahia de la ascencion
Castaño and Cadima 1993*	0.4	160	0	Nicaragua
Olsen adn Koblis 1975*	0.32	133	0	Virgin Islands, USA
Mateo & Tobias*	0.216	172.8	0.482	St. Croix
Leon et al. 2005	0.24	183.55	0.45	Cuba SW

*From FAO 2001, table 3.3

Fecundity at length (α, β)

Different fecundity-at-length relationships have been published for *P. argus* which vary mainly in egg estimates for larger sizes (Table S8.V). Here we used the function by Cox and Bertelsen (1997), which is currently used by SEDAR (SEDAR 2010), and is an intermediate function within the ones that have been observed for the basin. According to Cox and Bertelsen (1997) lobsters reach maturity at 50.16 cm or 1.78 years if using the length-at-age relationship of Leon et al. (2005) discussed above.

Table S8.V. Length-fecundity relationships published for *P. argus*. Also indicated the number of replicates and coefficient of determination (when present). Function used highlighted in bold font

Reference	Location	N	Equation
Fonseca-Larios & Briones-Fourzan 1998	Puerto Morelos, Mexico	157	BS=3.40 CL ^{2.5723}
Nascimento & Araujo 1984 ^{\$}	Rio Grande do Norde, Brazil	143	BS=9231.8519CL-477547.27, r ² =0.97
Cruz et al. 1987 ^{\$}	Gulf of Batabano, Cuba	269	BS=0.5911 CL ^{2.9866} , r ² =0.86
Cox and Bertelsen 1997	Dry Tortugas NP, USA	-	EC=91.88 CL²-231212
Cox et al. 1997 [°]	Florida Keys, USA	129	EC= 98.34 CL ² -1261651, r ² =0.91
Cruz and Bertelsen 2008	Cuba, Florida Keys, Dry Tortugas and Mexico	658	EC=2.668CL ^{2.709}
Donahue et al. 1998 [°]	-	-	EC=88.7CL ² -219200

\$ Cited in Fonseca-Larios and Briones-Fourzan 1998, used by SEDAR (2005)

° Cited in FAO 2001

Broods per year (b)

Large *P. argus* females produce several broods per year (Briones-Fourzán 2014, Cruz and Bertelsen 2008, Maxwell et al. 2009). Therefore, here we followed the approach used by Muller et al. (1997) and SEDAR (2010), and considered that female lobsters larger than 80 mm CL (i.e. 2.8 years using Leon et al. 2005 length-at-age equation) produce two broods per spawning season.

Weight at length (Γ , Δ)

Estimates of weight are needed to obtain yield. Many functions relating carapace length and tail weight have been published (Table S8.VI). With the exception of Mathews et al. (2003), Lyons et al. (1981) for males, and Wade et al. (1999) most functions are extremely similar. In this work we used the equation for both sexes published recommended by FAO (2001) in the absence of local data.

Table S8.VI. Some mass at length relationships published for lobster. Function used highlighted in bold

Reference	Location	N	Equation
Murray and Jennings-Clark 1998	St. Lucia	122	WTmale=0.030CL ^{2.216} , r ² =0.85
	St. Lucia	59	WTfemale=0.024CL ^{2.270} , r ² =0.91
Lyons et al. 1981	Florida	312	WTmale=0.00315CL ^{2.59934}
	Florida	258	WTfemale=0.00361CL ^{2.68379}
	Florida	570	WTboth=0.0042CL ^{2.64091}
Cruz et al. 1981§	Cuba		WTmale=0.00207 CL ^{2.792}
	Cuba		WTfemale=0.00279 CL ^{2.736}
	Cuba		WTboth=0.0046 CL^{2.630}
Munro 1983	Jamaica	100	WTboth=0.00271 CL ^{2.738}
FAO 2001	Florida		WTmale=0.00287 CL ^{2.71}
FAO 2001	Florida		WTfemale=0.00195 CL ^{2.81}
SEDAR 2005	Puerto Rico		WT=0.00921LC ^{2.4804}
Matthews et al. 2003	Florida		WTboth=0.0007762 CL ^{2.76273}
Olsen and Koblic 1975*	St. John		WTboth=0.0021 CL ^{2.778}
Clairouin 1980*	Martinique		WTmale=0.0023 CL ^{2.77}
Clairouin 1980*	Martinique		WTfemale=0.0021 CL ^{2.80}
Squires and Riveros 1978*	Colombia		WTmale=0.00516 CL ^{2.578}
Squires and Riveros 1978*	Colombia		WTfemale=0.00221 CL ^{2.7921}
Wade et al. 1999*	Belize		WTboth=0.0012 CL ^{2.689}

§ In FAO 2001

* In Matthews et al. 2003

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