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Conserving Spawning Stocks Through Harvest Slot Limits and No-Take Protected Areas

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Conserving spawning stocks through harvest slot limits and no-take protected areas

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Running head: MPA footprint

Article Impact Statement

Marine protected areas and harvest slot limits together can conserve large breeding individuals and support population sustainability.

Abstract

The key to the conservation of harvested species is the maintenance of reproductive success. Yet for

many marine species large, old individuals are targeted despite their disproportionate contribution

to reproduction. We hypothesized that a combination of no-take marine protected areas (MPAs) and

harvest slot limits (maximum and minimum size limits) would result in the conservation of large

spawning individuals under heavy harvest. We tested this approach under different harvest intensities with a 2-sex, stage-structured metapopulation model for the Caribbean spiny lobster (*Panulirus argus*). *P. argus* is intensively harvested in the Caribbean, and in many localities large, mature individuals no longer exist. No-take MPAs and harvest slot limits combined rebuilt and maintained large mature individuals even under high harvest pressure. The most conservative model (a 30% MPA and harvest slot limit of 75-105 mm) increased spawner abundance by $5.53E^{12}$ compared with the fishing status quo at the end of 30 years. Spawning stock abundance also increased by $2.76-9.56E^{12}$ individuals at a high harvest intensity over 30 years with MPAs alone. Our results demonstrate the potential of MPAs and harvest slot limits for the conservation of large breeding individuals in some marine and freshwater environments. Decisions on which management strategy best suits a fishery, however, requires balancing what is ecologically desirable with what is economically and socially feasible.

Conservación de Stocks Reproductivos por medio de Límites de Espacios de Producción y Áreas Protegidas de Cero Captura

Gnanalingam et al.

19-839

Palabras clave: área marina protegida, conservación, crianza, langosta, límite de tamaño

Resumen. La clave para la conservación de las especies en criaderos es la manutención del éxito reproductivo. Aún así, para muchas especies marinas los individuos grandes y viejos son seleccionados a pesar de su contribución desproporcionada para la reproducción. Nuestra hipótesis supone que una combinación de áreas marinas protegidas (AMPs) de cero captura y los límites de espacio de producción (límites máximos y mínimos de tamaño) resultaría en la conservación de individuos reproductivos grandes durante una producción intensiva. Probamos esta estrategia bajo diferentes intensidades de crianza con un modelo metapoblacional de dos sexos y estructurado por etapas aplicado a la langosta espinosa del Caribe (*Panulirus argus*). *P. argus* es producida intensivamente en el Caribe y en muchas de las localidades, los individuos grandes y maduros ya no existen. La combinación de las AMPs de cero captura y los límites de espacio de producción regeneró y mantuvo individuos grandes y maduros incluso bajo una presión alta de producción. El modelo más conservador (un 30% de MPA y un límite de espacio de producción de 75-105 mm)

incrementó la abundancia de individuos reproductivos por 5.53E^{12} comparado con el status quo de la pesca después de treinta años. La abundancia del stock reproductivo también incrementó por 2.76-9.56E^{12} individuos en una intensidad alta de producción durante 30 años sólo con las AMPs. Nuestros resultados demuestran el potencial de las AMPs y los límites de espacio de producción para la conservación de individuos reproductivos grandes en algunos ambientes marinos y de agua dulce. Sin embargo, las decisiones sobre cuál es la mejor estrategia de manejo para una pesquería requieren del equilibrio entre lo que es ecológicamente deseable y lo que es económica y socialmente factible .

通过捕捞箱大小限制和禁止捕捞的海洋保护区来保护产卵种群

【摘要】保护被捕捞物种的关键是保障其成功繁殖。然而，对于许多海洋物种来说，体型大的老龄个体尽管对繁殖贡献的比例更大，但仍是捕捞的目标。我们假设，将禁止捕捞的海洋保护区和捕捞箱限制（最大和最小尺寸限制）相结合，可以在捕捞量较大的情况下保护产卵的大型物种。我们用加勒比海的眼斑龙虾（*Panulirus argus*）两种性别、有年龄结构的复合种群模型检验了这一方法。眼斑龙虾在加勒比海地区被广泛捕捞，许多地点已不存在大型成熟个体。结果显示，结合禁止捕捞的海洋保护区和捕捞箱限制，即使在高捕捞压力下也能重建和维持成熟个体数量。最保守的模型（30%海洋保护区和75-105毫米的捕捞箱限制）相比于继续维持现状，在30年后产卵雌性的数量可以增加5.53E^{12}。而单独建立海洋保护区，也可以在30年的高捕捞强度下使产卵种群数量增加2.76-9.56E^{12}只个体。我们的结果证明，海洋保护区和捕捞箱限制在某些海洋和淡水环境中对大型繁殖个体具有较好的保护潜力。不过，对渔场的最适管理战略决策还需要在生态和经济、社会方面之间取得平衡。【翻译：胡怡思；审校：聂永刚】

关键词：海洋保护区，龙虾，尺寸限制，保护，捕捞

Introduction

The targeted harvest of a population's largest or oldest individuals can disrupt social hierarchies, mate choice, sexual competition, and resilience to environmental change, eventually undermining population stability and reproductive success (Whitman et al. 2004, Hsieh et al. 2006, Barnett et al. 2017). In many species, particularly in the marine environment, large and typically old individuals are the most fecund (Hixon et al. 2014). Where there is hyperallometric scaling, large individuals can contribute disproportionately to population replenishment (Barneche et al. 2018). Large individuals and old individuals can also produce offspring of higher fitness (Berkeley et al. 2004; Birkeland & Dayton 2005). Overharvesting of large, old, or more experienced individuals can

therefore shift the majority of reproduction and hence population survival to small, young, and less-experienced individuals. In extreme cases, overharvesting of the largest individuals has driven the selection of life-history characteristics favoring earlier size or age of first reproduction and has contributed to population collapse (Hutchings & Rowe 2008, Allendorf et al. 2008, Therkildsen et al. 2019). There are, however, management tools explicitly designed to protect mature breeding individuals from harvest, including prohibitions on the take of pregnant or nursing individuals, temporal or spatial closures, and maximum size limits (Hixon et al. 2014, Barnett et al. 2017).

Spatial closures (e.g., parks and reserves) were originally designed to conserve natural and cultural resources (IUCN 2008). Where harvesting in these areas is prohibited (e.g., no-take marine protected areas [MPAs]), closures are credited with increasing the density, biomass, size, and diversity of a number of species in their boundaries (Halpern & Warner 2002, Coetzee et al. 2014, Gill et al. 2017). With increases in body size translating to increases in per capita fecundity and reproductive output, MPAs have an enormous potential to replenish populations (Barneche et al. 2018, Marshall et al. 2019). No-take MPAs have been used to conserve and rebuild spawning biomass in species as diverse as Atlantic cod (*Gadhus morhua*) (Moland et al. 2013) and spiny lobsters (*Panulirus argus, Jasus edwardsii*) (Bertelsen & Matthews 2001, Cox & Hunt 2005, Jack & Wing 2013). Marine protected areas can also contribute to larval dispersal and movement of adults beyond their boundaries (Di Lorenzo et al. 2016, Kough et al. 2019, Marshall et al. 2019). Despite their potential to conserve spawning populations, however, they are generally too small, too few, and too poorly enforced to affect the sustainability of species whose populations extend beyond their borders (Steneck et al. 2009, Gaines et al. 2010, Krueck et al. 2018). Spatial closures are also often politically controversial (Sale et al. 2005).

Another means of protecting large individuals in exploited populations is maximum size limits (MSL) in which only individuals below a given size are harvested. Such measures are common in

recreational freshwater and shallow-water marine finfish fisheries (e.g., northern pike [*Esox lucius*], common snook [*Centropomus undecimalis*]), but less so in commercial marine fisheries. Maximum size limits are designed to conserve spawning individuals and are particularly well suited to species with high recruitment, slow growth, and moderate natural mortality. Slot limits (combined maximum and minimum size limits) in which individuals of an intermediate range may be harvested (harvest slot limits [open slot]) or protected (protected slot limit [closed slot]) are designed to protect young recruits and spawning individuals (Gwinn et al. 2013). They may be particularly useful when reproductive output or the provisioning of young increases with maternal size (Ahrens et al. 2020) and when harvesting depletes spawning biomass (McPhee 2008, Arlinghaus et al. 2010). The success of MSLs and harvest slot limits to reduce fishing mortality and increase spawning stock without severely restricting catch rates, however, may be limited by the size or sizes chosen for harvest. If the MSL is too high or the harvest slot is too broad, such regulations are unlikely to succeed because few individuals will make it through to protection, particularly if harvest is intense. If the MSL is too low or the harvest slot too narrow, then catch rates are likely to decline (Law et al. 2012).

Yet, if harvest slot limits and spatial closures were combined this integrated management strategy could rebuild exploited populations and conserve the most fecund individuals while allowing harvest (Steneck et al. 2009). The use of these mechanisms together, however, has not been assessed previously. We assessed the potential use of harvest slot limits and MPAs to rebuild spawning biomass of the Caribbean spiny lobster with a 2-sex, stage-based, matrix population model. The model linked *P. argus* populations from the 10 largest fisheries in the Caribbean and considered 4 management scenarios: fishing (status quo), MPAs + fishing, slot limits + fishing, and MPAs + slot limits.

P. argus supports some of the largest and most economically valuable fisheries in the Caribbean (CRFM, 2011), but decades of intense fishing has left many regional populations fully capitalized or overfished (Ehrhardt, 2010), and except in a few well-enforced MPAs, size-selective fishing has nearly eliminated the largest individuals (e.g., Bertelsen & Matthews 2001). These large individuals produce disproportionately more offspring of higher quality (MacDiarmid & Butler, 1999; Gnanalingam & Butler, 2018a). Management of *P. argus* is complicated by a long postlarval period (5-9 months), dispersal, and widespread distribution (Goldstein et al. 2008; Butler et al. 2011, Kough et al. 2013). Although some spatial genetic patchiness may exist in oceanographically retentive regions of the Caribbean, overall there is significant demographic connectivity among Caribbean nations (Kough et al. 2013; Truelove et al. 2017; Segura-Garcia et al. 2019). At present, however, no standardized management measures aim to rebuild or provide long-term conservation of *P. argus* spawning biomass in the Caribbean.

Methods

Our lobster metapopulation model included the 10 countries with the highest landings of *P. argus* (highest to lowest: Bahamas, Cuba, Nicaragua, United States, Dominican Republic, Honduras, Mexico, Haiti, Venezuela, Belize). Commercial landings from these 10 countries constitute approximately 95% of the total catch (CRFM, 2011). Because fisheries for *P. argus* are fully or overexploited (Ehrhardt, 2010), we considered landings (catch) a reasonable estimator of population abundance, thus we used landings as a relative estimate of population magnitudes. Populations were linked by larval connectivity as estimated by Kough et al. (2013), whose model results were corroborated with empirical data on larval supply and population genetic structure (Truelove et al. 2017). Larvae produced every year by each population were split among the 10 populations according to these larval-connectivity probabilities. Lobster demographics (growth, mortality, immigration, emigration, reproduction) in each population were depicted in a 2-sex, stage-specific model (Fig 1). Although demographic models typically model only female dynamics, we opted for

a 2-sex model to account for differences in vital rates, size-selective mating, and sperm limitation (MacDiarmid & Butler, 1999; Butler et al. 2015). Data for model inputs came from published literature (Supporting Information), except for fecundity estimates, which were derived empirically (Gnanalingam & Butler, 2018b).

Figure 2 shows the model's basic form. Where N_t is a vector of lobsters in each sex and stage class at time t, and A_t is the sex-specific life-history projection matrix composed of survival and fecundities for each sex and stage at time t (Caswell, 2001). Model stages reflect *P. argus*'s 4 main life stages: larvae, juvenile, subadult, and adult (Supporting Information). The adult stage is divided into 10-mm carapace length (CL) classes (males, A1-A15; females, A1-A10) to account for differences in reproductive output, growth, and mortality. We used a 6-month time step to constrain growth within these size classes. This necessitated the creation of reproductive and nonreproductive matrices to prevent overestimation of fecundities and the number of young produced every year. Annual survival and growth probabilities were adjusted to fit the 6-month time step so entire populations transitioned smoothly between matrices.

Sex ratio at birth is $\rangle$ (set to 0.5 for a 1:1 sex ratio). For stage i and sex s, $G_{i,s}$ is the probability of an individual surviving ($\sigma_{i,s}$) and moving to the next stage ($\gamma_{i,s}$). The $P_{i,s}$ is the probability of an individual surviving ($\sigma_{i,s}$) and remaining in its current stage ($1 - \gamma_{i,s}$), and f_i is stage-specific fertility (size-specific fecundity $\times$ $\sigma_{i,s}$ [probability of an individual surviving]). We estimated $\sigma_{i,s}$ as 1- ($M_{i,s} + F_{i,s}$), where $M_{i,s}$ is age-specific natural mortality derived from a decay function centered on a mortality of 0.51 for a 1-year-old irrespective of sex (Forcucci et al. 1994) (Supporting Information) and $F_{i,s}$ is average age and sex-specific fishing mortality based on estimates from the Florida Integrated Catch at Age model (SEDAR 2010). The matrix without reproduction was identical except for 0s in place of the fertility coefficients f_i. (Supporting Information contains further information on how reproduction was incorporated in the model.) Each simulation ran for at least 30 years.

Management scenarios

Four management scenarios (Table 1) were uniformly applied across populations and each was assessed at low (mean fishing mortality [*F*] = 0.18), intermediate, or status quo (mean *F* = 0.36) and high (mean *F* = 0.72) harvest intensities (Supporting Information). We applied *F* only to lobsters outside MPAs and between maximum and minimum size limits in slot limit scenarios. To account for effort displacement in scenarios with MPAs and slot limits, fishing effort that would have ordinarily applied to all size classes in a fishable population was redistributed equally across all fishable size classes outside MPAs (where implemented) in accordance with the fishery-squeeze assumption (Smith & Wilson 2003, Pelc et al. 2010). A minimum size limit of 75 mm CL (close to minimum legal size in several countries in the Caribbean) was applied in all 4 scenarios. Fishing mortality for subadult lobsters was included to account for the take of undersized lobsters (SEDAR 2010). At intermediate harvest intensity subadult *F* was 0.13 (SEDAR 2010), and it was adjusted proportionally to high and low intensities. Model response variables were total abundance (*N*), spawning stock abundance (SSA) (number of breeding individuals only), total egg production (RO) (reproductive output = number of breeding females × fecundity), harvest biomass (FB*)*, number of migrants moving from MPAs to harvestable areas (emigrants), and population growth rate (λ).

In scenarios with MPAs, a carrying capacity for the harvestable area (K_f) was based on the estimated area occupied by *P. argus* in the Caribbean multiplied by the highest densities of lobsters observed in a Florida MPA ($0.031/m^2$) (Eggleston & Parsons, 2008). We assumed habitat was homogenous. The carrying capacity of MPAs (K_p) was the percentage of the population protected × K_f. Emigrant mortality (spillover) was 0.8 regardless of fishing effort. Effort concentration at MPA boundaries regardless of catch rates in the fishable area can be high for spiny lobsters (Stobart et al. 2009, Goñi et al. 2010); thus, this rate was kept constant across all fishing efforts. Probability of movement between MPA and fished areas varied according to rates and patterns of movement

described by Bertelsen and Hornbeck (2009) for *P. argus* in the Florida Keys. (Supporting Information contains further information on how lobster movement was incorporated.)

The effect of stochasticity in 4 life-history parameters (natural mortality [*M*], larval and emigrant mortality, and fecundity) on model results was assessed with scenario 3: MPA with 30% no-take protection at an intermediate fishing intensity. The influence of larval connectivity and discard mortality was assessed in additional simulations (description and results in Supporting Information).

Results

Harvest intensity and management scenario affected response variables in all 10 populations. When harvest intensity was low (mean *F* = 0.17), *N,* SSA*,* RO*,* and FB increased exponentially regardless of management scenario (Table 2, Fig. 3, & Supporting Information). But when harvest intensity was high (*F* = 0.72), lobster populations under fishing status quo and slot limit only scenarios collapsed (Table 2, Fig. 3, & Supporting Information). Meanwhile, lobster populations in models with MPAs only and MPAs + slot limits increased after 3 years, following an initial decline at the highest intensity (Fig 3, Supporting Information). Regardless of harvest intensity, after 30 years, the most conservative management option (30% MPA + MSL 105 mm CL) performed the best, followed by the 30% MPA + MSL 135, in terms of *N,* SSA, and RO, even with inclusion of discard mortality for lobsters in the slot size classes (Table 2 & Supporting Information). The values produced by 30% MPA + MSL 105 were not merely additive of a 30% MPA and 105 MSL. For values produced by the 30% MPA + MSL 105 to be matched by an MPA alone, the proportion of the population requiring protection was >75% regardless of harvest intensity. Even the narrowest of slot limits (MSL 85) applied to all 10 populations could not produce a *SSA* that matched the *SSA* of the 30% MPA + MSL 105 scenario after 30 years. Harvestable biomass was the exception; 30% MPA + MSL 135 outperformed 30% MPA + MSL 105 at a medium harvest intensity and the 30%

MPA + MSL 105 FB value was lower than the other MPA + slot limit models and MPA models at high harvest intensity (Supporting Information). At low harvest intensity, it took 18 years for FB in scenarios 2-4 to overtake the value in the fishing status quo (10 years for MPA 30 + slot limit, and MPA 30), whereas at moderate harvest intensity it took 10 years (7 years for MPA 30 + slot limit, MPA 30, and MPA 10). At high harvest intensity, only MPA and MPA + slot limit models retained harvestable biomass by the end of 30 years (Supporting Information).

Depending on model run time and harvest intensity, MPAs and slot limits alone sometimes improved response values compared with the fishing status quo. At a high fishing intensity, for example, SSA doubled from its initial value with MPAs alone in 5-10 years, depending on MPA size (Fig 3). This change is somewhat obscured by the log scales in Fig 3, which are useful for discerning the long-term changes in SSA. Slot limit models also produced higher values for N, SSA, RO, and FB compared with the fishing status quo but only after 5-10 years at low and medium harvest intensities (Fig 3 & Supporting Information) and only if discard mortality was excluded (Supplementary Information). At high harvest intensity, slot limits alone failed to prevent population decline (Fig 3 & Supporting Information).

After 30 years, spawning individuals (A1-15 males, A1-10 females) represented a very small percentage of the total N regardless of management scenario. However, where MPAs were applied, large spawning individuals (>100 mm CL) were more protected than where they were not (Fig 4). For status quo and slot limit only scenarios at high fishing intensity, large spawning individuals were relatively unprotected, and by year 30 they were not present. The consequences for reproductive output were obvious when combined over time for these scenarios (Supporting Information) and demonstrated the importance of hyperallometric scaling in $P.$ $argus$. A single A9 female surviving to reproduce in a given year would produce 2.35×10^6 eggs, whereas a single A1 female would produce only 8.83×10^4. Thus, models with the highest numbers of the largest male

and female size classes (i.e., 30% MPA + MSL 105/135, followed by 30% MPA and 10% MPA) ensured reproductive output remained high over 30 years.

Populations inside MPAs, always reached carrying capacity by year 30, and individuals had to migrate into the fished population. Populations within MPAs typically maintained a high proportion of spawning individuals; thus, reproductive output inside MPAs remained high even when harvest intensity was high outside the MPA. Because the carrying capacities for the MPAs varied relative to the level of MPA protection, the number of migrants that spilled over into the fished areas also varied. However, without the additional protection of harvest slot limits , up to 41% of lobsters emigrating from MPAs would be lost to fishing mortality.

Discussion

Our model demonstrated that a combination of regulations (i.e., slot limits, MPAs, and a decrease in harvest intensity) can rebuild and conserve *P. argus* spawning-stock abundance and ensure population sustainability throughout the seascape. The most conservative model (i.e., largest MPA coverage and lowest maximum size limit) quickly rebuilt spawning biomass and produced the largest population abundance regardless of harvest intensity after 30 years. However, strong positive effects on lobster sustainability were also predicted for MPAs applied alone (2%, 10%, and 30%) at all 3 harvest intensities, just not to the extent of the 30% MPA + slot limit models.

The MPA + slot limit scenario produced the highest values for the response variables after 30 years, but this was not simply a reflection of the additive nature of increasing protection by combining MPAs and slot limits. Rather, it reflected interactions among several factors including the size classes that were protected, hyperallometric scaling in fecundity, reallocation of fishing effort to size classes that were not protected, and length of model run. Adding results of a 30-year run of the 30% MPA and MSL 105 models, for example, did not produce the values obtained in the 30%

MPA + MSL 105 model. Nor could the 30% MPA + 105 MSL values be matched by any MPA or slot limit scenario alone, unless the MPA covered >75% of the population. Results from the less-restrictive MPA + slot limit combinations (i.e., 2% MPA MSL 135) run over 30 years, however, were surpassed by a 10% or 30% MPA applied alone even at high fishing intensities - particularly if discard mortality was included (Supporting Information). Thus, MPAs + slot limits may not always be the best option for conserving spawning-stock abundance or reproductive potential in a population, and ultimately a balancing between what is ecologically desirable and what is economically feasible or acceptable to fishers will be required (Klein et al. 2008).

Slot limits, applied alone were less effective at rebuilding and maintaining spawning biomass. Fishing removed individuals before they could grow into the protected size classes and the loss of large individuals translated into poor reproductive output. For lobsters in Florida to reach the protection of a 105 or 135 mm CL MSL, they would have to avoid capture for at least 4-5 years if male and 5-8 years if female. Yet, approximately 90% of the lobsters caught in Florida are 1.5 - 2.5 years old (76 - 90 mm CL) (SEDAR, 2010). Lobsters >105 mm CL make up <0.2% of Florida's fishery landings (SEDAR, 2010). Hence, there is scant probability that lobsters in the currently intense Florida fishery could avoid harvest long enough to reach the size refuge offered by the MSLs modeled here. This problem has been empirically observed in other fisheries, including an experimental fishery for northern pike in Finland (Tiainen et al. 2017). Although harvest slot limits preserved mature age and size structure compared with minimum size limits applied alone, they could not prevent a decline in the abundance of large pike at high harvest intensity, and slow-growing fish were caught before they reached the MSL (Tiainen et al. 2017).

Our results also confirm the profound impact harvest intensity has on spawning individuals in the absence of management tools such as MPAs and slot limits. Lowering exploitation rates is the most direct way to ease pressure on harvested populations (Allendorf et al. 2008). When harvest intensity was halved from present-day levels without any other management measures, population size,

spawning abundance, and reproductive output increased 100-fold over 3 decades. Although a large reduction in harvest intensity is unlikely to be economically feasible, if lobster populations are severely depleted a reduction in fishing mortality may be the only way to rebuild populations. One need only look to species protected under the U.S. Endangered Species Act (e.g., American crocodile [*Crocodylus acutus*]) or the recovery of fish stocks in the North Sea during World War II for examples of species that recovered following cessation of intense harvesting (Beare et al. 2010, US Fish & Wildlife Service 2019). Typically, such drastic measures are poorly received by the public, but they can lead to dramatic recoveries, as was the case for the Atlantic striped bass (*Morone saxatilis*) following a 5-year moratorium on harvest in the 1980s in the eastern United States (Secor, 2000).

Of course, the effectiveness of all demographic models is constrained by the quality of data inputs and model assumptions. For example, good estimates of the spatiotemporal variation in natural mortality, growth, fecundity, and fishing effort around the Caribbean is currently lacking for *P. argus*. Therefore, we used the same values for every population based on the best available data. The growth function, for example, was derived from Ehrhardt (2008) and was based on tag recapture and molt increment data from south Florida, where growth is typically slower than it is for *P. argus* at lower latitudes. Likewise, our estimates of fecundity were based on a noninvasive technique that yields more conservative estimates of size-specific fecundity than those based on gravimetric methods (Gnanalingam & Butler, 2018b). Maternal effects on larval survival were ignored, as were density dependent effects because density dependence for *P. argus* has not been reported in the literature and may be uncommon in the wild (Behringer & Butler 2006). Therefore, we believe the results from our model are likely to be conservative.

In the Caribbean, the idea of using harvest slot limits and MPAs for the conservation of spawning biomass and the long-term sustainability of *P. argus* is gaining traction among fisheries managers

(e.g., St Georges Declaration 2015) and perhaps even fishers. In a preliminary survey we conducted of lobster fishers ($n = 25$) in the Florida Keys and The Bahamas, the majority of respondents (64%) were in favor of using slot limits and MPAs in their own area. Strikingly, 59% of those fishers were supportive of this management strategy throughout the Caribbean even if there was little or no obvious benefit to their own geographic area. However, the addition of any new management tool intended to constrain fishing mortality is likely to have a negative effect on catch rates in the short term, with commensurate effects for the fishers and those dependent on the fisheries. Potential economic losses will no doubt weigh heavily on the minds of fisheries managers and government officials looking to implement new policies. Ultimately, decision makers will need to decide what policy goals to pursue in the short and long term, particularly if it could take a decade or more for harvestable biomass to surpass levels under the fishing status quo. Any potential short-term loss, however, could be offset by other business opportunities (Sala et al. 2013, 2016; Davis et al. 2019), and over long periods, spillover could offset catch losses resulting from the reduction in area open to fishing (Goñi et al. 2010).

Regulatory mechanisms that restrict harvests are likely to be contentious (e.g., Jones et al. 2008), but the long-term benefits of protecting mature spawning individuals are undeniable. Large individuals are often more fecund and produce offspring of a higher fitness, and mature population structures provide resilience (the storage effect) when environmental conditions are unfavorable (Chesson & Warner 1981, Anderson et al. 2008). This is true for a number of harvested species, particularly in shallow marine or freshwater environments, where fishing-related barotrauma is less of a problem. We therefore advocate the use of MPAs, and MPAs + harvest slot limits for the rebuilding and long-term conservation of Caribbean spiny lobster spawning biomass and suggest that it be considered for other intensively harvested marine and freshwater species.

Supporting Information

Further details on model methods (reproduction, movement) (Appendix S1), an assessment of model stochasticity (Appendix S1), life-history stages (Appendix S2), data sources (Appendix S3), parameters used in stochastic models (Appendix S4), a results summary of models run with discard mortality (Appendix S5), reproductive output (Appendix S6), harvestable biomass (Appendix S7), and a summary of results of the stochastic models (Appendix S8) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1. Management scenarios and fishing restrictions for spiny lobster applied to each model run and the justification for the selection of each simulation.

Scenario	Fishing restrictions	Justification
1. Fishing status quo	min size limit 75 mm	minimum size limit similar to that in Florida (76 mm); no maximum size limit or MPAs
2. Slot limit	slot limit* 75 – 105 mm	105 mm CL is the size at which fisheries landings sharply decline in the Florida trap fishery
	slot limit 75 - 135 mm	135 mm CL is the point at which a significant number of female lobsters produce a 3rd clutch
3. Marine protected area (MPA)	min size limit 75 mm + 2% no take protection	2% = current area protected by MPA in the Caribbean (Knowles et al. 2015)
	min size limit 75 mm + 10% no take protection	10% = target for MPA protection from the Convention on Biological Diversity 1993, Aichi Target 11 2010.
	min size limit 75 mm + 30% no take protection	30% = target for MPA protection from the World Parks Congress 2014
4. MPA + slot limit	2% no take protection + slot limit 75 – 105 mm	as for scenarios 2 and 3
	2% no take protection + slot limit 75 – 135 mm	as for scenarios 2 and 3
	30% no take protection + slot limit 75 – 105 mm	as for scenarios 2 and 3
	30% no take protection + slot limit 75 – 135 mm	as for scenarios 2 and 3

* Combined minimum and maximum size limits between which lobsters are harvested.

Table 2. Summary of deterministic model runs incorporating management scenario and fishing

effort on total abundance (*N*), spawning stock abundance (SSA*)*, reproductive output (RO), harvest

biomass (FB*)* , number of migrants, and population growth rate (λ) for the 10 populations of spiny

lobsters combined over 30 years.

Management scenario	Scenario particulars	*n*	Spawning stock	Reproductive output	Harvest biomass (Mt)	Migrants[a]	λ[b]
Low harvest intensity fishing status quo		2.31E+12	1.34E+10	1.09E+15	3.20E+07	NA	1.26-1.28
harvest slot limits	MSL (maximum size limit) 105	8.53E+12	4.51E+10	3.68E+15	8.79E+07	NA	1.32-1.34
	MSL 135	3.85E+12	2.18E+10	1.77E+15	5.09E+07	NA	1.28-1.31
MPA (marine protected area)	2% coverage	1.14E+14	5.22E+11	6.66E+16	6.18E+08	8.77E+08	-
	10% coverage	2.38E+14	1.24E+12	1.74E+17	1.42E+09	1.66E+09	-
	30% coverage	5.37E+14	2.65E+12	3.64E+17	1.39E+09	2.04E+09	-
MPA + harvest slot limit[c]	MSL 105 + MSL 2%	1.39E+14	6.07E+11	7.32E+!6	6.96E+08	3.40E+09	-
	MSL 135 + MPA 2%	1.24E+14	5.78E+11	6.85E+16	7.97E+08	3.36E+09	-
	MSL 105 + MPA 30%	1.42E+15	6.09E+12	7.08E+17	4.14E+09	7.23E+09	-
	MSL 135 + MPA 30%	6.59E+14	3.05E+12	3.90E+17	2.48E+09	8.27E+09	-

Medium harvest

intensity

fishing status quo		1.80E+07	1.46E+05	6.95E+09	1.49E+02	NA	0.84-0.86
harvest slot limits	MSL 105	7.73E+08	5.06E+06	2.52E+11	4.12E+03	NA	0.94-0.96
	MSL 135	1.02E+08	7.62E+05	3.66E+10	7.89E+02	NA	0.88-0.91
MPA	2% coverage	8.24E+13	3.79E+11	4.83E+16	2.08E+08	1.06E+09	-
	10% coverage	1.60E+14	8.70E+11	1.30E+17	3.88E+08	3.63E+09	-
	30% coverage	2.05E+14	1.24E+12	2.03E+17	3.08E+08	6.67E+09	-
MPA + harvest slot limit	MSL 105 + MPA 2%	1.02E+14	4.20E+11	5.10E+16	2.60E+08	4.38E+09	-
	MSL 135 + MPA 2%	8.49E+13	4.13E+11	4.86E+16	3.41E+08	4.71E+09	-
	MSL 105 + MPA 30%	1.18E+15	4.54E+12	4.69E+17	1.04E+09	1.06E+10	-
	MSL 135 + MPA 30%	8.43E+14	2.99E+12	3.19E+17	9.99E+08	1.70E+10	-

High harvest

intensity

fishing status quo		0.00	0.00	0.00	0.00	NA	-
harvest slot limits	MSL 105	3.96E+06	2.14E+04	2.35E+09	0.00	NA	0.81
	MSL 135	2.43E+05	1.51E+03	5.90E+07	0.00	NA	-
MPA	2% coverage	6.84E+13	2.76E+11	3.94E+16	5.16E+07	1.02E+09	-
	10% coverage	1.36E+14	7.41E+11	1.15E+17	9.21E+07	3.96E+09	-
	30% coverage	1.65E+14	9.56E+11	1.83E+17	0.00	8.21E+09	-
MPA + harvest slot limit	MSL 105 + MPA 2%	5.27E+13	2.94E+11	4.00E+16	2.84E+08	3.46E+09	-
	MSL 135 + MPA 2%	6.85E+13	2.37E+11	3.94E+16	4.16E+08	4.89E+09	-
	MSL 105 + MPA 30%	2.90E+14	5.53E+12	3.32E+17	0.00	4.00E+11	-
	MSL 135 + MPA 30%	2.02E+14	2.93E+12	1.02E+18	0.00	6.22E+10	-

[a]Average number of lobsters that moved into the fishery minus emigrant mortality from MPAs for

the 10 populations over 30 years.

[b]A (-)indicates a fluctuating λ after 30 years.

[c] Combined minimum and maximum size limits between which lobsters are harvested.
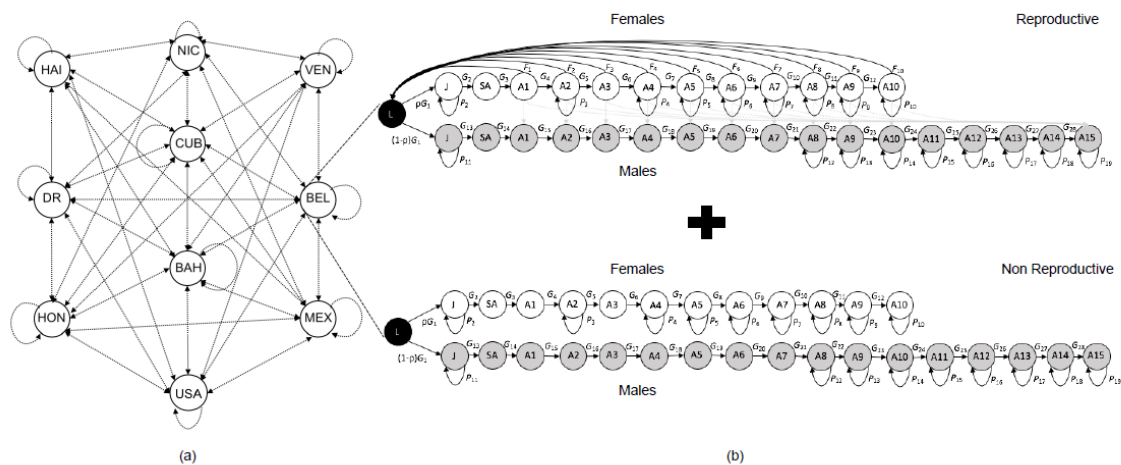
Figure 1. Stage-based matrix model of reproductive and nonreproductive cycles used for the 10 countries in the Western Atlantic that harvest the most *P. argus*: (a) larval connectivity matrix among the 10 countries (HAI, Haiti; BEL, Belize; DR, Dominican Republic; HON, Honduras; MEX, Mexico; BAH, Bahamas; CUB, Cuba; VEN, Venezuela; NIC, Nicaragua; USA, United States) and (b) sex- and stage-based structure of the model depicted for Belize, where reproductive (top) and nonreproductive (bottom) portions of the population are modeled separately before summing to obtain results for the entire population (arrows, individuals surviving and growing to the next stage [G_x] or probability of an individual surviving and remaining in its current stage [P_x]; F_x, stage-specific fertility; J, juvenile; SA, subadult; A, adult; numbered codes for life-history stages described in Supporting Information).

Figure 2. The model's basic form with reproduction included. $\mathbf{N_t}$ is a vector of lobsters in each sex and stage class at time t, and $\mathbf{A_t}$ is the sex-specific life-history projection matrix.

Variables (G, P, F, ρ) and life stages (L, J, SA, A for males [m] and females [f]) are defined in Methods
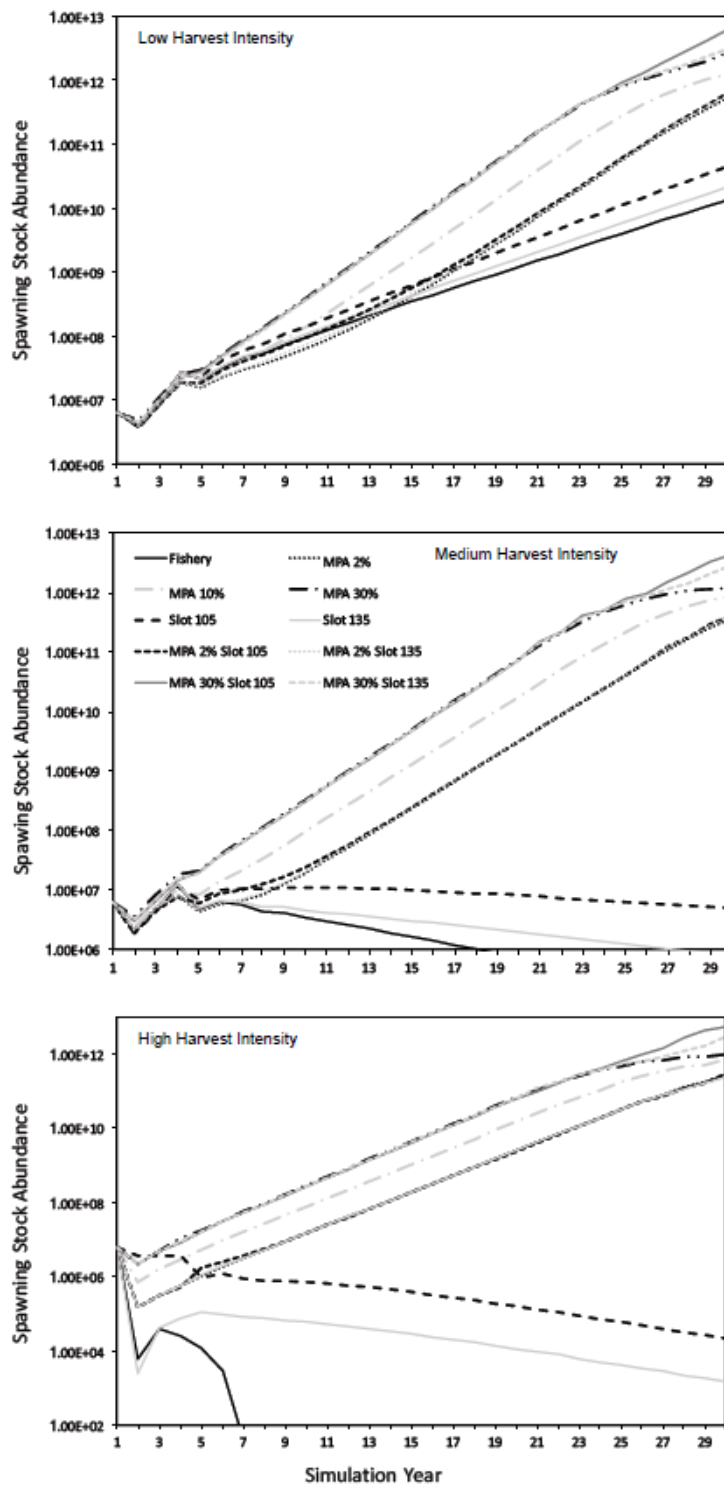
Figure 3. Effect of management scenario and harvest intensity on spiny lobster spawning stock abundance for the 10 modeled lobster populations combined over 30 years (MPA, marine protected area; slot, harvestable size range 75-105 or 135 mm carapace length [CL]). Logarithmic y-axis scales are used to permit easier visualization of results among scenarios.
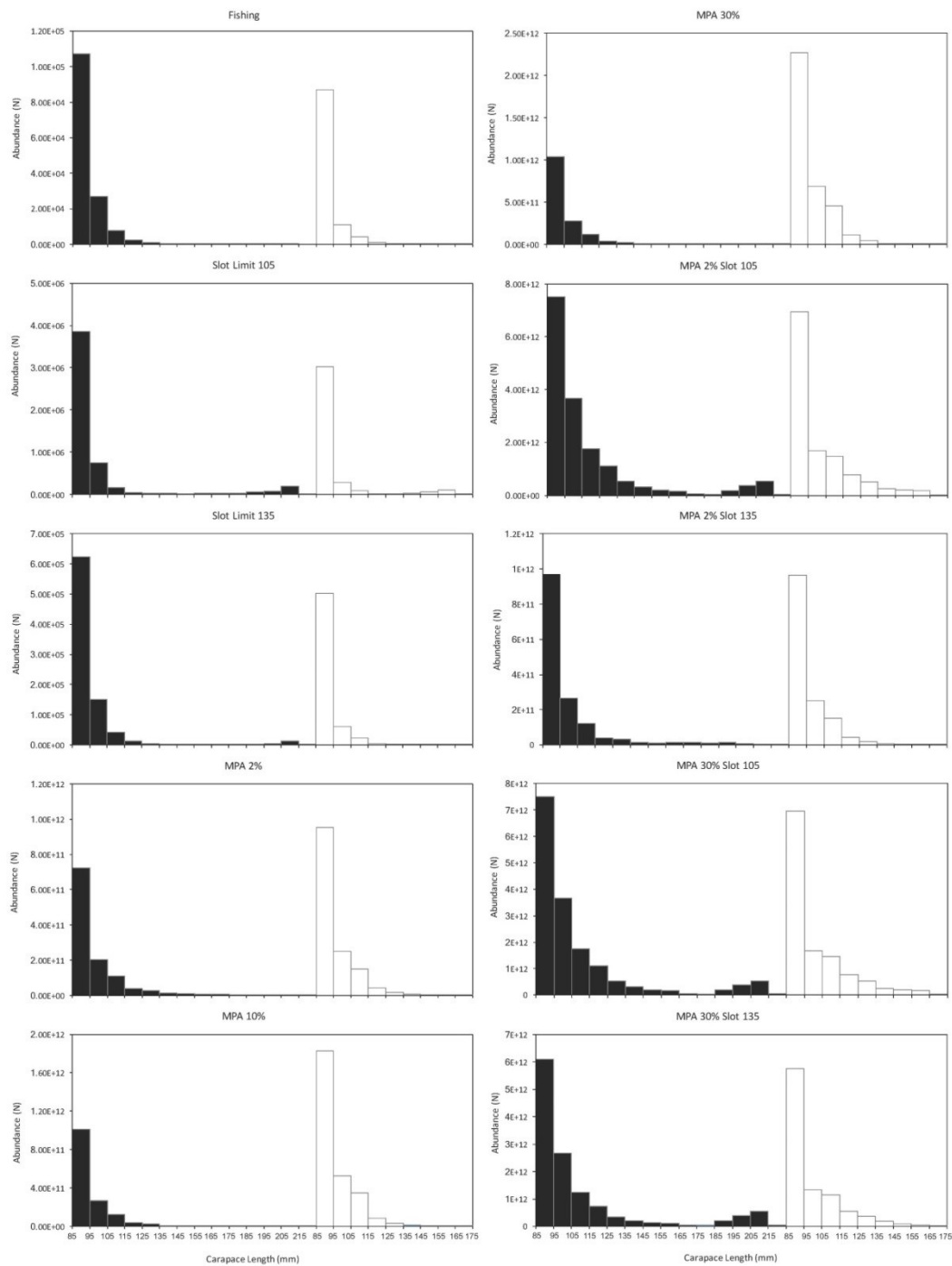
Figure 4. Stock structure of fisheries sized lobsters (> 85 mm carapace length [CL]) at year 30 for each of the management scenarios run at moderate fishing effort ($F = 0.34$) (MPA, marine protected area; slot, harvestable size range 75-105 or 135 mm CL; black bars, male; white bars, female). The smallest adult lobsters (75-85 mm CL) are not included in the figure because their much higher abundances obscured the stock structure of larger size classes. The y-axis scales differ to permit easier visualization of the relative results among scenarios.