# Underestimating the benefits of marine protected areas for the replenishment of fished populations

Dustin J Marshall[1]*, Steven Gaines[2,3], Robert Warner[2], Diego R Barneche[1,4], and Michael Bode[1,5]

Marine protected areas (MPAs) are important tools for managing marine ecosystems. MPAs are expected to replenish nearby exploited populations through the natural dispersal of young, but the models that make these predictions rely on assumptions that have recently been demonstrated to be incorrect for most species of fish. A meta-analysis showed that fish reproductive output scales "hyperallometrically" with fish mass, such that larger fish produce more offspring per unit body mass than smaller fish. Because fish are often larger inside MPAs, they should exhibit disproportionately higher reproductive output as compared to fish outside of MPAs. We explore the consequences of hyperallometric reproduction for a range of species for population replenishment and the productivity of exploited species. We show that the reproductive contribution of fish inside MPAs has been systematically underestimated and that fisheries yields can be enhanced by the establishment of reservoirs of larger, highly fecund fish.

Fish are an essential source of protein for a substantial proportion of the world's population. Wild fisheries are under intense pressure and landings of fish catches in global ports have largely flattened despite increasing effort (Kroodsma *et al.* 2018). Intense debate about the sustainability of wild fisheries continues, but improving their sustainability is a common goal (Pauly *et al.* 2002; Kroodsma *et al.* 2018). Increasingly, it seems that fish size plays an important role in replenishing

fish populations (Hixon *et al.* 2014). Larger fish have higher reproductive outputs than smaller fish and can produce offspring of higher quality (Dick *et al.* 2017). This has prompted calls to consider the role of "big, old, fat, fecund females" (BOFFFs; Hixon *et al.* 2014) in the management of fisheries, because fishing quickly reduces the relative abundance of BOFFFs.

Fishing decreases the average size of fish for two reasons. First, larger fish are more likely to be caught because of minimum size regulations, size-specific gear, and fisher preferences. Second, simply increasing the mortality rate beyond background levels results in a lower probability of fish surviving to a larger size (Cooper *et al.* 2013). The loss of the largest fish from a population is almost inevitable, even when fishing mortality is relatively low (Barnett *et al.* 2017). A wide variety of exploited fish species already exhibit reductions in average mass of up to 25% or more (Kopf *et al.* 2005; Fenberg and Roy 2008; Genner *et al.* 2010). Worse still, the increased mortality associated with fishing acts as a powerful selective force on maturation schedules and size (Swain *et al.* 2007). Intense fishing can induce evolutionary responses in fish to reproduce at a smaller size, an adaptation that increases reproductive success and offsets the increased risk of mortality (Fenberg and Roy 2008; van Wijk *et al.* 2013; Waples and Audzijonyte 2016). This size evolution negatively affects multiple desirable traits (eg larval viability, foraging behavior), and reduces the yield and replenishment of exploited populations relative to unexploited ones (Walsh *et al.* 2006). Given these negative consequences, how can managers maintain sustainable fisheries?

## Marine protected areas as management tools

Marine protected areas (MPAs) create localized areas of higher biomass and size distributions of larger fish relative to unprotected, fished areas (Lester *et al.* 2009; Edgar *et al.*

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**In a nutshell:**

- Debate continues around the efficacy of marine protected areas (MPAs) for managing and maintaining exploited fish stocks
- Fish are generally larger in MPAs, and a recent meta-analysis showed that larger fish produce disproportionately more offspring than smaller fish; however, models of fish populations do not typically take this difference in production into account
- Including the disproportionate reproduction of larger fish into models of fish replenishment increases the benefits of MPAs dramatically
- In terms of egg production, a single hectare of MPA is equivalent to 3–225 ha of unprotected area on average, depending on the fish species being considered

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[1]*Centre for Geometric Biology/School of Biological Sciences, Monash University, Melbourne, Australia *(dustin.marshall@monash.edu); [2]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA; [3]Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, CA; [4]School of Life and Environmental Sciences, The University of Sydney, Sydney, Australia; [5]School of Mathematical Sciences, Queensland University of Technology, Brisbane, Australia*

2014; Baskett and Barnett 2015). If designed correctly, networks of MPAs connected by larval dispersal may support a robust metapopulation of protected individuals that is relatively insulated from the impacts of fishing. Theory suggests that MPAs, if sufficiently widespread, can impede the evolution of harvesting-adapted phenotypes, maintaining the original phenotypic distribution of the exploited species (Baskett *et al.* 2005). Although these effects may be desirable from an ecological perspective, there are both benefits and costs for fishers (Fovargue *et al.* 2018).

MPA advocates argue that MPAs benefit fishers, not only by maintaining the population of the exploited species within the MPA network but also by promoting "spillover", whereby some fish or larvae leave the MPA and are eventually caught (McClanahan and Mangi 2000). The hope is that by maintaining higher biomasses within the MPAs, the spillover from those MPAs may offset the putative loss of catch associated with their establishment (Gell and Roberts 2003; Caselle *et al.* 2014). Despite these potential benefits, support from fishers is limited and MPAs remain contentious (Hilborn 2018). However, recent evidence suggests that the way in which managers account for fish reproduction leads to a systematical underestimation of some of the benefits of MPAs for the replenishment of fished populations.

## ◼ Modeling the contribution of MPAs to population replenishment

Models of fish replenishment almost invariably assume that fish reproduction scales isometrically with mass; that is, if fish mass increases by 10%, there will be a proportionate 10% increase in its reproductive output (Andersen *et al.* 2016; but see Marshall *et al.* 1998). Such assumptions were originally made when fisheries scientists had to calculate everything by hand, and modeling isometric reproduction made their analyses much simpler (Marshall *et al.* 1998). Moreover, assuming isometry had the additional benefit of reducing the amount of data that was required, as one needed only to estimate the total spawning stock biomass. The progenitors of fisheries models were uncomfortable with these assumptions even as they made them, believing them to be unrealistic (Beverton and Holt 1957), and yet, although there are exceptions (Scott *et al.* 2006; Cooper *et al.* 2013; Dick *et al.* 2017), the assumption of reproductive isometry continues to dominate models of fish replenishment (Zimmermann and Jorgensen 2015; Kell *et al.* 2016). Today's modelers probably make isometric assumptions for similar reasons: the mathematics is simpler, and the models are less data-hungry. However, some fisheries scientists have called for changes to this practice (eg Dick *et al.* 2017).

Although fisheries models have assumed reproductive isometry, fish biologists have repeatedly observed that reproduction in their particular species or group of species is hyperallometric rather than isometric (Hixon *et al.* 2014; Dick *et al.* 2017) – that

is, as fish size increases, fecundity increases disproportionately more. Yet, even though the incidence of hyperallometric reproductive scaling in fish has been noted sporadically for 40 years, it is rarely included in fisheries models (Barneche *et al.* 2018). Importantly, studies of the spillover effects of MPAs still assume isometry (eg Fovargue *et al.* 2018). Recent evidence, however, suggests that reproductive hyperallometry is in fact the rule across nearly all groups of marine fishes.

## ◼ Wrong assumptions about fish reproductive output

Barneche *et al.* (2018) demonstrated that, on average, reproductive output scales with fish size hyperallometrically in over 95% of fish species for which such data exist. In other words, a single 2-kg fish produces many more eggs than do two 1-kg fish. The average scaling exponent across all fish for which there are available data is 1.18, but can be as high as 1.56 for commercially important species like olive rockfish (*Acanthoclinus fuscus*). To put a scaling exponent of 1.56 into perspective, a single 5-kg fish produces 2.4 times as many eggs as five 1-kg fish. This reproductive hyperallometry is amplified further by the fact that larger fish also tend to produce larger offspring that contain more energy, and larger mothers are more likely to spawn repeatedly within a single season (Hixon *et al.* 2014).

Reproductive hyperallometry has troubling consequences for standard fisheries models, which generally assume that one unit of biomass has the same reproductive capacity as any other unit of biomass, regardless of whether it occurs in a smaller number of large fish or a larger number of small fish (Dick *et al.* 2017). Several studies have shown that an incorrect assumption of reproductive isometry results in the systematic overharvesting of exploited fish populations (Marshall *et al.* 1998; Cooper *et al.* 2013). This occurs because most models fail to account for the disproportionate loss of reproductive output that follows the loss of rare, larger individuals. The resulting overestimate of population replenishment encourages overharvesting. That is the bad news regarding reproductive hyperallometry; the good news is that if reproductive hyperallometry holds true, then MPAs may offer much greater benefits than previously believed.

## ◼ MPAs make outsized contributions to fish replenishment

Models of MPA spillover routinely assume that a fish's reproductive output scales isometrically with size (Fovargue *et al.* 2018). If the size distribution of fish within and outside of MPAs were identical, then this assumption would have no consequences. But as we noted earlier, there are systematic reasons as to why fish inside MPAs will be larger than fish outside MPAs. One meta-analysis showed that fish within MPAs are, on average, 28% longer than fish outside of MPAs (Lester *et al.* 2009).

Differences in fish size inside and outside a given MPA are often reported in terms of the mean length of fish (Lester *et al.* 2009). Reporting mean length makes sense because (1) length is a reasonable measure of fish size and (2) fish length is generally the actual metric that is recorded during surveys (Edgar *et al.* 2014). However, focusing on mean fish length risks underestimating the differences in fish reproduction between MPAs and fished areas for two reasons: such an approach overlooks the "two allometries" of fish size and reproduction, and fails to account for the principles of non-linear averaging embodied in "Jensen's inequality" (see below).

## Two allometries

Differences in length partially reflect differences in fish size and reproduction. Fish weight, which arguably is a more complete estimate of size, scales with fish length at an exponent of ~3 (ranging from 2.5–3.5 depending on species; Froese 2006). Therefore, length *L* relates to mass *M* via a cubic function:

$$M \propto L^3 \qquad \text{(Equation 1)},$$

such that the observed 28% difference in fish length yields a 109% difference in mass. Because humans generally have trouble thinking non-linearly, it may seem counterintuitive that increasing fish length by around a quarter more than doubles fish mass.

The risk of underestimating the difference in reproductive output between fish inside and outside MPAs is made worse by the hyperallometric relationship between fish mass and fish reproductive output. Because fish mass scales with reproductive output at an exponent of ~1.18 (Barneche *et al.* 2018), an increase in fish mass of 109% yields an increase in individual reproductive output of 139% (Figure 1). In other words, because length relates to mass allometrically, and mass relates to reproductive output allometrically, a moderate increase in fish length yields a massive increase in fish reproductive output. These estimates assume equal amounts of total fish biomass inside and outside MPAs when, in reality, total biomass is often higher inside the protected area (Lester *et al.* 2009).

## Jensen's inequality and fish reproduction

An even more counterintuitive consequence of comparing mean fish lengths inside and outside MPAs relates to Jensen's inequality and non-linear averaging. Because fish length relates to fish reproductive output non-linearly, the average difference in length (or mass) cannot necessarily be used to compute the average difference in reproductive output. Generally, a biological system's response to the average condition is not equivalent to the average of its responses to variable conditions (Denny
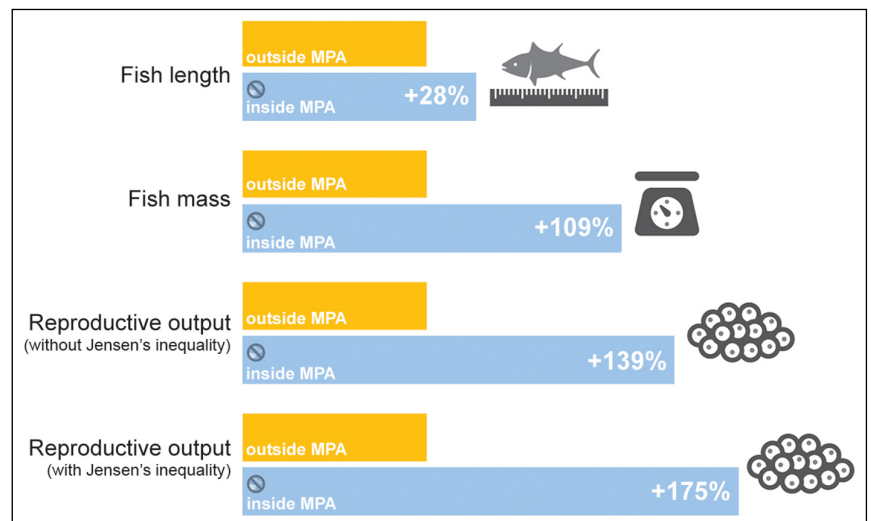


**Figure 1.** Effect of two allometries on fecundity differences between fished and protected areas based on the average difference in fish size between fished and reserved areas (from Lester *et al.* 2009). Yellow bars show length, mass, and reproductive output of fish of average size outside the protected area; blue bars show length, mass, and reproductive output of fish inside protected areas.

2017). Specifically for fish, the difference in reproductive output between fish inside and outside MPAs cannot be determined using the average size of fishes inside and outside the reserve. Because the relationship between fish size and reproductive output is non-linear, calculating reproductive output based on mean size underestimates reproductive output because it fails to account for the disproportionate contribution to reproduction made by larger individuals (see Figure 2). For example, assuming a log-normal distribution of fish sizes and a reproductive scaling exponent of 1.18, using the mean size to calculate reproductive output underestimates actual reproductive output by around a factor of $e^{0.11v}$, where $v$ is the variance in fish size (see WebPanel 1 for derivation). As such, the more variance in the population, the greater the risk of underestimating actual production when using mean size to infer reproductive output.

The effect of Jensen's inequality is enhanced because MPAs change the variance of fish length, as well as the average length. Because mortality reduces the chances of a fish surviving to an old age and large size, fish size distributions are naturally right-skewed, with more fish concentrated at smaller sizes and tapering off at the larger sizes. Higher survivorship will create reserve size distributions that have both higher averages and greater variance, because fish are more likely to grow older and become bigger when they are not subjected to fishing (Fovargue *et al.* 2018; Edgar *et al.* 2018). Fish length can vary twice as much inside MPAs as it does outside (Davidson 2001; Kleczkowski *et al.* 2008) so we parameterized the equation $e^{0.11v}$ assuming log-normal size distributions, an exponent of 1.18, and a two-fold difference in variance in size. In this case, using mean sizes to estimate reproductive outputs underestimates production inside MPAs by a further 35%, even if the two allometries (the allometric relationships between length and mass, and mass and reproduction) are accounted for (Figure 1).
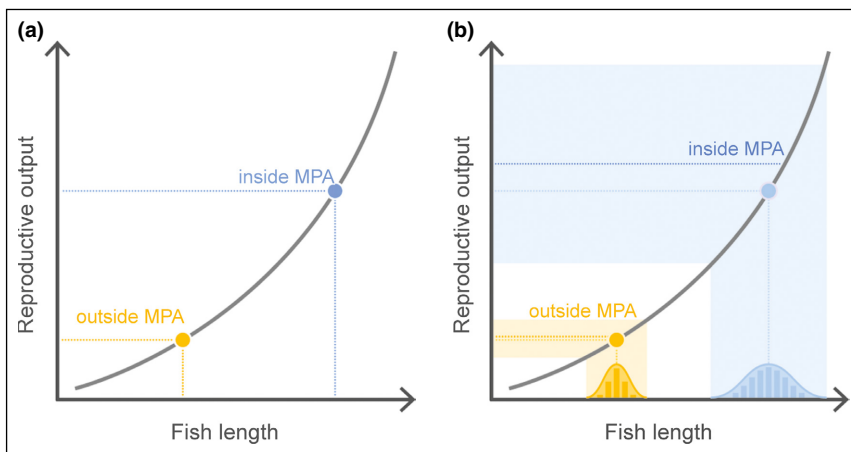
**Figure 2.** Jensen's inequality for fish reproduction. (a) The benefit of MPAs for average fish reproduction driven by differences in mean size. (b) The benefits of MPAs are enhanced by greater size variation being present inside the MPA and Jensen's inequality, resulting in higher reproductive output than what would be predicted based on differences in average size alone.

Combining the effects of allometry and Jensen's inequality shows how easy it is to underestimate the reproductive enhancement offered by MPAs if only the average length difference is reported. A 28% difference in average fish length yields a 109% difference in average fish mass, which yields a 139% difference in fish reproductive output, or a 175% difference when differences in size variance and Jensen's inequality are also included. In other words, considering only a difference in length underestimates the true percentage differences per unit of biomass in reproductive output by about sixfold (28% versus 175%; Figure 1).

In the case of species for which we know both relative biomass densities and reproductive scaling, to what degree have

models of MPA spillover been underestimating MPA reproduction? Figure 3 shows the relative rates of egg production inside and outside MPAs for several different species of fish. Even if the cumulative density of biomass inside and outside a given MPA were the same, the relatively smaller number of larger fish inside the MPA would produce far more eggs than fish outside the MPA (Figure 3a). Because fish total biomass also tends to be higher within an MPA, total egg production (TEP) per unit area inside the MPA far outstrips the TEP per unit area outside the MPA (Figure 3b).

To put this in perspective, on average, 1 ha of MPA produces at least five times as many offspring than 1 ha of fished area across most of our examples. Importantly, bioeconomic modeling for at least one fishery suggests that spillover from this increased production of recruits results in much higher yields for fishing fleets, because replenishment is that much greater (Panel 1). The benefits of this increase in production of young from MPAs expand even further with the level of overfishing outside the MPAs, because the fished populations will depend more strongly on recruitment from protected adults in the MPAs.

## ◼ Caveats

Our inferences here are based on a number of assumptions. First, we conservatively estimate that the recruitment potential of offspring from larger and smaller fish is equivalent. It is possible that the offspring of larger mothers are better provisioned to survive the difficult processes of dispersal and
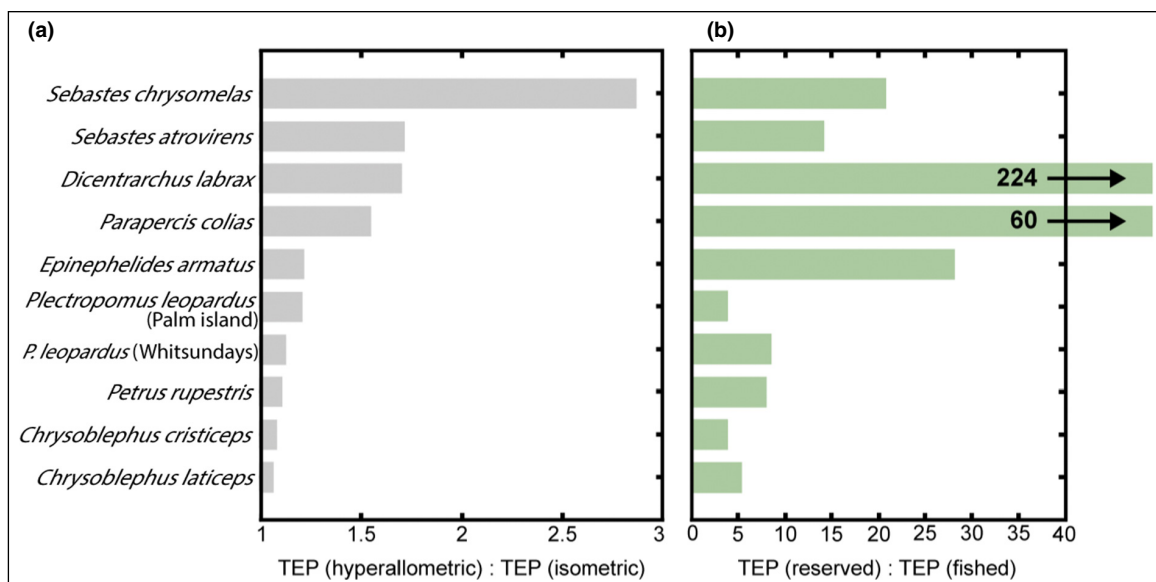


**Figure 3.** Impact of assuming hyperallometry versus reproductive isometry for nine marine fish species. (a) Underestimates of marine reserve egg output resulting from an incorrect assumption of isometry. Bars show the ratio of egg production estimated using parameterized hyperallometric models relative to isometric predictions. (b) Ratio of total egg output from marine reserves, relative to fished areas, based on hyperallometric reproduction and differences in size and total biomass of fish within MPAs versus outside. For example, based on surveys of blue cod (*Parapercis colias*) length distribution and abundance in New Zealand (Davidson 2001), it is estimated that blue cod in MPAs will produce 60 times as many eggs than in fished areas of equivalent size.

**Panel 1. Bioeconomic model of the Great Barrier Reef fishery**

Accounting for hyperallometry could allow managers to accurately calculate the per-capita and total production of eggs in reserve areas, as demonstrated by Equation 1 in WebPanel 1 and by Figure 4. A number of factors may alter the magnitude of this potential benefit, reducing its impact on fishery yield and total stock biomass. First, not every fish in the reserved population will experience the same increase in length. Second, for the additional larvae produced in reserved areas to translate into additional fishery yield, they must first disperse from no-take reserves into fished areas (usually as larvae). Thus, yield will be affected by species' dispersal characteristics, regional hydrodynamics, and the heterogeneous size and configuration of the marine reserve network. Third, the benefits of enhanced egg production will be undermined by density-dependent mortality processes. In other words, the additional eggs produced by fish in marine reserves may simply create more recruitment mortality, rather than more fish.

To assess these factors, we used a bioeconomic model (for details see Fovargue *et al.* [2018]) of a Great Barrier Reef (GBR) line fishery to translate the enhanced egg output of hyperallometric organisms into changes in fisheries yield. The model is a deterministic, spatial model of an open-access commercial fishery that exploits a population of demersal reef fishes across the length of the GBR (see WebPanel 2 for details). Fishing vessels allocate their effort across patch reefs to maximize profits. Total fishing effort is unregulated, and more vessels will therefore enter the fishery if its productivity increases. Fishing yields are calculated using an age-structured metapopulation model, broadly parameterized for coral trout (*Plectropomus*) species, a key target of the commercial fishing industry.

Using this model, we numerically solve for the bioeconomic equilibrium first under the standard assumption of isometric fecundity, and then the average across-species hyperallometric exponent of $\beta_1 = 1.18$ for marine fish (Barneche *et al.* 2018). We report for both exponents the relative egg production density in both fished and reserved areas, and the total equilibrium yield. We measure and report the variation between reefs that results from the heterogeneity in fish density caused by the variation in larval dispersal patterns and fishing effort (Figure 4).
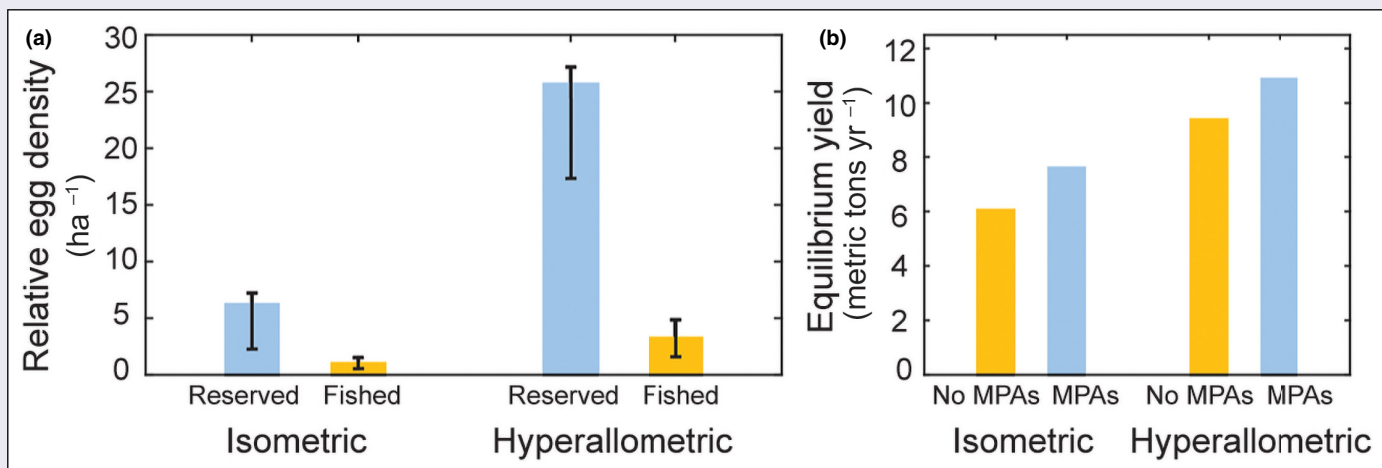


**Figure 4.** Consequences of isometric model assumptions for a bioeconomic model of the Great Barrier Reef (GBR) coral trout (*Plectropomus* spp) fishery (see WebPanel 1 for details). (a) Modeled relative egg production density (bars show 95% output density distribution from model) inside and outside the reserves under isometric and hyperallometric scaling. All values are scaled to egg production density in isometric fished reefs. (b) Predicted equilibrium yield of an open-access fishery targeting coral trout based on the presence of MPAs versus no MPAs under isometric and hyperallometric reproduction.

recruitment (Barneche *et al.* 2018). However, the question of whether these offspring also perform better than offspring from smaller mothers remains controversial and unresolved – only more empirical work (eg Cameron *et al.* 2016) will shed light on this issue.

Second, we make the standard assumption that MPAs export juveniles to fished areas. If recruits are not free to disperse outward from MPAs, either because of hydrodynamic barriers to dispersal or because the MPA is very large and therefore has a small periphery-to-area ratio, the benefits of hyperallometric reproductive output from reserves would be reduced. For the vast majority of MPAs, however, neither of these constraints is likely to be overwhelming.

Third, these inferences depend on the assumption that density dependence is not very strong outside MPAs, so that recruitment rather than resource availability limits population growth. Assuming weak density dependence outside MPAs is contentious but at the very least it seems unlikely that MPAs have limited reproductive output, which would render them less effective in fisheries management (Hilborn 2017). Given the logistical challenges of protecting larger individuals from fishing, MPAs emerge as a particularly useful tool for creating reservoirs of larger, highly
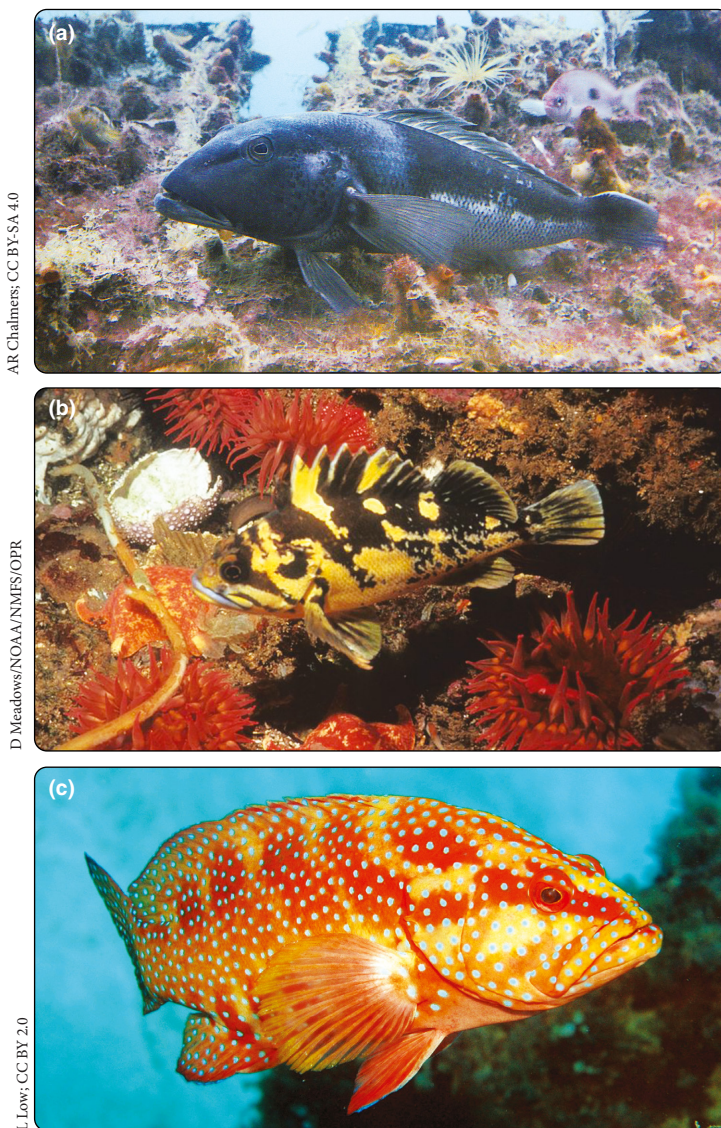
**Figure 5.** (a) Blue cod (*Parapercis colias*), (b) black and yellow rockfish (*Sebastes chrysomelas*), and (c) coral trout (*Plectropomus leopardus*) increase in both size and abundance in response to the establishment of MPAs, such that reproductive output increases dramatically in reserved areas.

fecund fish. Notably, however, any activity or mechanism that preserves larger individuals in exploited populations should have disproportionate benefits for population replenishment.

## Conclusions

Our discussion of the role of MPAs in replenishment has been restricted solely to fish, because this is the group for which hyperallometry has been formally demonstrated to occur ubiquitously (Barnecehe *et al.* 2018). Nevertheless, hyperallometric reproduction also occurs in marine invertebrates, including commercially important species of crabs and abalone (Somers 1991; Campbell *et al.* 2003). Clearly, formal tests of reproductive hyperallometry in marine

invertebrates are necessary, but initial indications suggest that, as with fish, protecting larger individuals inside MPAs should benefit exploited marine invertebrates.

The discovery of ubiquitous hyperallometric reproduction in fish has revealed that the potential of MPAs to replenish populations has been systematically underappreciated (Figure 5). We join a long line of researchers (Marshall *et al.* 1998; Hixon *et al.* 2014; Dick *et al.* 2017) who contend that larger fish play a disproportionate role in driving the dynamics of fish populations, and should therefore be accounted for accordingly. MPAs represent an essential tool for protecting larger fish, and it is our hope that a more accurate accounting of the value of MPAs will increase support for their use by a wide variety of stakeholders.

## Acknowledgements

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## ◼ Supporting Information

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