The Regional Effects of Marine Protected Areas

Daniel Ovando[a,1], Jennifer E. Caselle[b], Christopher Costello[b], Olivier Deschenes[b], Steven D. Gaines[b], Ray Hilborn[a], and Owen Liu[b]

[a]University of Washington, School of Aquatic and Fishery Sciences; [b]University of California, Santa Barbara

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. Despite the expanding role of MPAs in marine resource management, we lack a clear understanding of what the regional effects of MPAs might be, and how we might detect them in scientific studies. We used a bio-economic simulation model to demonstrate how the regional effects of MPAs are affected by a suite of economic and environmental drivers and show how commonly used methods to measure inside-MPA effects are likely to fail to capture the regional impacts of protection. We present an empirical strategy for estimating regional MPA effects on biomass density using 16 years of data from inside and outside of MPAs within the Channel Islands, California, USA. We find no statistically clear effect of MPAs on aggregate mean biomass densities of targeted finfish throughout the study region. To make meaningful progress on MPA design and evaluation, the next generation of MPA science must address the challenge of understanding and estimating the regional effects of MPAs across the diversity of species in the ecosystem.

Marine Protected Areas | Conservation | Bio-economic modeling | Program Evaluation

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) rely on the belief 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.

What is the scientific evidence of the conservation effects of MPAs? 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. To address this gap, this study examines two critical questions: 1) What do we expect the regional-scale conservation effects of MPAs to be and 2) When (and how) can we expect to empirically detect these effects? We answer these questions using a simulation

Significance Statement

Healthy marine ecosystems are critical to the well-being of the planet. Marine protected areas, parts of the oceans protected from human activities such as fishing, are increasingly being used in an effort to conserve and manage these ecosystems. Our study pairs theory with empirical methods to examine the regional effects of MPAs on conservation outcomes. Using simulations, we show that the regional effects of marine protected areas can be highly variable and dependent on human drivers. We find no statistically clear effect of a network of MPAs after 13 years of protection, which our simulation analysis suggests is actually to be expected. Our results lay a foundation for future research on the design and monitoring of marine protected areas.

www.pnas.org/cgi/doi/10.1073/pnas.XXXXXXXXX

PNAS | October 16, 2019 | vol. XXX | no. XX | 1–9

analysis to frame the theoretical regional conservation impacts of MPAs. We then present an empirical test of the evidence for regional-level conservation effects of MPAs resulting from a network of closures put in place in the Channel Islands, California, USA, in 2003.

What Are the Regional Effects of MPAs?. Much of the literature on the effects of MPAs 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).

We used a simulation model to examine the regional conservation effects of MPAs under a wide array of conditions that might reasonably be expected to affect these outcomes. The model explores combinations of MPA designs, life histories, and fishing fleet dynamics (See Table.S1 for a complete description of simulation variables). We use this model to explore how different drivers interact to affect the conservation outcomes of MPAs.

Theoretical Conservation Effects. As a thought experiment, imagine a region that has driven its fish populations to near extinction and then places 100% of its waters inside a no-take MPA. In that setting, we would expect the regional-scale conservation benefits to be massive. On the other hand, imagine implementing an MPA in an area where a sedentary species has been only lightly fished. In that setting, it is possible to create a small net conservation loss if the concentration of fishing pressure outside the reserve has a greater effect than the biomass buildup inside the reserve. Within these broad bounds, numerous factors can act to affect the regional effects of MPAs. These include the scale of adult and larval dispersal relative to the size of the MPAs (22–25), 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 activity and management responds to the implementation of the MPAs (4, 8, 26–32). 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, 33).

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 (4%). For ecosystems fished near MSY levels (depletion of 40%-60%), the median conservation effect was 28%, while for overfished ecosystems (without-MPA depletions above 60%) the median regional conservation effect was over 100% (Fig.1-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 (34), though works that include a broader range of fisheries estimate that 50% or more of stocks to fall into the heavily fished category (35, 36).

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 (37–40) (Fig.1-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 (94% of simulations), the 6% 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.

How Can We Detect Regional Effects?. How can we empirically measure the regional effects of MPAs? Intuition and bio-economic theory tells us that the regional conservation effects of MPAs are likely to be highly context dependent across locations and across species within locations, so careful thought must be devoted to an empirical design to detect their effects. The perfect experiment would involve two parallel worlds that were identical, except for the implementation of an MPA. In world "A", no MPA would be implemented, and in the facsimile world "B", the MPA would be implemented. Both worlds would be tracked before and after MPA implementation, and the conservation and fishery outcomes would be compared after treatment. Instead of two parallel worlds, a similar experimental design would involve random placement of MPAs.

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 (41, 42).

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 (43) 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?

Control sites used in density or biomass ratios are often selected based on abiotic or ecological traits such as habitat characteristics (41). 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 (44), the MPA evaluation literature has by and large been unable to adequately address them, often due to the very real challenges of acquiring the necessary data (41).

Failure to account for these spillover effects can result in a biased estimate of the true effect of a policy such as MPA placement (42). 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.2-A). In this idealized case, the response ratio is often a reasonable estimator for the regional conservation effect.
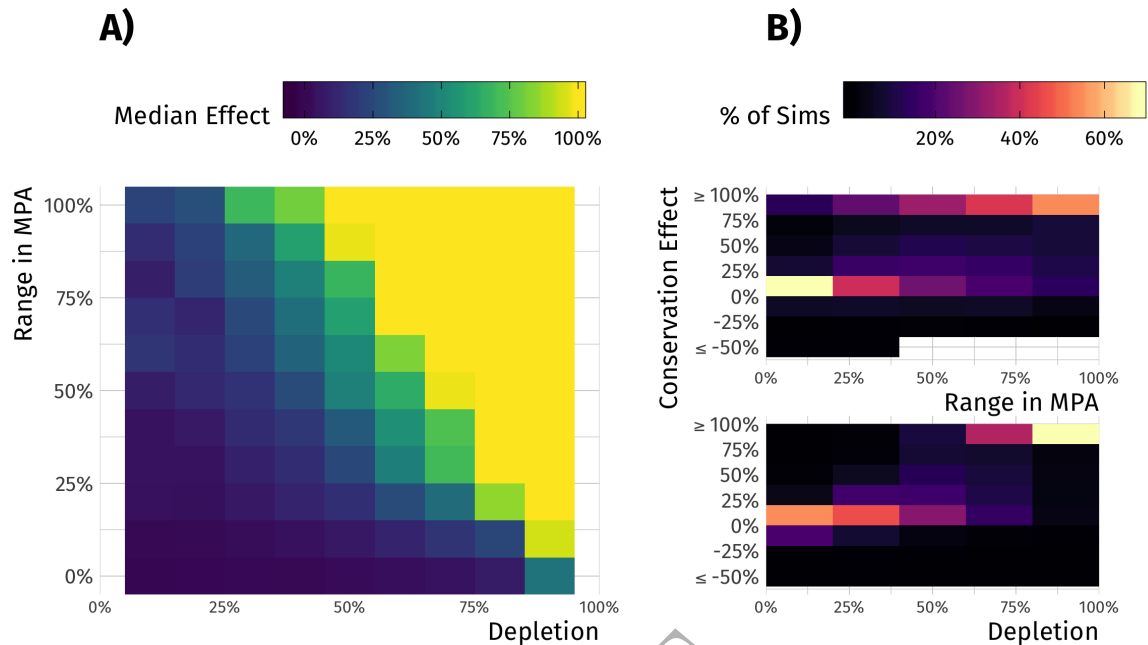
What happens when the "control" sites are in fact affected by the application of the MPA through biological spillover and fishing concentration? In order to address this possibility, we calculated a new response ratio as the mean density inside MPAs relative to the mean density outside the MPAs (both 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.2-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.

MPA Effects in the Channel Islands. Given these challenges, what is a viable alternative for estimating the conservation effects of MPAs? In a manner similar to (38), we use a difference-in-difference estimator comparing densities in finfish species targeted by fishing effort (i.e., those potentially affected by an MPA) from those not targeted before and after MPA implementation (42). 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 (45, 46). But, we must note that 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). 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

373
374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389
390
391
392
393
394
395
396
397
398
399
400
401
402
403
404
405
406
407
408
409
410
411
412
413
414
415
416
417
418
419
420
421
422
423
424
425
426
427
428
429
430
431
432
433
434

435
436
437
438
439
440
441
442
443
444
445
446
447
448
449
450
451
452
453
454
455
456
457
458
459
460
461
462
463
464
465
466
467
468
469
470
471
472
473
474
475
476
477
478
479
480
481
482
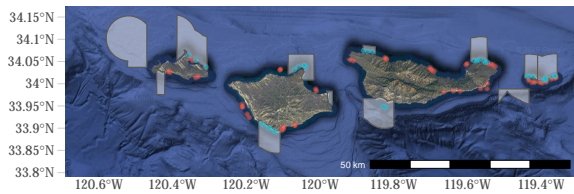483
484
485
486
487
488
489
490
491
492
493
494
495
496

Fig. 1. Median (A) and range (B) of equilibrium regional MPA conservation effects (percent change in total biomass with MPAs relative to without MPAs) across a range of depletion and MPA sizes (and incorporating the full range of scenarios included in our study). "Range in MPA" is the percent of patches covered by an MPA, "Depletion" is the depletion that would have occurred in equilibrium without the MPA. Colors in panel B represent the percentage of simulations that fell into an effect size bin at each x-axis bin, such that the sum of all percentages for a given x-axis bin is 1.
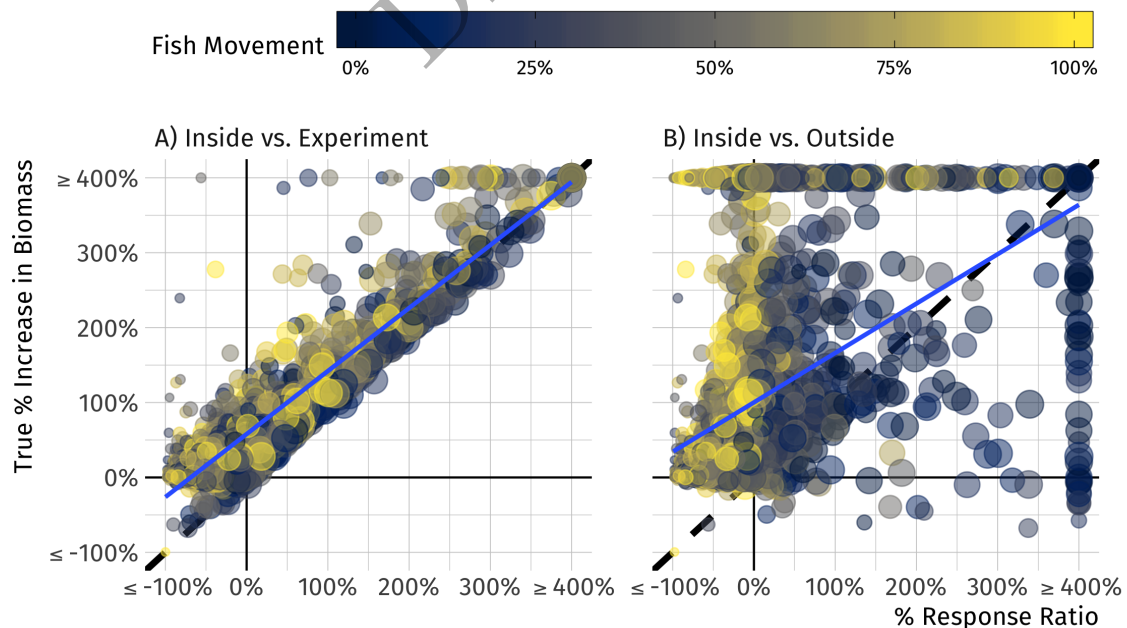
Fig. 2. Simulated MPA-size weighted response ratios (x-axis) plotted against true regional change in biomass caused by MPAs (y-axis). Each point represents a simulation, and color represents the movement rate of fish in the simulation (expressed as a percentage of the patches a fish is likely to move in one time step). The black line shows the one:one fit line, the blue line is a linear fit of the relationship between observed response ratios and true regional change in biomass. Inside vs. Experiment simulates a true control, while Inside Vs. Outside uses a control that may be affected by the treatment.

497
498
499
500
501
502
503
504
505
506
507
508
509
510
511
512
513
514
515
516
517
518
519
520
521
522
523
524
525
526
527
528
529
530
531
532
533
534
535
536
537
538
539
540
541
542
543
544
545
546
547
548
549
550
551
552
553
554
555
556
557
558

559
560
561
562
563
564
565
566
567
568
569
570
571
572
573
574
575
576
577
578
579
580
581
582
583
584
585
586
587
588
589
590
591
592
593
594
595
596
597
598
599
600
601
602
603
604
605
606
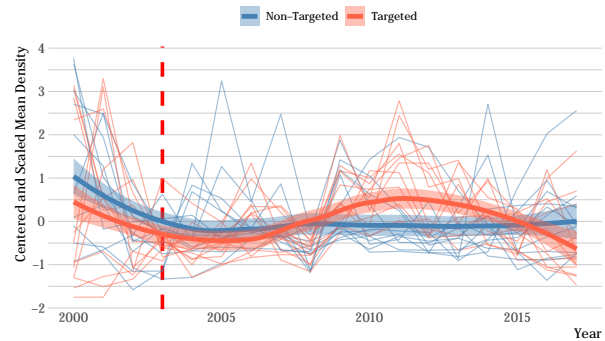607
608
609
610
611
612
613
614
615
616
617
618
619
620

Fig. 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)

Fig. 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.

Fig. 5. Estimated divergence in biomass densities of targeted and non-targeted fishes throughout the Channel Islands (integrated across inside and outside of MPAs). MPAs are implemented in 2003 (red dashed line). Colored cells in the background indicate the frequency of MPA conservation effects predicted by our simulation modeling for MPAs similar in design and species composition to the Channel Islands in each year.

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 (16 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.
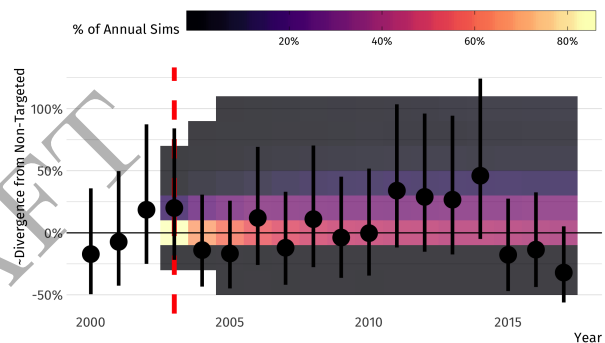
We applied this difference-in-difference strategy to a large dataset in California. We used empirical kelp forest survey data from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) monitoring in the Northern Channel Islands with the ultimate goal of testing the regional effects of MPAs in a real world 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 (47), (48), (49), and (50) 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).

Although the Islands do not encompass the full population of any of these species, they encompass a large enough area to assess the regional MPA conservation effects we might see in the Channel Islands after 13 years of protection (the time span covered by our model). The median regional conservation effect produced by our simulation model after 13 years of protection by MPAs covering between 15%-20% of a population's range was 25%. This projected effect has an an interquartile range of 8% and 100%, although values as high as a 200% increase and as low as a 50% decrease were also produced. Our expectation then is that all else being equal we are likely looking for a modest but positive effect size.

The raw trends in the biomass densities appear to show parallel trends in the densities of targeted and non-targeted fishes pre-MPA, with the targeted group diverging first positively and then negatively over time (Fig.4). However, these raw trends could be caused by any number of confounding variables besides the effects of the MPAs themselves, from changes in observer skill and sampling locations, to shifts in environmental conditions. Using our difference-in-difference

model in an effort to control for these factors, we found no significant difference in the biomass densities of targeted and non-targeted fishes pre-MPA (before 2003). Following the implementation of the MPAs in 2003, we see evidence of an increasing trend in densities of targeted relative to non-targeted fish, reaching a peak value in 2014. After 2014, densities of targeted species appear to have declined relative to what we would expect based on the non-targeted group (Fig.5).

Discussion. 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 94% of our simulations (Fig.1). 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 36% stands in contrast to the large within-MPA effects on biomass densities reported by (51) 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 (52, 53), 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.5). 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.1 scaled by absolute population size). Beyond these challenges, the median estimated age at sexual maturity for the targeted species included in this study is 5 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.5). 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 (54). 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 (55). 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.1). 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 (41) and (42) 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 (42) 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 (39). 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.5) 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.

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 (56). Our main difference-in-difference model was fit using Template Model Builder in R (57). Code needed to replicate results can be found here.

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 (58) package in R. We pair these data with randomly selected values between 0.6 and 0.95 for Beverton-Holt steepness (59), 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 (60):

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.

Difference in Difference Regression. We use a difference-in-difference regression style regression to attempt to estimate the causal effect of MPAs on regional targeted fish biomass.

Ovando *et al.*

PNAS | **October 16, 2019** | vol. XXX | no. XX | **7**

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

$$log(d_i) = \beta_0 + \beta_1 T_i + \beta_2 MPA_i + \beta_3 T_i MPA_i + e_i \quad [1]$$

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 (61, 62).

We used convergent cross mapping (CCM), in the manner of (63), 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.

1. Johannes RE (1978) Traditional Marine Conservation Methods in Oceania and Their Demise. *Annual Review of Ecology and Systematics* 9(1):349–364.

2. IUCN (1976) *IUCN yearbook, 1975-76 : Annual report of the International Union for Conservation of Nature and Natural Resources for 1975 and for January-May 1976.*

3. Watson JEM, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. *Nature* 515(7525):67–73.

4. Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing Marine Reserve Networks for Both Conservation and Fisheries Management. *Proceedings of the National Academy of Sciences* 107(43):18286–18293.

5. Lester S, et al. (2009) Biological effects within no-take marine reserves: A global synthesis. *Marine Ecology Progress Series* 384:33–46.

6. Halpern BS, Warner RR (2003) Review Paper. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London Series B: Biological Sciences* 270(1527):1871–1878.

7. Edgar GJ, et al. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506(7487):216.

8. Gerber LR, Heppell SS, Ballantyne F, Sala E (2005) The role of dispersal and demography in determining the efficacy of marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 62(4):863–871.

9. Goni R, Hilborn R, D\'ıaz D, Mallol S, Adlerstein S (2010) Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Prog Ser* 400:233–243.

10. Halpern BS, Lester SE, Kellner JB (2009) Spillover from marine reserves and the replenishment of fished stocks. *Environmental Conservation* 36(04):268–276.

11. Kay MC, Lenihan HS, Kotchen MJ, Miller CJ (2012) Effects of marine reserves on California spiny lobster are robust and modified by fine-scale habitat features and distance from reserve borders. *Marine Ecology Progress Series* 451:137–150.

12. Stobart B, et al. (2009) Long-term and spillover effects of a marine protected area on an exploited fish community. *Marine Ecology Progress Series* 384:47–60.

13. McClanahan TR, Mangi S (2000) Spillover Of Exploitable Fishes From A Marine Park And Its Effect On The Adjacent Fishery. *Ecological Applications* 10(6):1792–1805.

14. Russ G, Alcala A (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* 132:1–9.

15. Thompson AR, Chen DC, Guo LW, Hyde JR, Watson W (2017) Larval abundances of rockfishes that were historically targeted by fishing increased over 16 years in association with a large marine protected area. *Royal Society Open Science* 4(9):170639.

16. Baetscher DS, et al. (2019) Dispersal of a nearshore marine fish connects marine reserves and adjacent fished areas along an open coast. *Molecular Ecology* 28(7):1611–1623.

17. Pelc R, Baskett M, Tanci T, Gaines S, Warner R (2009) Quantifying larval export from South African marine reserves. *Marine Ecology Progress Series* 394:65–78.

18. Costa BH e, et al. (2013) Fishers' Behaviour in Response to the Implementation of a Marine Protected Area. *PLOS ONE* 8(6):e65057.

19. Mason J, Kosaka R, Mamula A, Speir C (2012) Effort changes around a marine reserve: The case of the California Rockfish Conservation Area. *Marine Policy* 36(5):1054–1063.

20. Murawski SA, Wigley SE, Fogarty MJ, Rago PJ, Mountain DG (2005) Effort distribution and catch patterns adjacent to temperate MPAs. *ICES Journal of Marine Science* 62(6):1150–1167.

21. McDermott GR, Meng KC, McDonald GG, Costello CJ (2019) The blue paradox: Preemptive overfishing in marine reserves. *Proceedings of the National Academy of Sciences* 116(12):5319–5325.

22. Gaines SD, Gaylord B, Largier JL (2003) Avoiding Current Oversights in Marine Reserve Design. *Ecological Applications* 13(sp1):32–46.

23. Botsford LW, et al. (2008) Connectivity, sustainability, and yield: Bridging the gap between conventional fisheries management

and marine protected areas. *Reviews in Fish Biology and Fisheries* 19(1):69–95.

24. Di Franco A, et al. (2018) Linking home ranges to protected area size: The case study of the Mediterranean Sea. *Biological Conservation* 221:175–181.

25. McGilliard CR, Hilborn R (2008) Modeling no-take marine reserves in regulated fisheries: Assessing the role of larval dispersal. *Canadian Journal of Fisheries and Aquatic Sciences* 65(11):2509–2523.

26. Hilborn R, Punt AE, Orensanz J (2004) Beyond band-aids in fisheries management: Fixing world fisheries. *Bulletin of Marine Science* 74(3):493–507.

27. Hilborn R (1992) Can fisheries agencies learn from experience? *Fisheries* 17(4):6–14.

28. Walters CJ, Martell SJ (2004) *Fisheries ecology and management* (Princeton University Press).

29. Hastings A, Botsford LW (2003) Comparing Designs Of Marine Reserves For Fisheries And For Biodiversity. *Ecological Applications* 13(sp1):65–70.

30. Gerber LR, et al. (2003) Population Models For Marine Reserve Design: A Retrospective And Prospective Synthesis. *Ecological Applications* 13(sp1):47–64.

31. Hilborn R, et al. (2004) When can marine reserves improve fisheries management? *Ocean & Coastal Management* 47(34):197–205.

32. Botsford LW, Micheli F, Hastings A (2003) Principles for the Design of Marine Reserves. *Ecological Applications* 13(sp1):25–31.

33. Costello C, Lynham J, Lester SE, Gaines SD (2010) Economic incentives and global fisheries sustainability. *Resource* 2.

34. FAO (2018) *The State of World Fisheries and Aquaculture 2018: Meeting the sustainable development goals* (FAO, Rome, Italy).

35. Costello C, Gaines S, Gerber LR (2012) Conservation science: A market approach to saving the whales. *Nature* 481(7380):139–140.

36. Rosenberg AA, et al. (2017) Applying a New Ensemble Approach to Estimating Stock Status of Marine Fisheries around the World. *Conservation Letters*:n/a–n/a.

37. Starr RM, et al. (2015) Variation in Responses of Fishes across Multiple Reserves within a Network of Marine Protected Areas in Temperate Waters. *PLoS ONE* 10(3):e0118502.

38. Caselle JE, Rassweiler A, Hamilton SL, Warner RR (2015) Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. *Scientific reports* 5:14102.

39. Nickols KJ, et al. (2019) Setting ecological expectations for adaptive management of marine protected areas. *Journal of Applied Ecology* 0(0). doi:10.1111/1365-2664.13463.

40. Villaseñor-Derbez JC, et al. (2019) An interdisciplinary evaluation of community-based TURF-reserves. *PLOS ONE* 14(8):e0221660.

41. Ferraro PJ, Sanchirico JN, Smith MD (2018) Causal inference in coupled human and natural systems. *Proceedings of the National Academy of Sciences*:201805563.

42. Larsen AE, Meng K, Kendall BE (2019) Causal analysis in controlImpact ecological studies with observational data. *Methods in Ecology and Evolution* 0(0). doi:10.1111/2041-210X.13190.

43. Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. *Ecology Letters* 5(3):361–366.

44. Halpern BS, Gaines SD, Warner RR (2004) Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecological Applications* 14(4):1248–1256.

45. Costello C, et al. (2010) The value of spatial information in MPA network design. *Proceedings of the National Academy of Sciences* 107(43):18294–18299.

46. Rassweiler A, Costello C, Hilborn R, Siegel DA (2014) Integrating scientific guidance into marine spatial planning. *Proceedings of the Royal Society B: Biological Sciences* 281(1781):20132252.

47. Osmond M, Airame S, Caldwell M, Day J (2010) "Lessons for marine conservation planning: A comparison of three marine protected area planning processes". *Ocean & Coastal Management* 53(2):41–51.

48. Kirlin J, et al. (2013) California's Marine Life Protection Act Initiative: Supporting implementation of legislation establishing a statewide network of marine protected areas. *Ocean & Coastal Management* 74:3–13.

49. Botsford LW, White JW, Carr MH, Caselle JE (2014) Chapter Six - Marine Protected Area Networks in California, USA. *Advances in Marine Biology*, Marine Managed Areas and Fisheries., eds Johnson ML, Sandell J (Academic Press), pp 205–251.

50. Hilborn R (2012) The role of science in MPA establishment in California: A personal perspective. *Environmental Conservation* 39(03):195–198.

51. Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* 13(sp1):117–137.

52. Alonzo S, Key M, Ish T, MacCall AD (2004) *Status of the California Sheephead Stock for 2004*.

53. Dick EJ, et al. (2017) *The Combined Status of Blue and Deacon Rockfishes in U.S. Waters off California and Oregon in 2017* (Pacific Fishery Management Council, Portland, OR).

54. Gentemann CL, Fewings MR, García-Reyes M (2017) Satellite sea surface temperatures along the West Coast of the United States during the 20142016 northeast Pacific marine heat wave. *Geophysical Research Letters* 44(1):312–319.

55. Freedman R (2019) Understanding the Efficacy of Spatial Management on Emerging Threats. PhD thesis (University of California, Santa Barbara).

56. R Core Team (2019) R: A Language and Environment for Statistical Computing.

57. Kristensen K, Nielsen A, Berg CW, Skaug H, Bell BM (2016) **TMB** : Automatic Differentiation and Laplace Approximation. *Journal of Statistical Software* 70(5). doi:10.18637/jss.v070.i05.

58. Thorson JT, Munch SB, Cope JM, Gao J (2017) Predicting life history parameters for all fishes worldwide. *Ecological Applications*:n/a–n/a.

59. Mace PM (1994) Relationships between Common Biological Reference Points Used as Thresholds and Targets of Fisheries Management Strategies. *Canadian Journal of Fisheries and Aquatic Sciences* 51(1):110–122.

60. Babcock EA, MacCall AD (2011) How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? *Canadian journal of fisheries and aquatic sciences* 68(2):343–359.

61. Babcock RC, et al. (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences* 107(43):18256–18261.

62. Pershing AJ, et al. (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* 350(6262):809–812.

63. Clark AT, et al. (2015) Spatial convergent cross mapping to detect causal relationships from short time series. *Ecology* 96(5):1174–1181.