The Regional Effects of Marine Protected Areas

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Abstract

Marine Protected Areas (MPAs) cover between 3-7% of the world's oceans, up from less than 1% in the year 2000. The Convention on Biological Diversity calls for 10% of coastal waters to be protected inside MPAs by 2020, while the International Union for Conservation of Nature calls for 30% protection by 2030. It is often clear that MPAs produce conservation benefits inside their borders, but many MPAs are also justified on the grounds that they also benefit the broader region outside their borders. The conservation effects of MPAs are most commonly evaluated using response ratios—measures of biomass densities inside their borders, relative to biomass densities in reference sites outside their borders. Studies of this nature have provided broad evidence that MPAs produce conservation benefits within their borders. While these gains can be vitally important, marine populations are rarely contained entirely within the borders of MPAs; therefore a critical question is not only do MPAs produce conservation gains inside their borders, but how do they affect the broader region in which they are located? The Channel Islands National Marine Sanctuary provides a clear example of this challenge. A network of MPAs covering roughly 20% of the Islands' waters was put in place in 2003, with a goal of providing regional conservation and fishery benefits. Response ratios from the region indicate that the Channel Island MPAs have increased biomass densities inside the MPAs. However, we are unable to find a clear effect of these same MPAs at the regional scale across multiple species.Building off of existing theory, we use a bio-economic simulation model to explain this discrepancy, and demonstrate under what conditions we likely can and cannot clearly estimate the regional conservation effects of MPAs. We show that MPA networks covering 25% or less of a region are likely to produce regional increases in fish biomass on the order of 10%-20%, a meaningful effect but also one that can easily be overwhelmed by environmental shocks. Our results provide a novel assessment of the regional effects of a large and iconic Marine Protected Area network, and provide guidance for managers charged with monitoring and adapting MPAs.

Contents

as we move away from "set it and forget it" management towards adaptive management of marine ecosystems, it is critically important that we develop robust strategies for monitoring the effectiveness of our management intercentions

No-take Marine Protected Areas (MPAs), spatial regions of the ocean in which fishing is prohibited, have a long history in the management of marine resources. Traditional cultures in Oceania utilized - often temporary - MPAs as "fish banks" for times of need (1). Modern MPAs were first established primarily as marine analogs to the terrestrial protection of iconic landscapes like Yellowstone or Kruger National Parks (2, 3). Over time our goals and expectations for MPAs have evolved; while all MPAs are expected to deliver conservation benefits within their borders, many modern MPAs are also established to bolster fish populations throughout the region in which they are located (4).

Indeed, many recent agreements to expand MPAs (most proximately, the Convention on Biological Diversity's Strategic Plan for Biodiversity, which calls for 10% of coastal waters to be protected inside MPAs by 2020 and the International Union for Conservation of Nature call for 30% by 2030) are based on the expectaion that well-designed MPAs will achieve benefits both within, and outside, their borders. Despite these assumptions, our collective scientific understanding of the regional-scale conservation and fishery impacts of current and future MPAs is surprisingly limited.

Numerous studies provide evidence that well-enforced and appropriately sized MPAs can produce conservation benefits within their borders (5–8). As these conservation benefits accrue inside MPAs, theory holds that MPAs can affect the waters beyond their borders through the spillover of adult and larval fish from the protected to the fished areas, as well as through displacement of fishing effort. Several studies have documented empirical evidence for the existence of adult or larval spillover affecting both abundance and fisheries (9–17), as well as alteration of fishing effort in reaction to (18–20) and in anticipation of (21) MPA placement. The potentially more important question, however, is not whether spillover occurs (it must to some degree in any realistic scenario), but what the net effects of spillover are and whether those effects are empirically detectable. From a fishery perspective, are spillover benefits sufficient to offset losses in fishing grounds and changes in responses of displaced fishers caused by an MPA? From a conservation perspective, how much does the buildup of fish inside an MPA increase biomass outside the protected area? Overall, what are the regional effects of MPAs?

As stakeholders around the world increasingly seek to use MPAs in marine resource management portfolios, and the performance of existing MPAs is evaluated, it is critical that we develop a better understanding of the magnitude and drivers of regional-scale MPA effects. The Channel Islands National Marine Sanctuary, California, USA provides an ideal case study to address this need. A network of protected areas covering approximately 20% of the Islands' waters qas put in place in 2003 (see (22), (23), (24), and (25) for information on the creation of these MPAs). We use data from the first 14 years of protection to provide what is to our knowledge the first large-scale empirical assessment of the regional effect of a large MPA network on a wide array of fin-fish species. In contrast to clear differences in biomass densities observed inside and outside of well protected MPAs (5), we are unable to detect a clear regional effect from the Channel Islands MPAs. We build off of existing MPA theory to consider why this might be, and provide guidance for scientists and managers as to when and how we might expect to estimate the regional conservation effects of MPAs.

What Are the Regional Effects of MPAs?

The empirical MPA literature focuses on assessing the conservation effects within the borders of protected areas (7). While these within-MPA effects are vitally important for protecting rare species, biodiversity, critical habitats, and often tourism, they paint an incomplete picture of the overall population effects of MPAs. The organisms within the borders of protected areas are generally part of a broader biological stock, connected through adult movement and larval dispersal. If the goal of conservationists or natural resource managers is to increase the total abundance or productivity of a resource, a broader question we should ask of MPAs is not just are there more fish inside their borders, but also how have the reserves affected abundances throughout the region in which they are located? This logic, that MPAs will have conservation benefits for most species beyond their borders, is implicit in all multilateral calls for MPA expansion.

We define the regional conservation effects of MPAs as the change in total biomass of fish (summing inside and outside of MPAs) relative to the total biomass of fish that would have occurred without the MPAs (acknowledging that other outcomes such as increased biodiversity or resiliency are also important to conservation but are beyond the scope of this analysis).

Numerous factors can affect the regional effects of MPAs. These include the scale of adult and larval dispersal relative to the size of the MPAs (8, 26–29), larval dispersal patternss and the strength and timing of density dependence in the population (e.g. pre- or post-settlement, **???**), how overfished the population would be without the MPA, and how fishing and management responds to the implementation of the MPAs (4, 30–39). In addition, even for the same total area of MPAs, the location and spacing of the MPAs can have a profound influence on their cumulative impact through habitat and network effects (4, 40).

Given this existing body of theory, what should we expect *a priori* the effect size of the Channel Islands MPAs to be? While we know many parameters will affect the expected effects of the MPAs, theory suggests that life history, adult and larval dispersal relative to MPA size, and fishing pressure will be key drivers. The targeted species in our database span a range of life histories, but are largely made up of fishes in the genus XX (e.g.) and **Sebastes** (e.g.), with a median Von Bertalanffy growth coefficient of XX, and a median age at maturity of XX (41). The MPAs in this study cover roughly 21% of the the waters of the Northern Channel Islands, a region spanning roughly 90km east to west. While detailed dispersal studies are not available for all of the species covered by our study, what information we have suggest that while adults of some of these species are likely to exhibit some site fidelity (42), larvae are likely distributed beyond the northern Channel Islands (43). Therefore, if we assume that the population of the targeted species is at least equal to the extent of the Northern Channel Islands, we can assume that at most the MPAs cover roughly 20% of the targeted populations' ranges. Turning to the critical question of fishing pressure, formal stock assessments are largely lacking for these species. However, what evidence we have suggests mostly moderate fishing pressure, with some species such as California sheephead (XX) and blue rockfish (xx) experiencing high levels of fishing mortality / biomass levels beloe target levels during the early 2000s pre-MPA (44, 45).

Considering the combinatino of slow growth, 20% or lower MPA coverage, and moderate fishing pressure, we might expect that the northern Channel Islands MPAs would produce a small to moderate effect size over time. However, theory also tells us that many other variables can interact to affect the outcomes of MPAs. To address this, we utilized a spatial bio-econonomic model to simulate the expected effects of an MPA network stylized to resemble the Channel Islands on the group of targeted species covered in our analysis (See SI for details of simulation framework).

reference HARKing, of course DiD and theory matching together doens't prove anything, but it's an important step to take

0.1 How Can We Detect Regional Effects?

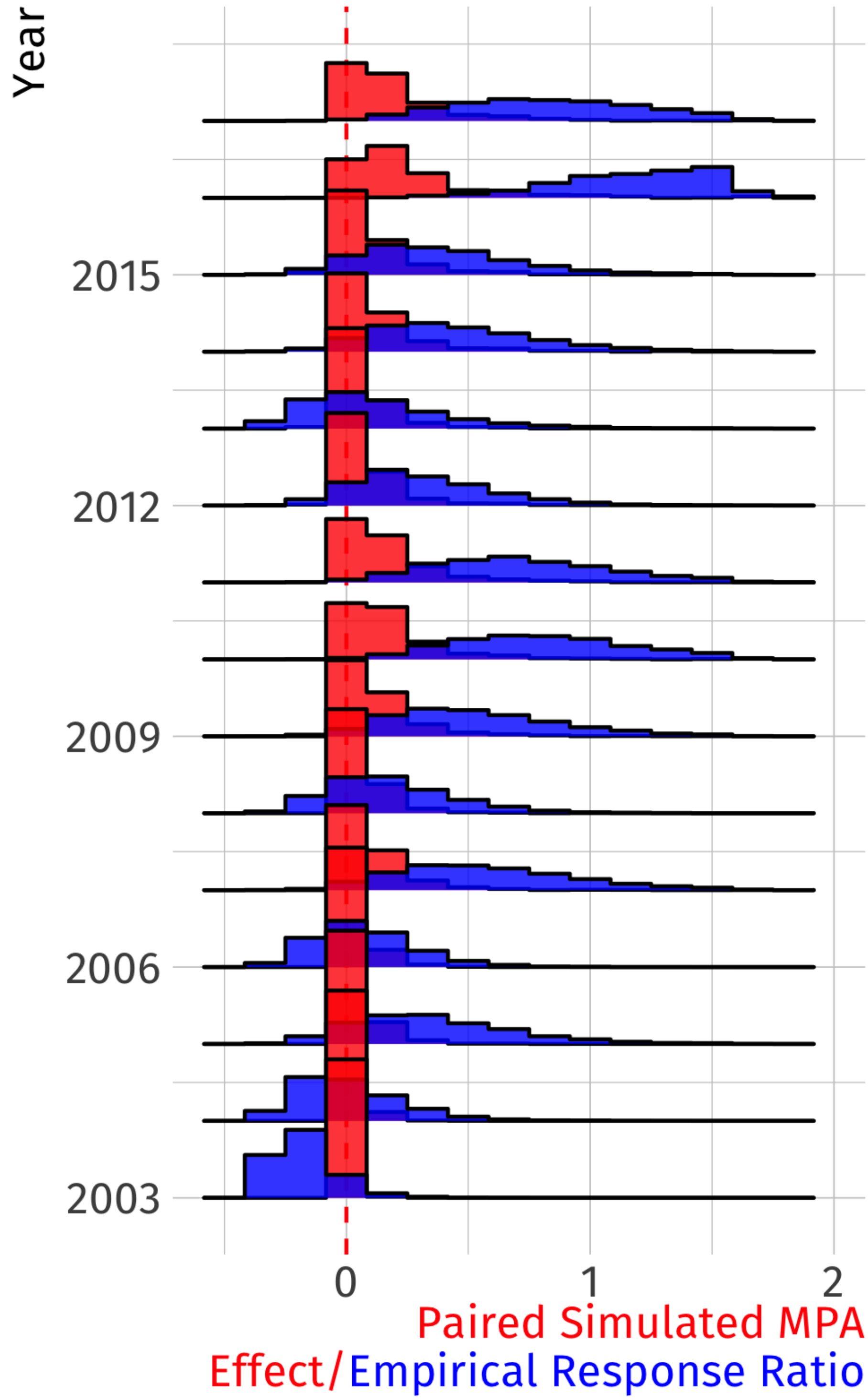
Having established a theoretical grounding for the likely effect of the Channel Island MPAs, what empirical evidence do we have for the effects of this protected area network? **???** examined changes in biomass densities of species targeted by fishing activity inside and outside of the MPAs over time (a measurement generally termed "response ratios"), and compared these changes to the trends in non-targeted species. They found a statistically significant increase in the response ratios of targeted speices over time, and evidence that this increase is smaller in the non-targeted species. Updating the results of (46) through 2017 shows the same increasing trend in the resonse ratios of targeted species (Fig.**??**).

Why do these response ratio results not serve as sufficient evidence for the regional effects of the Channel Island MPAs? Control sites used in calculating response ratios are often selected based on abiotic or ecological traits such as habitat characteristics (47). However, selection of control sites is further complicated by the very spillover that MPAs are often intended to create. Export of adults or larvae from the MPA to the "control" site affects their status as controls, as does displacement of fishing effort from MPAs to control sites. In theory, control sites far enough away to negate both biological spillover and concentration by the fishing fleet could be selected, but finding suitably far sites that are also appropriate proxies for the ecological and economic context of the MPAs may be challenging. While these concerns have been stated previously (48), the MPA evaluation literature has by and large been unable to adequately address them, often due to the very real challenges of identifying and sampling adequate control sites that are truly independent of the MPAs in question (47).

In the case of the Channel Islands MPAs, control sites are often located within only a few kilometers of an MPA, suggesting that they are susceptible to biological spillover and concentration of fishing effort resulting from the MPAs. Given these complications, we can certainly interpret the response ratios reported in (46) and updated here as evidence that the MPAs are indeed providing effective protection of targeted fish biomass inside their borders, particularly in light of the general increase in respones ratios over time. However, it is unclear how well these response ratio results serve as in indicator of overall regional effects of the MPAs.

To illustrate this problem, we used our bio-economic model to simulate response ratio trajectories for species and MPA coverage representative of the northern Channel Islands. These simulations cover the life-histories and MPA sizes seen in the Channel Islands, but vary in key unknowns such as the actual degree of fishing pressure, the timing of density dependence, and the fleet responses to the MPAs. For each year of protection, we paired our simlated response ratios to the estimated posterior probablity distributinos of the Channel Island response ratios. For example, if the mean response ratio in the year 2006 is 1, we found all simulations with three years of protection that had simulated response ratios near 1, and then pulled out the "true" regional MPA effect from each of those simulations. This provides us with a distribution of simulated regional MPA effects that could plausibly generate the types of response ratios actually observed in the Channel Islands.

As reported in (46), we see evidence for an increasing trend in respones ratios of targeted species over time (Fig.**??**). This provides strong evidence that the MPAs are providing protected for targeted species within their borders. However, our simulation results show thatresponse ratios trends we observe in the data could plausibly be produced by a wide range of regional MPA effects (Fig.**??**). Response ratios well over 1 were associated with regional MPA effects generally elss than 25%, and many simulations produced large response ratios but regional MPA effects close to zero. This can occur if for example fishing pressure is only moderate, adult movement is low, larval dispersal is high, and displaced fishing effort concentrates around the border of the MPAs.



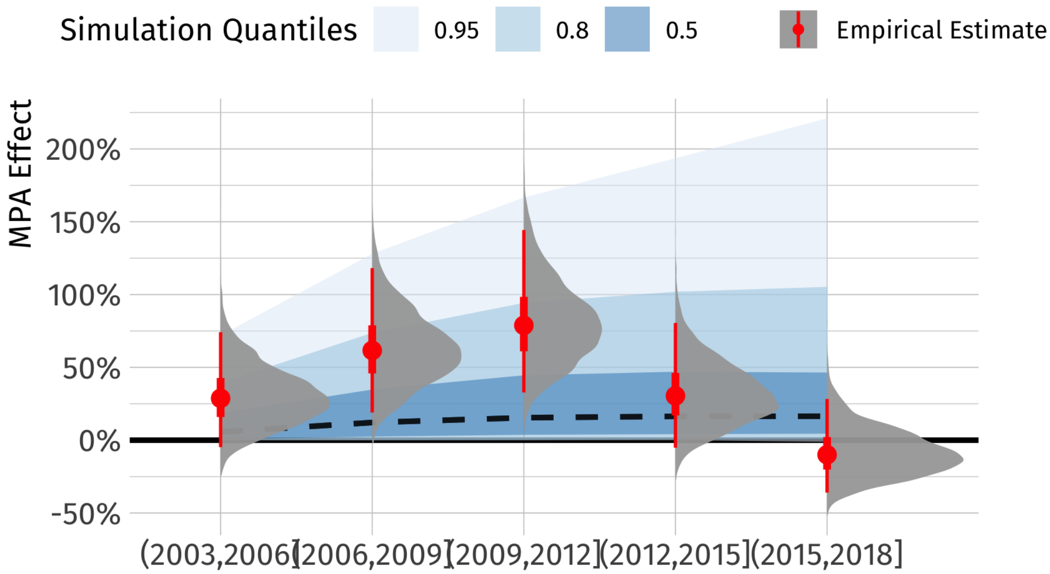
\begin{figure}%[tbhp]
\caption{90% Posterior probability distributions of response ratios for targeted species (x-axis) over time

(y-axis) in blue. Simulated MPA effects associated with simulated response ratios matched to empirical response ratios in red. For response ratios, a value of zero indicates that biomass densities of targeted and non-targeted species are identical inside and outside MPAs, a value of 1 indicates that biomass densities of targeted species are 100% greater inside MPAs than outside. For MPA effect, a value of zero indicates that mean biomass densities are identical in the with- and without- MPA scenarios. A value of 1 indicates that mean biomass densities are 100% greater in the scenario with MPAs than the scenario without MPAs.} \end{figure}

While we see empirical evidence of increasing response ratios of targeted species in the Channel Islands, theory indicates that this may not be a reliable indicator of the regional effect of the MPAs. An ideal "control" for estimating the regional effects of MPAs would a) control for regional environmental shocks unrelated to the MPAs b) be unaffected by treatment bias (e.g. preferential placement of MPAs in ideal habitat) c) be unaffected by the MPAs themselves. While spatial response-ratios can help control for environmental shocks and, in theory, treatment bias, at the scale of the Channel Islands it is unlikely that we can strongly say that outside-MPA sites are themselves unaffected by the MPAs we are trying to evaluate.

Building off of (46), we propose an alternative identification strategy utilizing biomass densities of species that are not directly targeted by fishing as our control group (non-targeted), and biomass densities of species targeted by fishing as our treatment group. Targeted species in the Northern Channel Islands, California, include commercially important finfish such as California sheephead (*Semicossyphus pulcher*), and copper (*Sebastes caurinus*) and blue (*Sebastes mystinus*) rockfish. Each of these targeted species was the subject of prior bio-economic modeling related to the effects of MPAs in southern California (49, 50). But, the analysis omits species from important invertebrate fisheries including red urchin (*Mesocentrotus franciscanus*) and spiny lobster (*Panulirus interruptus*). Non-targeted species include garibaldi (*Hypsypops rubicundus*), halfmoons (*Medialuna californiensis*), and blacksmith (*Chromis punctipinnis*) (See Table.S2 for a complete list of species). We use a Bayesian difference-in-difference estimator to estimate any difference in mean total biomass densities of finfish species targeted by fishing effort (i.e., those potentially affected by an MPA) and those species not targeted by fishing before and after MPA implementation (51). The result of this regression is an estimate of the effect of the MPAs on the mean total biomass densities of targeted species throughout the Channel Islands.

As conventional wisdom and theory would suggest, over the first three years of implementation (2003-2006), the effects of the MPAs is unclear, with support for a small negative effect to a substantially positive effect (with much higher probability of a small positive effect). Over the next six years we see signs of an increasingly positive MPA effect, peaking in 2009-2011 with a median estimate of MPA effect of 75% on mean total bioamss of targeted species. These empirical estimates are in line with the range of outcomes that our simulation model suggests are plausible given the rough characteristics of the northern Channel Island MPAs. However, in the subsequent years the trend reverses itself, and for the years 2015-2017 we once again see no clear effect of the MPAs Fig.**??**



\begin{figure}*%[tbhp]*
\caption{Results of difference-in-difference regression estimating the regional effect of the northern Channel Island MPAs on mean total biomass densities of targeted species (difference in mean total biomass density of targeted species over time relative to expected levels using non-targeted species as a control). Grey distibutions show 90%XX posterior probability distribution of estimated MPA effect; red point is median estimated effect, thicker red section 50% credible interval, thinner red line 90% credible interval). Blue distributions in background show range of MPA effects produced by simulation model tuned to reflect the dybnamics of the Northern Channel Island MPAs (black dashed line is median simulated value). Results are estimated in three blocks, including years greater than or equal to left-hand value and less than right-hand value.} \end{figure}

Discussion

1. Why are the results from the channel islands imporant and what do they tell us
2. Put the channel islands results in context -

Ideally then we want a control for broad environmental shocks to the region that is independent of factors such as selection bias, biological spillover, and fishing concentration.

1. multiple lines of evidence
2. Theory before empirics
3. Patience

The network of MPAs implemented in the Northern Channel Islands in 2003 provides an ideal opportunity to examine the regional effects of proteced area networks. This analysis is to our knowledge the first empirical estimate of the regional effects of such a large MPA network on a broad assemblage of targeted finfish. Despite the well enforced nature of these MPAs [xx], and the presence of a rigorous scientific monitoring program, we are unable to estimate a clear effect of protection. While response ratios have targeted species have increased over time, providing evidence of effective *within MPA* protection, these response ratios are on their own an unrealible indicator of the regional conservation effects of the MPAs. Our difference-in-difference estimates a high probability of increasinly positive MPA effects over the first nine years of protection, only to see these estimated gains reversed from 2012 to 2017. For the most recent time period, we can detect no clear positive or negative effect of the Channel Island MPAs Fig.**??**

How can we explain these results? The estimated effects from 2003 to 2014 are well in line with theoretical expectations given the species and network in question. How might we explain the most recent results though? One explanation may lie in fleet dynamics. Much of the theoretical literautre on MPAs assumes that all else being equal bigger reserves produce bigger conservation gains (**???**). However, to our knowledge all of these models simulate fleet dynamics through assumptions about fishing mortality rates (e.g. concentration of fishing mortality (48)). The assumption of these models is that fishers determine an amount off effort to exert, and distribute that effort outside the MPA in response to some function.

An alternative and to our knowledge unexplored (in the context of MPAs) fleet model though is a "constant-catch" strategy. Under this model, fishers have a catch objective, and exert as much (or little) effort as needed to achieve that objective. While a constant-catch greater than MSY is not possible over the long-term under the assumptions of our model, over the short-term a constant-catch scenario is not implausible. Subsistence fisheries may use a constant-catch style policy over the short-term, as they seek to ensure that their food needs are met. More industrial fisheries may have pre-arranged agreements with buyers to deliver set amounts of fish. Constant-catch dynamics might also occur in fisheries with constraining quotas that are not updated after the implementation of MPAs. Interestingly, when we simulated the effects of MPAs under different fleet models, the "constant-catch" scenario stood out as the only way for MPAs to actually produce a net conservation loss (Fig.**??**). While open-access fishing strategies can result in "scorched earth" scenarios where the only fish left are found inside the reserve, across all 9252 simulations the net effect of the reserves was still positive. Under a constant-catch scenario though, fishers have to fish much harder than before to get the same catch from a smaller part of the population, reducing the size structure of the population and, under XX% of our constant-catch simulations producing a net conservation loss (Fig.XX). XX

Can the the non-trivial probability that the Channel Islands MPAs caused a net conservation loss (taking the difference-in-difference results at face value) in the most recent years be explained by the local fleets following a constant-catch strategy? While we do not have access to fine scale fishing data from the islands directly, reported catches for the species of interest in the Santa Barbara region in fact exhibit an overall downward trend in the years post reserve (see SI, XX). We can most likely rule a negative MPA effect caused by a constant-catch fishing strategy then. What then is another explanation? The parallel trends assumption of our model appears to be valid initial years of protection, and we do not detect any clear evidence of interaction between the targeted and non-targeted species (e.g. depressed levels of non-targeted species as a result of predation from increased biomass densities of targeted species, see Fig.SXX).

However, the Santa Barbara Channel experience a massive heatwave in XX. The Channle Islands represent the warmest edge of the distribution of many of the targeted species in our study. Conversely, many of the represented non-targeted species are sub-tropical. As a result, we hypothesize that the blob even of XX broke down the parllel trends assumption between the targeted and non-targeted species in our study, as the targeted species were more negatively affected by the warming temperatures. This is supported by the fact that we observe similar declines in targeted species both outside and inside the reserves (Fig.XX). Assuming that the reserves are sufficiently well enforced and large to protect targeted species biomass (an assumption supported by the response ratio results), if the cause of recent declines was due to increases in fishing pressure we would expect to see substantial declines only in the fished areas (Fig. XX).

0.1.1 When Can We Detect the Effects of MPAs?

The Northern Channel Islands would appear to be an ideal system to study the effects of MPA networks on regional conservation outcomes. Simulation analysis built on existing MPA theory suggests that these reserves were likely to have a positive but modest effect (50% of simulated effects sizes less than 20% after 15 years of protection) on mean total biomass of targeted species. From 2003 (the year of MPA implementation) to 2011, our empirical results estimate a a highly uncertain but overall positive effect of the Channel Islands MPA, roughly in line with what MPA theory would suggest. However, these gains dissapear over the most recent years of available data, a phenomenon likely due to dramatic changes in the Channel Islands environment over the last decade that disproportinately affected the targeted species complex. Combined with the challenges we have demonstrated of using response ratios as a measure of regional impacts, we are left with an unclear picture of the overall effect of the Channel Island MPAs on biomass densities of targeted species after 14 years of protection.

What does this result in a system as well-studied and well-enforced as the Channel Islands suggest for our ability to assess the effects of other MPAs around the world? First, much of the empirical MPA literature has focused on the relatively clear signals provided by response ratios [(5);]. While we often see biomass densities of targeted species on the order of 400% higher inside MPAs than outside, as discussed in (47) and expanded on here response ratios even as high as these are not a reliable indicator of the regional effects of MPAs. While response ratios can provide important evidence as to the effectivness of the MPAs in protecting fishes within their borders, if our interest is in estimating the effect of MPAs on the broader ecosystems in which they are located we must look for additional lines of evidence.

The difference-in-difference strategy utilized here presents an alternative strategy, that while not without its own strict caveats presents some potential improvements over response-ratios as a means of estimating regional conservation effects. Given the natural variability of marine ecosystems, and the strong challenges of obtaining accurate samples from marine environments, how large of an effect would an MPA network have to allow a difference-in-difference strategy such as this to be a reliable measure of MPA effects?

To provide guidance on this important question, we simulated data from a range of scenarios with increasing MPA effect size along with varying degrees of observation error and natrual recruitment variation. As an added measure, we include scenarios in which the sampled species go through recruitment regimes, which may be positive for both targeted and non-targeted species, or positive for non-targeted species and negative for targeted species. We then used a simlpe Bayesian difference-in-difference regression on these simulated data and estimated the percent error in the true MPA effect.

XX . Mean absolote percent error dropped below XX% once the true MPA effect exceeded XX%. While this if of course no guarantee that any study of such an effect size will be successful (many model runs still ahd high error even at this effect size), our results help illustrate the effect size that may be required if managers which to have a given degree of confidence in their results. XX This is merely an illustrative exercise, omitting clearly critical factors such as detection probability and sampling strategy. However, since nearly any omission which one can think of would make an MPA effect harder to detect, not easier, these results serve as a useful floor for the likely uncertainty in estimating MPA effects.

This finding begs an important question then: when should we expect to see MPA effects big enough to stand a reasonable chance of detection? To address this, we simulated 9252 MPA scenarios across a wide range of life histories, network designs, and fishing dynamics (see SI for a full description of scenarios). Using these simulations, we can consider what we might expect the regional effects of an MPA network to be under a with range of plausible circumstances. Interested users can explore the use of this model for simulation at danovando.shinyapps.io/simmpa.

Suppose that we are willing to tolerate a MAPE of XX%. Two of the most critical drivers of MPA performance are the size of the MPA and the degree of fishing pressure. Looking across these two variables, our simulations suggest if the MPA network covers XX% or more of a species range and/or pre-MPA depletion is greater XX we might expect an effect size with a reasonable chance of detection. While recently some extremely large MPAs have been enacted that may indeed reach into the higher levels of MPA coverage, for commercial finfish many coastal MPA networks are likely to cover areas more in line with the Channel Islands (20%) (Fig.**??**).

These results would seem to suggest some rather simple rules of thumb: put an MPA of sufficient size on a fishing population and one can expect large results. However, as discussed earlier, the MPA literature has highlighted a large number of variables beyond simply size and fishing pressure that can affect performance. To address this, we can

plot error as a function of MPA effect.

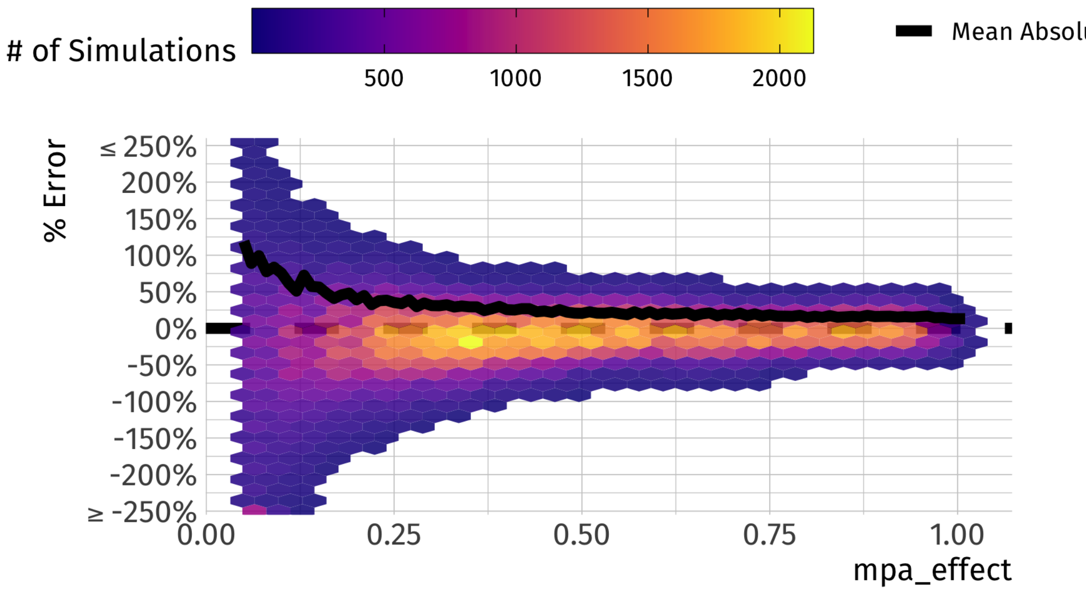


Figure 1: Validation

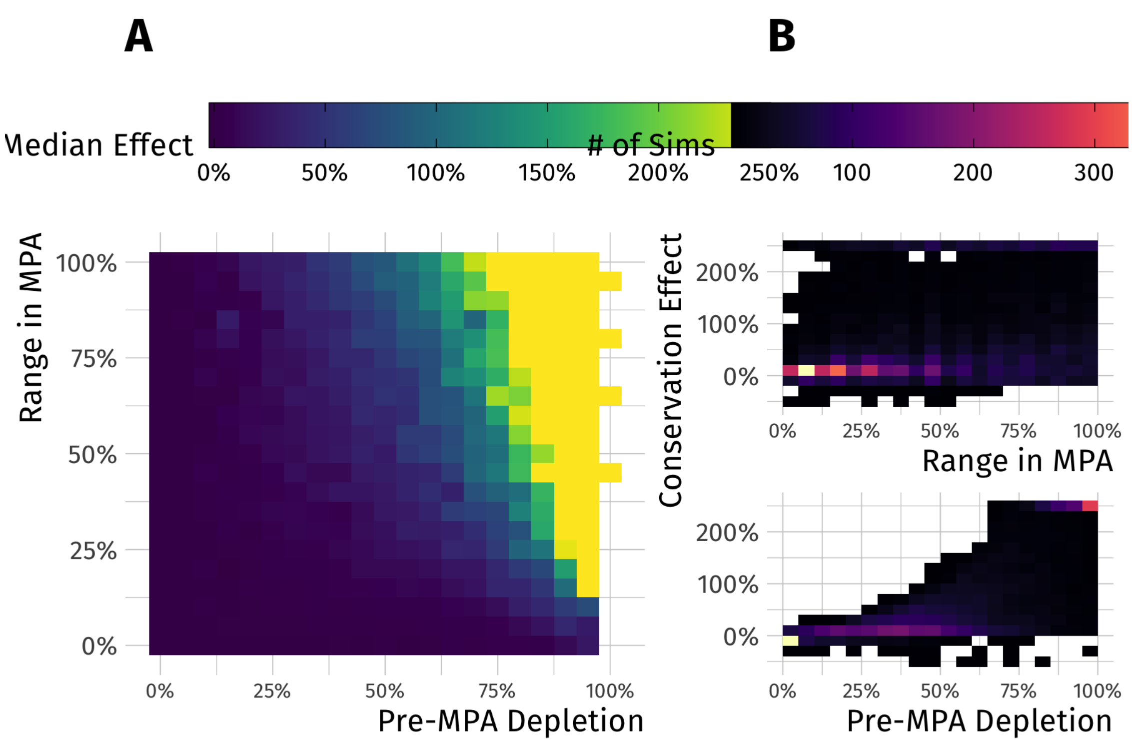


Figure 2: Expectation

we hav shown that even in a well studied network, MPA effects on the order 0f 0-25% will be very challenging to detect. Under what circumstances might we expect MPA effects large enough to facilitate detection even in the face of observation and process error?

THe persistently high response ratios suggest that despite overall decreases in targeted biomass densities inside and outside MPAs, the MPAs may still be providing protection within their borders. However

we hav shown that even in a well studied network, MPA effects on the order 0f 0-25% will be very challenging to detect. Under what circumstances might we expect MPA effects large enough to facilitate detection even in the face of observation and process error?

We tested the effects of different combinations of these theoretical drivers of MPA conservation effects using over 10,000 simulated MPA scenarios. A striking outcome of this simulation analysis is how the level of fishing pressure can cause dramatic and predictable shifts in conservation outcomes. We measure fishing pressure by the degree of simulated depletion (percent of unfished biomass gone, such that a depletion of 0% means the population is at 100% of unfished biomass, 100% means 0% of unfished biomass remains) in the scenario without MPAs. When MPAs were placed in relatively unexploited fisheries (depletions less than 40%), the median regional conservation effect was barely noticeable (2%). For ecosystems fished near MSY levels (depletion of 40%-60%), the median conservation effect was 33%, while for overfished ecosystems (without-MPA depletions above 60%) the median regional conservation effect was over 120% (Fig.**??**-A). Across all of these groups though, effects as low as declines of -50% and as high as an increase of more than 100% were possible. It should be noted though that these runs represent the range of scenarios evaluated in our simulation, and that certain types of scenarios may be much more likely than others in the real world. To put these results into context, the FAO estimates that 7% of the worlds fisheries with status estimates fall into the relatively unexploited category, 60% fall into the fully fished category, and 33% fall into the heavily fished category (52), though works that include a broader range of fisheries estimate that 50% or more of stocks to fall into the heavily fished category (53, 54).

These simple results support the intuitive conclusion that bigger MPAs on overfished populations produce large positive conservation outcomes. However, when combined with other factors such as fleet dynamics, life history, and MPA size, the conservation effects of MPAs can vary widely in magnitude and timing, a finding corroborated by empirical evidence (46, 55–57) (Fig.**??**-B). As the area protected inside MPAs increases, positive effects become more likely, but even MPAs protecting most of a population's footprint can produce conservation effects as low as 0% and as high as 200%. The degree of depletion (i.e. fishing pressure) has a clearer signal, with small conservation benefits of MPAs when depletion is low, and larger effects when depletion is high, but again even for severely depleted populations the conservation effects of MPAs can vary widely (although nearly always with population benefits).

While positive conservation outcomes were much more likely to occur across our simulations (88% of simulations), the 12% of runs that produced net conservation losses are of particular interest. These runs occurred almost exclusively when the simulated fleet followed a "constant-catch" fishing strategy. Under the constant-catch fleet model, fishing communities (or fishery policies) seek to catch the same amount regardless of the presence of an MPA. While a constant-catch greater than MSY is not possible over the long-term under the assumptions of our model, over the short-term a constant-catch scenario is not implausible. Subsistence fisheries may use a constant-catch style policy over the short-term, as they seek to ensure that their food needs are met. More industrial fisheries may have pre-arranged agreements with buyers to deliver set amounts of fish. Constant-catch dynamics might also occur in fisheries with constraining quotas that are not updated after the implementation of MPAs. These patterns suggest that coupling MPA implementation with appropriate management reforms that reduce the effects of constant-catch strategies can move the predicted conservation effects of MPAs to being nearly uniformly positive. The possibility of constant-catch strategies to result in net MPA conservation losses highlights the critical importance of understanding the broader management context in which MPAs are placed.

0.1.2 How can we use response ratios

Unfortunately, neither of these experimental designs has been implemented, because parallel worlds do not exist and MPAs are never placed at random. Careful causal inference requires some other means of controlling for biases introduced by factors such as the MPA siting process and biological spillover and concentration of fishing effort (47, 51). Conservation effects are typically estimated by comparing organism densities or biomass inside MPAs to densities or biomass in selected control sites outside MPAs, which we will refer to as response ratios. (5) and (58) present meta-analyses of hundreds of such studies. These results often find massively higher densities and biomasses inside MPAs than outside (5). While response ratios are intended as a measure of the effectiveness of reserves within their borders, these result stand in contrast to the smaller region wide effect sizes predicted by our simulation model. This raises the question: How reliable are density or biomass ratios as estimators of regional conservation effects?

Failure to account for these spillover effects can result in a biased estimate of the true effect of a policy such as MPA placement (51). In an ideal setting, the control site used in a response ratio would be a perfect counterfactual for what would have occurred without the MPA. We used our simulation model to approximate this scenario, calculating the response ratio as the ratio of densities inside the MPAs relative to the overall density from the paired simulation without MPAs multiplied by the area of the population in an MPA (to account for the fact that we would expect the effectiveness of a response ratio as a proxy for regional conservation effects to scale with the size of the MPA relative to the range of the species, Fig.**??**-A). In this idealized case, the response ratio is often a reasonable estimator for the regional conservation effect.

What happens when the "control" sites are in fact affected by the application of the MPA through biological spillover and fishing concentration? In order to address this possibility, we calculated a new response ratio as the mean density inside MPAs relative to the mean density outside the MPAs (both weighted by distance from MPA borders and scaled by MPA size). We only include simulations in which habitat and larval dispersal rates are identical inside and outside of MPAs, to approximate a scenario in which treatment and control sites have been paired by ecological characteristics. Under these circumstances the response ratio is a somewhat biased and very inaccurate estimator of the true regional effect of MPAs.

While on average high response ratios correspond with high true regional effects, the variance is high, so the response ratio alone cannot be used as a reliable proxy for the true regional effect, without accounting for the sources of biases discussed here. For higher movement rates, response ratios were frequently near 0% (potentially leading stakeholders to conclude that the MPA had been ineffective), when in fact in many cases the true effect of the MPA was highly positive. For highly sedentary species, extremely high response ratios could create the appearance of massive conservation gains when in fact the net effect on the regional population has been near zero or even negative (Fig.**??**-B).

We note that spatial before-after-control-impact (BACI) studies present a potential improvement over response ratios, controlling for differences in mean densities in the treated and control regions as well as MPA independent trends, but are much rarer due to the need for extensive pre-MPA monitoring. However, spatial BACI still requires that the MPAs do not affect the control sites, and as such has many of the same limitations as response ratios as an estimator of regional conservation effects.

MPAs are an important part of the marine resource management toolbox. Under ideal circumstances they can protect individual species and ecosystem linkages, while supporting local economies through tourism and fishing opportunities. One rationale for the expansion of MPAs is that they will deliver net conservation benefits both inside *and outside* their borders. To date, this assumption is insufficiently tested, and this is the focus of our paper. Our results show that regional conservation benefits of MPAs are highly context dependent and in many circumstances, are likely to be so small that they are nearly impossible to detect empirically. Indeed, this is exactly what we found in our empirical case study from the Channel Islands, California, USA.

We find regional conservation gains from MPAs in 88% of our simulations (Fig.**??**). MPAs covering less than 25% of the population range were unlikely to produce regional conservation gains above 10% unless the stock would have been severely overfished without the MPA. Given that few marine species on the planet have more than 25% of their entire range protected in MPAs, this suggests that large regional gains are unlikely to be common unless the overall extent of MPAs grows globally. Large MPAs protecting highly depleted stocks almost always produced large regional conservation gains, as should be expected.

The median conservation effect of 29% stands in contrast to the large within-MPA effects on biomass densities reported by (59) and (5). This difference is due in part to the fact that within-MPA effects are likely to be much larger than regional-MPA effects, but may also reflect the many challenges of translating response ratios into regional conservation effects. Our simulation analysis shows that without proper controls (in particular for the effects of fleet redistribution), response ratios well over 100% are entirely plausible even when the actual conservation effect is much lower (and *vice versa*).

We were not able to detect a statistically significant difference in the densities of targeted and non-targeted finfish species over the 13 years of MPA protection in the Channel Islands covered by our analysis. The data (and model assumptions) provide support for both negative and positive MPA effects, although the size of these estimated effects is well within the range that our simulation analysis suggests are plausible. At face value, this lack of a clear result may seem surprising given the size and carefully studied nature of this MPA network.

Our simulation analysis suggests that this result should perhaps be expected. The Channel Islands MPAs cover approximately 20% of the waters in the Channel Islands, and while formal stock assessments are not available for many of the targeted species in our analysis, what evidence we have suggests that, as a group, these fish are on average not heavily overfished. Some species, such as California sheephead and blue rockfish were likely below target levels during the period (44, 45), but projections based upon the overall average response across all species will likely suggest modest benefits even if a subset of species could experience much larger population gains. Harkening back to our simulations, we expect the average percentage difference in densities of targeted species with and without MPAs to be modest (Fig.**??**). Effects of this size are likely to be challenging to detect empirically given the large natural variation of marine ecosystems (especially temperate reefs) and the observation error inherent in infrequent annual survey programs such as those provided by PISCO.

In addition, our simulations examine percentage increases in biomass densities. As an extreme example, an increase in biomass densities from 2kg/m^2 to 4kg/m^2 would be reported as a 100% increase. While this chance produces a large percentage increase, this is a small change in absolute biomass densities relative to the variance in the observation process itself (see Fig.S1 for a companion to Fig.**??** scaled by absolute population size). Beyond these challenges, the median estimated age at sexual maturity for the targeted species included in this study is 6 years, meaning that the span of this analysis represents less than three generations of MPA protection for half of the the measured species. Ongoing monitoring may yet reveal clearer effects. Analysis of more rapidly growing and maturing species, e.g. spiny lobster, may also reveal clearer signals.

While the MPA effect estimated by our model was not significant in any one year, the positive trend from 2005 to 2014 is evident, as is the sharp decline from 2015-2017. To what should we attribute this apparent shift? We cannot reject the parallel trends assumption between the targeted and non-targeted species in the years before the MPAs (Fig.**??**). But, the Channel Islands region (and the entire West coast of the USA) experienced a dramatic ‘marine heatwave’ beginning in 2014 and persisting through 2016, resulting in part in extremely elevated water temperatures throughout the region (60). Biogeographic differences in the distributions of targeted and non-targeted species may confound the observed effects of MPAs. Many of the non-targeted species have warm thermal affinities and have increased in numbers since the heatwave (61). The targeted group is made up mostly of fishes with cold-water affinities, such as members of the genus *Sebastes*. As such, we hypothesize that the recent evidence for a decline in densities of targeted species is due to environmental conditions that disproportionately affect the targeted group (and not for example due to concentrated fishing pressure outside the reserves). This hypothesis is supported by the sharp declines in densities of targeted species seen inside the MPAs themselves (see Fig.S27-S29), suggesting a driver other than fishing may be at play.

What do our results imply about the future of MPA science? Our simulation model is by no means exhaustive (for example it ignores features such as species interactions, habitat effects, and climate feedback), but captures many of the core factors theorized to affect MPA performance. Our results show that while attributes such as MPA size and fishing pressure are important factors in determining the effects of protection, local fleet dynamics and the movement rates of adult fish can dramatically affect the outcomes of protected areas as well (Fig.**??**). Far from being a simple tool with clear outcomes, the effects of MPAs can be highly context dependent, requiring - we would argue - a bio-economic model of at minimum the complexity presented here to help communities design and set expectations of MPAs at the tactical level. While users may not be able to parameterize every aspect of a model such as that presented here, working with stakeholders to visualize the implications of, for example, different fleet responses to MPA implementation is a critical step in MPA design. Readers can use our simulation model to explore the effects of MPAs through an interactive web application available here.

Once simulation models have been used to help design an MPA, how can users evaluate whether it is achieving their objectives? Response ratios are commonly used as evidence for conservation outcomes of MPAs (5), but as suggested in (47) and (51) and demonstrated here, without careful attention to the design of control sites (accounting for example for the displacement of effort by MPAs), response ratios may be highly unreliable estimators of regional MPA effects. As (51) suggests, there are many potential alternatives for estimating the effects of MPAs that better account for the challenges of causal inference. We applied one such approach here (a difference-in-difference estimator), and yet were still unable to reach robust conclusions as to the effect of MPAs on the density of targeted species in the Channel Islands, due to the likely small size of the true effect relative to the strength and variability of environmental drivers.

While this does not mean that all MPAs will face similar challenges in estimating their effects, our results in the rigorously studied Channel Islands system make clear that in many instances empirically detecting a clear regional effect of MPAs may not be possible. How then should stakeholders go about adaptively monitoring and managing MPAs? Simulation modeling can help inform the range of effect sizes that may be expected, and monitoring programs can perhaps be tuned to focus on the species groups that have the highest chance of a detectable effect size (56). Expanding data collection to include robust monitoring of fleet dynamics may help statistical approaches to isolate the true effect of MPAs on conservation outcomes by allowing for improved control of the effects of fishing dynamics, and allow managers to take into account potential negative interactions between MPAs and fleet dynamics such as those that may occur under constant-catch dynamics. Whenever possible monitoring programs should be implemented prior to MPA implementation to provide a pre-treatment benchmark. Non-equilibrium analyses (Fig.**??**) also help set expectations for effect sizes over time. Beyond that, educating communities about the challenges of estimating the effects of MPAs can help set expectations, so that a lack of a clear effect is not necessarily viewed as a failure of the program, but rather considered in the context of reasonable expectations. While this paper has focused on the conservation outcomes of MPAs, future work must also address the challenge of predicting and estimating the fishery impacts of protected areas.

As the number and size of global MPA networks increase, it is critical that we both set appropriate expectations for their outcomes, and plan how we will monitor the performance of these protected areas over time. While the history of MPA science has made important strides in helping us understand the dynamics of protected areas, the future of MPA science must directly tackle the challenge of evaluating the performance of these MPAs, and adapting their design as needed to best achieve objectives. Commonly employed metrics such as response ratios may be applicable in some circumstances, but can have severe shortcomings as metrics of regional conservation effects. Dependence on unreliable estimators of MPA effects may lead to stakeholders incorrectly attributing negative environmental shocks as MPA failures, or interpreting data arising from scorched-earth fishing outside MPAs as a conservation success. Bio-economic modeling can help frame community expectations, reducing the potential for a reduction in support if unrealistic conservation or fishery gains are not realized. Statistical approaches that explicitly address complications such as the spatial spillover effects of MPAs (such as the difference-in-difference approach used here) may give users an improved understanding of the performance of their MPAs. Effective use of simulation and statistics to clearly communicate what we should expect and what we can detect from MPAs is critical in ensuring that MPAs play effective roles in fisheries management and marine conservation.

0.2 Materials and Methods

We present here critical characteristics of our simulation model and regression approach. Further details can be found in the Supplementary Information. All analysis were conducted in R (62). Our main difference-in-difference model was fit using Template Model Builder in R (63). Code needed to replicate results can be found here.

0.2.1 Simulation Model

Our bio-economic model simulates the effect of MPAs on a spatially explicit age-structured representation of a single species. Readers can explore the functionality of the model using an online tool available here. See Table.S1 for a complete description of simulation states. The model consists of 25 patches with wrapped edges (picture the waters around a circular island). For any one simulation we randomly pull a species and its associated life history from the `FishLife` (41) package in R. We pair these data with randomly selected values between 0.6 and 0.95 for Beverton-Holt steepness (64), as well as larval and adult dispersal rates. We also randomly assign whether adults have density dependent movement, as well as one of three potential types of density dependence (65):

1. Local density dependence: Density dependence occurs independently in each patch, and recruits then disperse to nearby patches
2. Global density dependence: Density dependence is a function of the sum of spawning biomass across all patches, and recruits are then distributed according to habitat quality
3. Post-dispersal density dependence: Larvae are distributed throughout the system, and then density dependence occurs based on the density of adult biomass at the destination patch

We allow for three potential siting strategies for MPAs. In the first, MPAs are randomly placed. In the second, we assume that MPAs are placed in preferentially better habit (unfished recruitment is four times greater inside MPA locations). In the third, we allow for scenarios in which MPAs are placed in hotspots of larval dispersal. In this scenario, patches in which MPAs will be placed have larval dispersal rates four times greater than patches that do not become MPAs.

Along with the fleet dynamics model, each simulation is assigned a random fleet dispersal scenario: uniform dispersal (where the total effort of the fleet is divided evenly among all open patches), catch dispersal (where the total effort of the fleet is divided according to the catchable biomass in each available patch), and profit dispersal (where the total effort of the fleet is divided according to the profit per unit effort in each available patch).

Lastly each simulation is assigned an MPA scenario, defined by the number and size of MPAs, the placement of those MPAs, and the year that the MPAs are put in place. Each simulation starts the population off at unfished equilibrium and then beings to apply the fleet model. The MPAs are then placed during the randomly selected start year, allowing some runs to explore how the early dynamics of the MPA play out when the fishery and population they are placed on is not already at equilibrium. Fishing effort in displaced by MPAs can either concentrate outside or leave the fishery. Each simulation is run to equilibrium with and without the selected MPA strategy (holding all else constant). We then measure the difference in biomass and fishery catches in each time step in the scenario with and without the MPAs to calculate the conservation and fishery effects of the MPAs over time.

0.2.2 Difference in Difference Regression

We applied this difference-in-difference strategy to a large dataset in California. We used empirical kelp forest survey data from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) monitoring in the Northern Channel Islands with the ultimate goal of testing the regional effects of MPAs in a real world

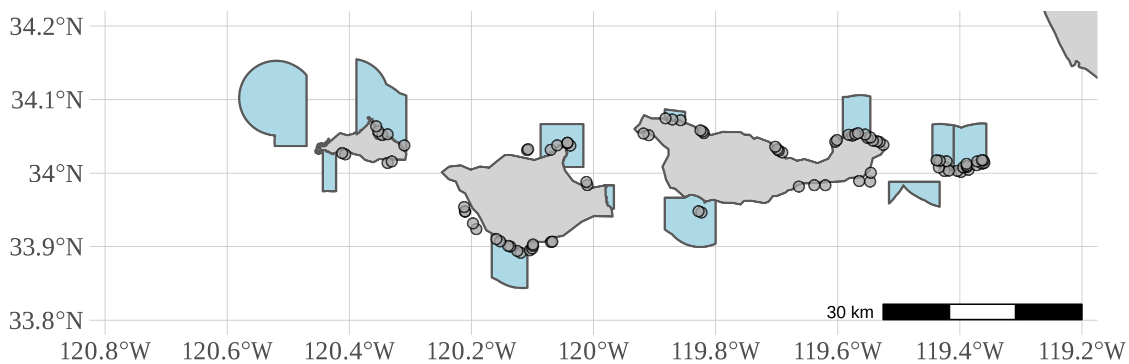


Figure 3: Map of PISCO sampling locations within the the Channel Islands National Marine Sanctuary, California, USA. Grey boxes indicated MPAs, points sampling locations, with color representing whether the site is inside an MPA (blue) or not (red)

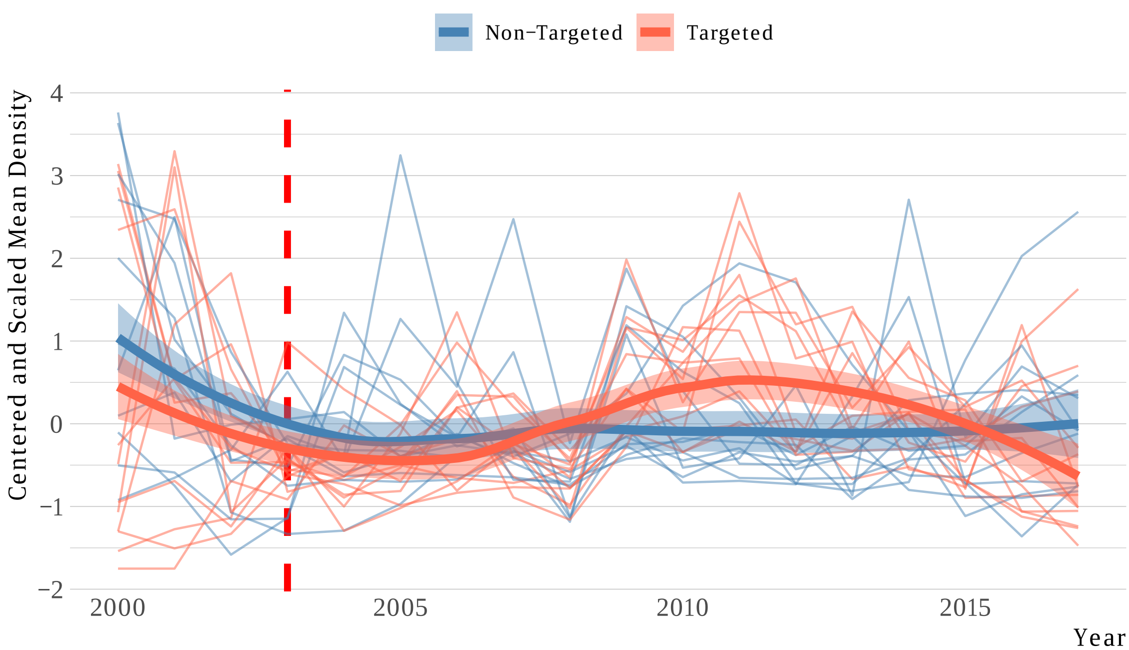


Figure 4: Centered and scaled mean annual biomass densities of included targeted (red) and non-targeted (blue) fish species (faded lines) and smoothed means with 95% confidence intervals over time (darker lines and ribbons). Vertical red dashed line shows year of MPA implementation.

context. A network of MPAs covering approximately 20% of the islands' waters was put in place in 2003 as part of the California Marine Life Protection Act (MLPA) (see (22), (23), (24), and (25) for information on the creation of the MLPA). PISCO conducts visual SCUBA surveys at a large number of rocky-reef and kelp forest sites inside and outside of MPAs throughout the Channel Islands, producing estimates of densities of fishes that are both targeted and non-targeted by fishing (Fig.3-4).

The key assumptions of this approach are that a) within the time-frame of the model there are no significant interaction effects between the targeted and non-targeted species (which in fact we do not detect, see SI), and b) that in the absence of the MPAs both the targeted and non-targeted groups of species would have exhibited similar trends in densities. The advantage to this approach is that given the time-frame of the model (18 years), we believe that spillover effects of MPA placement on the non-targeted species are likely to be much less severe than the effects of biological spillover and fishing concentration that may bias the performance of estimators such as a response ratios or a spatial BACI design.

We use a difference-in-difference regression style regression to attempt to estimate the causal effect of MPAs on regional targeted fish biomass. Empirically, this amounts to estimating the pre-post MPA difference in the biomass densities of targeted species net the same difference for non-targeted species in the Channel Islands.

The simplified form of this model is

$$log(d_i) = \beta_0 + \beta_1 T_i + \beta_2 MPA_i + \beta_3 T_i MPA_i + e_i \tag{1}$$

where d_i is the biomass density at observation i, T indicates whether the observation i is for a targeted ($T = 1$) or non-targeted ($T = 0$) species, and *MPA* marks whether observation i is in a pre MPA ($MPA = 0$) or post MPA ($MPA = 1$) state. Under the assumptions of this model, β_3 is the causal effect of the treatment (*MPA*) on the treated (targeted species). The full form of the estimation model is much more involved, integrating uncertainty in a hierarchical model from the individual observation level up to the mean trends of targeted and non-targeted species. See SI for details of estimation model.

We briefly assess two of the most critical assumptions of this model here: that the treated and non-treated groups have parallel trends, and that the effect of the treatment on the treated does not tangentially affect the untreated. While the parallel trends assumption cannot be formally proven, we can examine its validity using the data from the years before the MPAs were put in place in 2003. We do not detect any significant differences in the trends of the biomass densities of the targeted and non-targeted species in the years before the MPAs.

With regards to the second assumption, all of the species in this empirical analysis exist within an ecosystem, and as such affect each other through mechanisms such as predation, competition, and habitat modification. We find it unlikely that these effects have had enough time to manifest in a meaningful way in the 13 years of post-MPA data used in our analysis (66, 67).

We used convergent cross mapping (CCM), in the manner of (68), to test for the possibility of the trophic cascades biasing our results. Generalizations of Takens' theorem indicate that if two variables are part of the same dynamic system, their individual dynamics should reflect their relative causal influence. Convergent cross mapping (CCM) tests for causation by using the attractor/manifold built from the time series of one variable to predict another (hence the "cross-mapping"). CCM then allows us to test for causal relationships in the timeseries of densities of targeted and non-targeted species. Our results found no significant cross-mappings between targeted and non-targeted species, indicating that while clearly there are interactions between these groups on some level, the effects within the timespan of the data are not pronounced enough to be of concern to our results (see SI for additional information in CCM testing). However, the longer MPAs are in place, the greater the possibility that substantial species interactions that can affect use of non-targeted species as a control may arise.

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