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Setting ecological expectations for adaptive management of marine protected areas

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Abstract

1. Marine Protected Areas (MPAs) are being implemented worldwide, yet there are few cases where managers make specific predictions of the response of previously harvested populations to MPA implementation.

2. Such predictions are needed to evaluate whether MPAs are working as expected, and if not, why. This evaluation is necessary to perform adaptive management, identifying whether and when adjustments to management might be necessary to achieve MPA goals.

3. Using monitoring data and population models, we quantified expected responses of targeted species to MPA implementation and compared them to monitoring data.

4. The model required two factors to explain observed responses in MPAs: (a) pre-MPA harvest rates, which can vary at local spatial scales, and (b) recruitment variability before and after MPA establishment. Low recruitment years before MPA establishment in our study system drove deviations from expected equilibrium population size distributions and introduced an additional time lag to response detectability.

5. *Synthesis and applications*. We combined monitoring data and population models to show how (a) harvest rates prior to Marine Protected Area (MPA) implementation, (b) variability in recruitment, and (c) initial population size structure determine whether a response to MPA establishment is detectable. Pre-MPA harvest rates across MPAs plays a large role in MPA response detectability, demonstrating the importance of measuring this poorly known parameter. While an intuitive expectation is for response detectability to depend on recruitment variability and stochasticity in population trajectories after MPA establishment, we address the overlooked role of recruitment variability before MPA establishment, which alters the size structure at the time of MPA establishment. These factors provide MPA practitioners with reasons whether or not MPAs may lead to responses of

targeted species. Our overall approach provides a framework for a critical step of adaptive management.

KEYWORDS

adaptive management, environmental stochasticity, fishing, integral projection model, marine conservation, marine reserve, population dynamics, *Sebastes mystinus*

1 | INTRODUCTION

Marine protected areas (MPAs) are an increasingly popular tool for marine resource management and conservation (Watson, Dudley, Segan, & Hockings, 2014). Global meta-analyses show that *on average* we can expect MPAs to eventually lead to increased abundance of harvested marine species inside MPAs (Edgar et al., 2014; Lester et al., 2009). However, there is a wide range of individual outcomes in those analyses: in any single MPA abundances may remain the same or even decrease, defying expectations (Edgar & Barrett, 2012; Lester et al., 2009). Lack of population increase inside MPAs could be due to a number of factors, such as poor design (Claudet et al., 2008; Edgar et al., 2014) or weak enforcement (e.g. Giakoumi et al., 2017). In addition, MPA responses may not be detectable for reasons unrelated to MPA management. If the area was lightly harvested prior to MPA implementation, the cessation of harvest should not lead to an increase in harvested populations (Micheli, Halpern, Botsford, & Warner, 2004). Stochastic variability in the population can make a response difficult to detect (Blowes & Connolly, 2012; De Leo & Micheli, 2015), and particularly for some long-lived species, adequate time since implementation is needed to detect a response (Molloy, McLean, & Cote, 2009; Starr et al., 2015). Indirect effects, such as competition or predation from other increasing species, can also prevent positive responses of species within MPAs (e.g. Micheli et al., 2004; Babcock et al., 2010).

Distinguishing the drivers of observed responses to MPA implementation, and differentiating between MPA management-dependent and -independent factors, is necessary to evaluate MPA success and engage in adaptive management. Adaptive management is an approach to policy implementation in which ecological responses to management actions are monitored and compared to expected responses, then differences between observations and expectations are used to refine management in an iterative process (Walters, 1986). Such evaluation provides a first step in determining the factors impeding successful responses to MPA implementation. For MPAs, if a mismatch between outcomes and expectations occurs, refinement of management action could include adjusting the size, location, level of protection or degree of enforcement. Despite the consensus that adaptive management holds great promise to improve outcomes in ecosystem management (Allen, Fontaine, Pope, & Garmestani, 2011; Rist, Campbell, & Frost, 2013), including MPAs (Carr et al., 2017; Sale et al., 2005), there are few published cases that compare outcomes of management actions (i.e. observations from monitoring surveys) to expectations (i.e., predictions from population models) in any system (Westgate, Likens, & Lindenmayer, 2013).

From a management perspective, a lack of prior predictions makes it impossible to quantify whether an MPA has met expectations. Management actions generally take place on a regional to local spatial scale and managers and stakeholders are often interested in evaluation of potential success on short-time scales (<10 years). Therefore, adaptive management must place goals and expectations within the appropriate spatial and temporal context to avoid scale mismatch between ecological systems and decision-making (Grafton & Kompas, 2005; Wilson et al., 2016). Projecting the future response to MPAs sets the time-scale of change in an MPA, allowing managers to plan an appropriate time-scale for assessment.

Different mechanistic modelling approaches are appropriate for different phases of MPA management. Typically, population models used for MPA design focus on the long-term, *equilibrium* response of populations inside MPAs (e.g. White, Botsford, Moffitt, & Fischer, 2010). More recent models have focused on the short-term, transient responses of fish populations following MPA implementation (Brown, Abdullah, & Mumby, 2014; Hastings, 2016; White et al., 2013). These efforts show that short-term responses depend critically on the prior harvest mortality rate, which sets the rate for filling-in of the size/age distribution that was truncated by harvest as individuals are allowed to grow older and larger. Unfortunately, harvest mortality rates are usually estimated in stock assessments at the scale of hundreds of kilometres, rather than the local scale of MPAs where harvest rates vary due to distances from ports and other factors. Additionally, as a consequence of time lags associated with increases in reproductive output of populations in MPAs, trajectories of transient responses of population abundance and biomass may be flat or even decreasing during the short-term, despite long-term predicted increases (Hopf, Jones, Williamson, & Connolly, 2016; White et al., 2013). This delay in population increase is more likely for species that are long-lived with older ages of maturity, slow growth rates and/or infrequent recruitment events. While such delayed response can be more prominent when harvest mortality rates were high prior to MPA implementation, high harvest mortality also leads to a greater eventual magnitude of response with greater detectability.

In addition to these deterministic drivers, the population response will depend on stochastic effects of environmental variability. In many coastal marine populations, an important source of stochasticity are post-larval recruitment rates, which can fluctuate widely on seasonal or interannual scales due to ocean conditions and lead to large differences in cohort strength (Carr & Syms, 2006; Caselle, Wilson, Carr, Malone, & Wendt, 2010). This variability influences the initial age structure at implementation, seen as gaps (or peaks) in certain size classes corresponding with years of poor (or

high) recruitment, which determine transient population trajectories (Mangel, 2000). Environmental stochasticity also causes uncertainty in future recruitment, complicating predictions of near-term responses.

Here, we apply a Bayesian state-space integral projection model (IPM; Kimbro, White, & Grosholz, 2018; White et al., 2016) to pre-MPA size frequency data to estimate parameters for a mechanistic model that we used to assess the response of a common nearshore fish to establishment of three California no-take MPAs. We estimated both deterministic (local harvest rate) and stochastic (variable recruitment) components of the response. We used these estimates to compute deterministic and stochastic forward projections of population trajectories, which we then compared to monitoring data in an adaptive management process. We first evaluate which factors are necessary in order to correctly predict the observed responses. This analysis informs the adaptive management step of determining whether observed responses are due to natural factors or management actions, and whether changes in management actions might be necessary to achieve MPA goals. We then show how pre-MPA harvest rates, variability in recruitment and initial population size structure determine when response to MPA establishment will be detectable. This analysis informs the adaptive management step of determining when an evaluation of MPA efficacy for consideration of management adjustment is biologically reasonable. Our approach expands existing MPA theory focused on long-term, equilibrium outcomes to descriptions of short-term, transient responses that can then be compared to actual monitoring data to evaluate MPA efficacy.

2 | MATERIALS AND METHODS

2.1 | Monitoring data

We focus on three regions within central California containing well-enforced no-take MPAs established in 2007 and mandated to be monitored and managed adaptively: Point Lobos, Big Creek and White Rock (Botsford, White, Carr, & Caselle, 2014; Figure 1). The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) has conducted annual surveys of kelp forest fishes in Central California since 1999, spanning MPA implementation in 2007. We focused on the numerically dominant species of rockfish, blue rockfish, *Sebastes mystinus*, which experienced both commercial and recreational harvest in this region (Key, MacCall, Field, Aseltine-Nellson, & Lynn, 2008; Starr, Carr, Malone, & Greenley, 2010). Blue rockfish are long-lived (>40 year; Laidig, Pearson, & Sinclair, 2003) and have small home range sizes < 2 km^2 (Freiwald, 2012; Starr et al., 2015). Since MPA implementation in 2007, no clear increase in blue rockfish density or size within nearshore MPA locations has been evident at any of the three regions (Figure S1 in Supporting Information).

Kelp forest fish surveys were conducted during June-August each year, including the early post-recruitment season (June) of blue rockfish. Fish were counted and sized to the nearest cm along multiple 30 × 2 × 2 m transects at two levels throughout the water column, benthic and mid-water, where blue rockfish were numerically
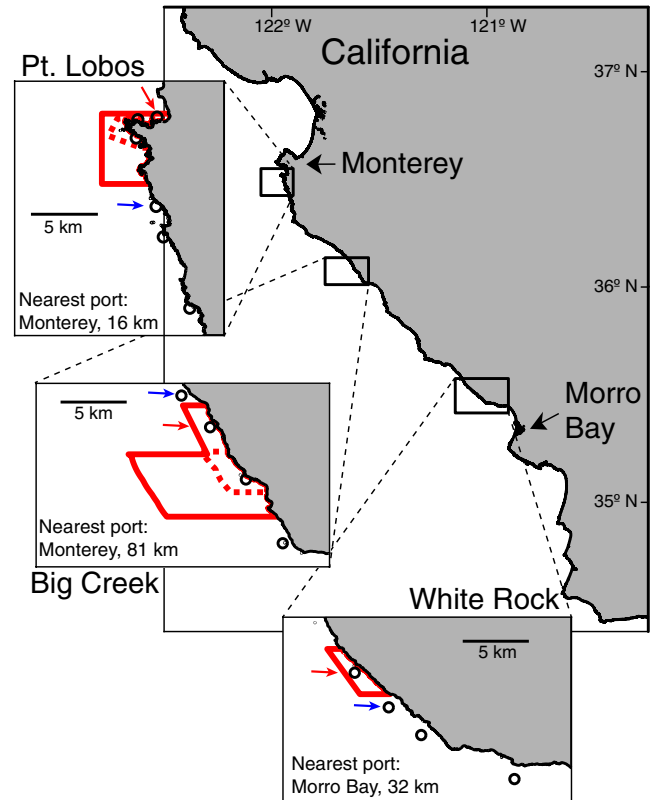

FIGURE 1 Map of study area along the California Central Coast with insets of study regions. Red dashed lines designate boundaries of no-take MPAs prior to 2007, and red solid lines designate boundaries of no-take MPAs implemented in 2007. Open circles indicate the centre of fish abundance monitoring areas. Black arrows show locations of the two closest ports to the MPAs; distance to port is indicated in each region's inset. Red arrows indicate locations that became MPAs in 2007 used for forward projections and comparisons to model output in Figure 3. Blue arrows indicate locations with continued harvest used for comparisons to model output in Figure 3

predominant. Because the number of transects varied slightly among years and locations, we normalized data by the number of transects. Data used for the state-space IPM come from six locations in the Point Lobos region and four locations each in the Big Creek and White Rock regions, with half of the locations inside a no-take MPA and half of the locations open to harvest. Data used for forward model projections came from one location in each region that became a MPA in 2007. We compare these projections to data from that site and the closest sampled harvested area.

2.2 | Integral projection model

We used an IPM to represent size-structured blue rockfish populations. An IPM is conceptually similar to a traditional age-structured Leslie matrix model, but it is an integrodifference model in which the state variable is a continuous size distribution (rather than a discrete age distribution), and the transition probabilities from size x to size y over a discrete time interval (including growth and survival) are

continuous, size-dependent functions (Ellner, Childs, & Rees, 2016). Blue rockfish populations are likely to be demographically open at the scale of our study sites due to their long planktonic dispersal period of 3–5 months (Love, Yoklavich, & Thorsteinson, 2002). We constructed a demographically open IPM that describes the population density $N(y,t)$ at size y, time $t + 1$, as a product of the current population density and the projection kernel $K(y,x)$ (the probability density of surviving and moving from size x to size y), integrated over all biologically reasonable sizes (Ω). New recruitment is added as the product of the density of juvenile recruits arriving at t, $R(t)$, and the probability density function for initial recruit size $\rho(y)$. Given our assumption of an open population with recruitment decoupled from local population size, we do not include density dependence in recruitment. A process error term $\nu(y,t)$ represents deviations from predicted densities due to variability in survival or growth for a given size at t (see Table 1 for list of symbols). The size-structured population dynamics are as follows:

$$N\left(y,t+1\right)=\int_{\Omega} K\left(y,x\right) N\left(x,t\right) dx + R\left(t\right)\rho\left(y\right)+\nu\left(y,t\right).$$

$K(y,x)$ included a von Bertalanffy growth function and size-independent mortality post-recruitment, both taken from independent data (Key et al., 2008; Laidig et al., 2003). Full details of the IPM are described in White et al. (2016).

2.3 | Estimation of pre-MPA harvest and recruitment rates

We fit the IPM to PISCO size data using a Bayesian state-space framework to estimate harvest rate and the annual recruitment magnitude during the pre-MPA time period (1999–2007) for each region (Appendix S1; White et al., 2016), using harvest rate, F, from the regional stock assessment as the Bayesian prior ($F = 0.09$ per year; Key et al., 2008). The model fitting process explicitly included both process error (e.g. interannual variability in growth, mortality and recruitment) and observation error (e.g. variation

TABLE 1 Symbols used in this study

Symbol	Definition
$N(y,t)$	Probability density of individuals of size y at time t
$K(y,x)$	Projection kernel giving the probability density of moving from size x to y
Ω	Set of biologically reasonable sizes, x
$R(t)$	Number of recruits in year t
$\rho(x)$	Probability density function for initial recruit size
$\nu(y,t)$	Process error from deviations in densities due to variability in survival or growth
N	Number of simulations
F	Harvest rate (per year)

in fish counts due to visibility, chance variation in observing fish aggregations).

2.4 | Simulating responses of populations to MPA implementation

We then used the IPM in a forward, non-estimation mode to simulate fish population trajectories, following the above equations and parameters. The IPM was initialized in two ways: (a) starting from the expected stable size distribution under harvest (the expected starting point in the absence of monitoring data) and (b) starting with the size distribution from monitoring data for an individual location within each region that became protected in 2007 (Monastery, Point Lobos region; Dolan, Big Creek region; White Rock, White Rock region; Figure 1). We characterized detection of increases in population density after MPA implementation by simulating fish population trajectories under two scenarios: no harvest mortality, corresponding to the expected conditions inside an effective MPA, and with continued harvest at the estimated pre-MPA harvest rate, such as would be expected if the MPA had not been implemented. For areas outside MPAs, responses will depend on whether harvest rates increase as effort is displaced (Byers & Noonburg, 2007; De Leo & Micheli, 2015); such displacement would lead to a greater inside:outside difference in density as outside densities decrease from additional harvest. Our estimated trajectory without MPA establishment, simulating harvest rates at pre-MPA levels, likely represents a conservative estimate of densities in sites outside of the MPA. The IPM tracks density at each size, accounting for the size structure of the population at each time step; we present results as the total density (abundance per area) of fish greater than or equal to the size limit for blue rockfish over time. We report density, as opposed to biomass, because calculations of biomass from length data would amplify any errors in length estimation.

When starting simulations from the expected stable size distribution under harvest, we first ran deterministic simulations then added noise for stochastic simulations. The major source of stochasticity in this system is recruitment, which does not show evidence for interannual autocorrelation (Dorn, 2002). Deterministic simulations had constant annual recruitment, allowing determination of the expected impact of pre-MPA harvest on population responses to MPAs. We used the stochastic case to investigate the additional impact of variable recruitment on population trajectories by running 1,000 model simulations in which each model simulation received a yearly recruitment density drawn from a Poisson distribution with the mean equal to the mean recruitment density estimated within each region from 1999 to 2007. We determined the number of simulations to run by generating 10 replicate sets of n simulations, with n increasing from 50 to 1,000. The standard deviation of the median population abundance in year 20, taken across each set of 10 simulations, was stable for $n > 500$ simulations with variability across sets of simulations <1% of the median population density. Erring on the side of caution we used $n = 1,000$ simulations for all reported results.

We determined the expected stable size distribution without harvest by first running the model for 100 years with constant recruitment each year at the mean recruitment estimated within each region from 1999 to 2007; 100 years was more than required to reach >99% of the asymptotic population density. We then introduced each region's pre-MPA harvest mortality rate for 30 years (a timescale achieving <1% deviation from the asymptotic population density) to obtain the stable size distribution under harvest for the deterministic simulations. For the stochastic simulations, we began with the stable size distribution after harvest for 30 years with constant recruitment, which was similar to the median of 1,000 simulations with variable recruitment after harvest for 30 years.

To test for impacts of the initial size structure on population trajectories in addition to recruitment variability, we began stochastic simulations with the observed size distribution from 2007 at locations that became MPAs in the three regions. Stable size distributions under harvest and the size distributions from 2007 monitoring data are shown in Figure S2.

2.5 | Calculating detectability of MPA responses

Receiver Operating Characteristics (ROC; Hanley & McNeil, 1982; Boettiger & Hastings, 2012) are a means of translating distributions of harvested and unharvested population trajectories at each point in time into a plot of the probability of a true positive (MPAs have led to greater density within the MPA, and that is detected) versus the probability of a false positive (MPAs have not led to greater density within the MPA, but an increase is detected).

We calculated ROC curves for the distributions of simulated density with a MPA and with continued harvest (no MPA) at a given site at 5, 10, 15 and 20 years post-MPA implementation. The probability of detecting a true positive versus false positive depends on the "cutoff value": the difference in abundance between harvested and unharvested populations that is required to declare whether there has been an increase. Each ROC plot consists of a plot of these two probabilities as the cutoff threshold values range from the minimum density in the no-MPA distribution to the maximum density in the MPA distribution; each set of cutoff threshold values would be unique to the scenario being analysed. For each cutoff value, we calculated the proportion of the no-MPA distribution that was greater than the cutoff (false positive) and the proportion of the MPA distribution that was greater than the cutoff (true positive). The ROC curve plots those pairs of values across the range of possible cutoff values. If the two distributions between which the response is being assessed are quite similar (i.e. same mean, standard deviation) the ROC plot will be a straight line on the diagonal. If the distributions have little overlap (i.e. the difference in means is greater than the combined standard deviations), the ROC plots will be bowed toward the upper left-hand corner.

All analyses were performed using MATLAB software version R2015a.

3 | RESULTS

3.1 | Estimation of pre-MPA harvest and recruitment rates

Across the three regions, using the value of pre-MPA harvest rate from the regional stock assessment as the Bayesian prior (F = 0.09 per year; Key et al., 2008), the posterior estimates of F ranged from near zero to twice the value in the regional stock assessment (Big Creek, $F = 1.1 \times 10^{-4}$ per year; White Rock, F = 0.10 per year; Point Lobos, F = 0.19 per year) and were inversely related to distance from port (see Figure 1 for distances).

Both modelled and observed recruitment magnitudes showed a general pattern of boom and bust years of recruitment that was echoed across the three regions and was close to zero leading up to and including 2007, the year the MPAs were implemented (Figure 2).

3.2 | Effects of pre-MPA harvest rates

The results of deterministic forward projections with no recruitment variability show the impact of pre-MPA harvest rates alone on population responses to MPAs. As predicted from White et al. (2013), the expected increase in blue rockfish density after MPA implementation was greater at sites with higher pre-MPA harvest rates (Figure 3a–c; dot-dashed lines). The saturating nature of the unharvested trajectories in Figure 3a–c reflects the filling-in of the previously harvested size distribution as unharvested cohorts reach larger sizes, eventually saturating at an equilibrium determined by the recruitment rate. The projected return to the unharvested size distribution occurred within 10–15 years at Point Lobos and White Rock. There was no discernible difference between projected harvested and unharvested populations at Big Creek because of the near-zero pre-MPA harvest rate in that region. However, none of these projections matched the observed patterns of density in post-2007 monitoring data (data points in Figure 3a–c), indicating that additional processes needed to be accounted for.
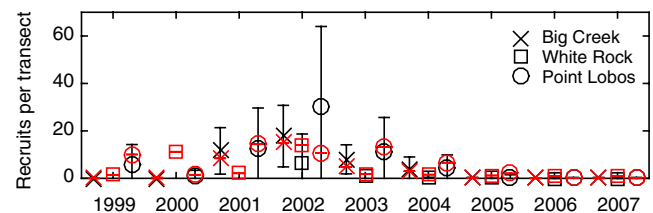

FIGURE 2 The number of blue rockfish recruits per transect at Big Creek (x), White Rock (□) and Point Lobos (O) from 1999 to 2007, leading up to implementation of the MPAs. Observed mean and standard deviation across all monitoring locations within each region (both inside and outside MPAs) are indicated with black symbols and error bars. Recruitment estimated from the state-space IPM are indicated with red symbols. Note that observed data for all three regions were not available until 2002, and that from 2005 to 2007 observation and modelled data overlap at zero for all sites. Recruits were counted as fish <10 cm
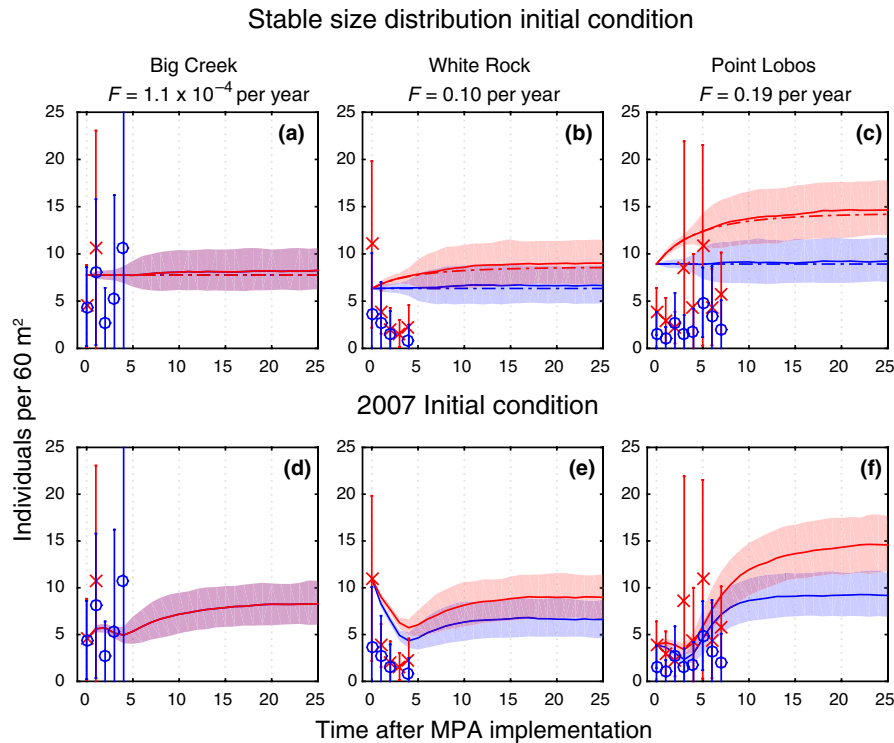
Stable size distribution initial condition

FIGURE 3 Forward projections of blue rockfish densities of fish greater than the fished size in the Big Creek (left), White Rock (middle), and Point Lobos (right) regions under scenarios with continued harvest at estimated pre-MPA harvest rates, *F*, (blue lines with shading) or as a no-take MPA (red lines with shading). The population densities in (a–c) start from equilibrium abundances of the stable size distribution with harvest. The population abundances in (d–f) start from densities observed in 2007, when MPAs were implemented. Dot-dashed lines in (a–c) indicate abundances with constant recruitment magnitude each year. Shaded areas indicate the envelope of outcomes from 5%–95% of all simulations with variable recruitment with the median of outcomes shown by the solid line. Note that dot-dashed and solid lines overlap. Markers indicate monitoring data from no-take MPA (red) and harvested (blue) sites, displayed as means with standard deviation computed for transects across zones within a location. For Big Creek (panels (a) and (d)), the red and blue lines and shading overlap. Note that we are addressing whether a harvested population would respond to MPA implementation as compared to a population where harvest persisted. We show data from a nearby site outside the MPA (blue markers) to show that predictions for continued harvest match those of a nearby harvested site

3.3 | Effects of variable recruitment and initial size structure

Recruitment variability, while not altering the mean population outcome across simulations, obscured differences between harvested and unharvested populations (overlap of blue and red shaded regions in Figure 3a–c). The amount of overlap was inversely related to pre-MPA harvest rates: at Point Lobos the trajectories eventually diverged, as opposed to White Rock and Big Creek. Still, the monitoring data did not match model projections (data points in Figure 3a–c).
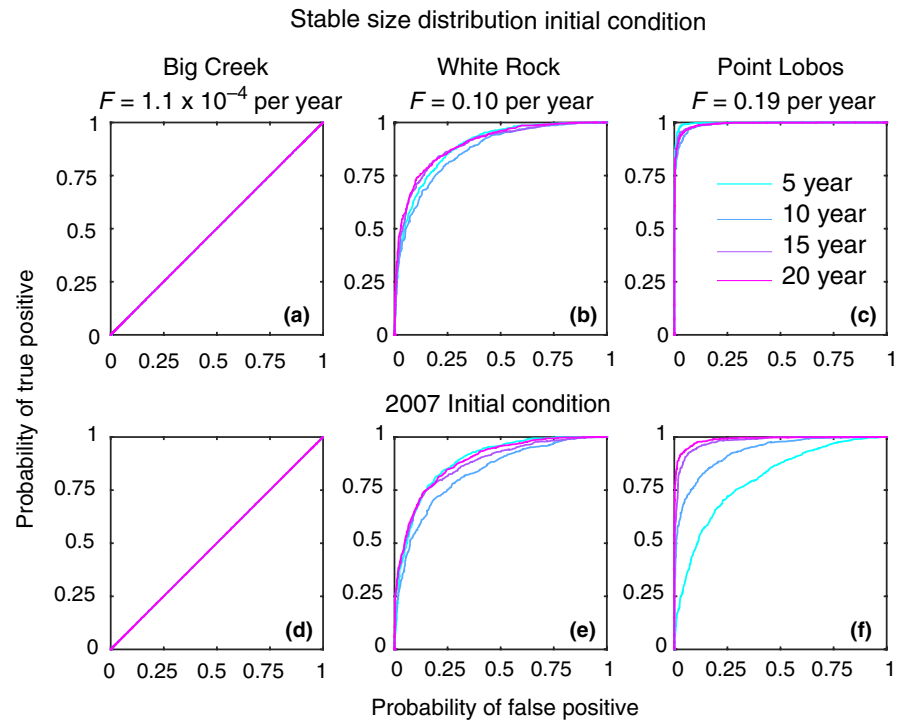
When simulations started with the observed 2007 size structure, forward projections with variable recruitment more closely resembled the monitoring data (Figure 3d–f). In these projections, the overlap in distributions of stochastic trajectories reduces the ability to detect a difference between unharvested populations and harvested populations for well over 15 years, if at all (Figure S3 provides density distributions for specific time points). At Big Creek where pre-MPA harvest was low, there was no expectation of increased

density (Figure 3d). For sites with detectable harvest before reserve establishment, simulations predicted initial decreases after MPA implementation (Figure 3e,f) due to the gap in size structure created by years of repeatedly low recruitment prior to implementation (Figure 2). The model over-predicted densities at White Rock, where observed recruitment continued to be close to zero through 2014, however the model captured the shape of the empirical trajectory in the monitoring data.

3.4 | Time-scale of response detectability

Correct detection of MPA effects is more likely with a higher pre-MPA harvest rate (Figure 4), and when the projection starts from a steady-state condition (Figure 4a–c). With low pre-MPA harvest rates, accounting for the actual initial conditions of the populations provides more realistic conditions, but only slightly changes the ROC detectability (Figure 4d,e). At Big Creek, with low pre-MPA harvest, we cannot ever expect to detect a difference in density between the harvested and MPA scenarios. At White Rock, the ROC curve

Stable size distribution initial condition

Big Creek
$F = 1.1 \times 10^{-4}$ per year

White Rock
$F = 0.10$ per year

Point Lobos
$F = 0.19$ per year

- 5 year
- 10 year
- 15 year
- 20 year

2007 Initial condition

Probability of true positive

Probability of false positive

converges on the same result obtained under assumed stable-state initial conditions, which indicates lower detectability than at Point Lobos where the harvest rate was highest. The ROC curve at White Rock does not improve, even 25 years after implementation. At Point Lobos, the ROC plots indicate steadily increasing detectability through time, however, departure from the stable-state greatly diminishes detectability (Figure 4f); high probabilities of correct detection (>80%) are only possible with high probabilities of false positives (>25%) until ≥15 years after implementation, when the ROC curve steepens.

4 | DISCUSSION

We found that spatial variability in harvest rate and temporal environmental stochasticity are crucial to accurately predicting expected responses to MPA establishment and therefore to adaptive management. Local pre-MPA harvest rates varied substantially across our study regions, and harvest rates were inversely related to proximity to fishing ports. Assuming uniform harvest rates across the Central California area would lead to erroneous predictions of responses to the cessation of harvest in the MPAs.

Accurate transient projections further require not only incorporating the complexity of variable future recruitment in this system, but also accounting for past variability that can cause departure from the steady state size distribution at the time of MPA implementation. The year the Central Coast MPAs were implemented corresponded with the end of a three-year period of exceptionally low recruitment across all regions (Figure 2; such patterns of high interannual recruitment variability is common for nearshore rockfish

species; Johnson, 2007; Caselle et al., 2010). These low recruitment years caused initial decreases in abundance after MPA implementation, as low recruitment years travelled through the size distribution and impacted future year's abundances. This echoes previous models demonstrating how perturbation from a stable size structure can lead to transient population decrease, even in populations that will increase in the long-term (Cohen, 1979; White et al., 2013). Given its effects on both the initial conditions and the spread of possible post-MPA trajectories, recruitment variability has the potential to double the predicted time-scale over which post-MPA population increases become detectable. Stochasticity likely plays a role in other locations around the globe where responses to MPAs have been variable and detectability of the response increases over time (Babcock et al., 2010; Russ & Alcala, 2004).

Setting expectations for adaptive management of MPAs implies consideration of the goals for which the MPA was established. California MPAs have a broad range of goals, such as "to protect the natural diversity and abundance of marine life" and "to help sustain, conserve and protect marine life populations" (CDFW, 2016). However, in California, as elsewhere, abundance serves as an initial proxy for the achievement of these broader goals (Whiteman et al., 2013). If the MPAs are not meeting expectations, the cause would be either ineffective management or inappropriate expectations. If the former, possible actions include increased enforcement, changes in MPA status (e.g. partial and no-take), and changes in MPA boundaries; if the latter, the relevant action is to update expectations based on improved scientific knowledge. Here, we show that simply expecting an increased abundance in the MPAs analysed can be a misleading expectation. Big Creek would not show an increase in abundance because its isolated location potentially made it a de facto MPA prior

to 2007 with little harvest. While it might at first seem counter-intuitive for a reserve to be placed in an area of no fishing, local fishing mortality rates were unknown during the reserve planning process, and many factors, ranging from socioeconomic costs to biodiversity goals, informed the siting process (Botsford et al., 2014). These results can help clarify which goals different MPAs might address; Big Creek may not help rebuild depleted marine populations, but it may serve to protect natural diversity and abundance (CDFW, 2016).

A wide array of MPA goals depend on the initial "filling in" response modelled here, but additional goals will also depend on dynamics ignored here in our focus on the most immediate and direct expected MPA response. MPA responses such as increased reproduction, spillover to harvested areas and subsequent effects on fishery yield, and cascading community-level changes will depend on further uncertain processes such as larval connectivity, fisher behaviour in terms of redistributed effort, movement of target species, and species interactions (Baskett & Barnett, 2015; White et al., 2011). Our findings of how the uncertain processes of local harvest mortality and recruitment variability significantly affect expectations demonstrate the potential challenges in creating expectations for longer-term and larger-scale responses as uncertainty propagates.

We developed a framework that can be used by managers to build expectations of responses of targeted species to MPA implementation, which includes producing robust estimates of pre-MPA fishing mortality rates, recruitment variability and size-structure, then using these estimates to build a size-structured demographic model to project population dynamics with and without MPA implementation. Such predictions will allow managers to develop expectations for how long it may take before a significant increase in population abundance and size is expected, and how big that increase might be. Key to this approach is the availability of long-term monitoring data. Our results show the value of before:after comparisons, especially in regards to stochastic events prior to implementation (Russ & Alcala, 2004). Ideally, a full before-after-control-impact (BACI) design can be used, increasing the ability to control for spatial and temporal heterogeneity (Halpern, Gaines, & Warner, 2004). Comparing observations from a BACI study to model outputs can validate hypothesized drivers of outcomes, such as whether stochastic population dynamics explain any observed non-monotonic trajectories, as is the case here. Indeed, even with a full BACI comparison, one would still need to know how pre-MPA harvest rates varied over space, both to ensure that "control" sites are representative and to estimate statistical power to detect before:after changes. When stock-recruit relationships are unknown, projections with competing models may be compared over time to the response. If a population is closed, trajectories might show even more intensified initial decreases than that reported here (White et al., 2013).

An important part of the adaptive management process is that as additional monitoring data are collected, managers can update projections with new information, adjust models and identify additional drivers of population responses that require consideration. The steps we describe here – predicting the initial post-implementation trajectory—are only the beginning of an ongoing adaptive management cycle. For example, new information on the actual levels of post-MPA recruitment could adjust projected trajectories, narrowing the range of uncertainty for ongoing assessment. Additionally, if appropriate information became available, site-specific growth and natural mortality rates could be incorporated (e.g. Hamilton, Wilson, Ben-Horin, & Caselle, 2011).

Projections may also help identify management gaps, such as lack of enforcement and poaching (Brown et al.., 2018), and can be used to explore how responses might change if MPAs are adjusted through adaptive management or as climate change impacts populations (e.g. if recruitment is reduced). In this example, we did not investigate the potential role of poaching, and assumed that the MPAs were well-enforced, but poaching would further decrease detectability. Using the framework we describe, managers could make projections that include poaching for comparison to monitoring data. In addition, for MPAs where harvest is allowed, projections could be run for different levels of harvest.

Evaluation of MPAs is a necessary step in ecosystem management, yet examples of adaptive management studies that incorporate monitoring data, let alone adequate data on the appropriate time scales for ascertaining responses to management, are lacking (Westgate et al., 2013). The combination of data and models provides an opportunity to investigate the mechanisms behind observed patterns (Hastings, 2016) and can advance the development of expectations and monitoring plans (Moffitt, White, & Botsford, 2013). Without such model predictions, monitoring can only inform a noise-sensitive "trial and error" approach to management that bases future choices on what is observed to work best, as opposed to a more proactive approach where managers can improve both management and scientific understanding based on gaps between predictions and reality (Walters & Hilborn, 1978; Walters & Holling, 1990). The integration of expectations into an adaptive management framework can help managers move from interpreting population responses after management actions to including predictions in MPA design and in the adaptive management policy itself (Schindler & Hilborn, 2015), thereby avoiding unforeseen costs of adjusting management actions (Morris & Green, 2014). The methods and framework we have developed here can be used to set expectations for MPA adaptive management, especially for systems where observational data are available but recruitment variability complicates the interpretation of patterns.

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AUTHORS' CONTRIBUTIONS

K.J.N., J.W.W., M.H.C., M.L.B., A.H. and L.W.B. designed research. D.M., R.M.S. and M.H.C. collected data. K.J.N. and J.W.W. analysed data and led the writing of the manuscript. All authors contributed to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and model code available from Zenodo http://doi.org/10.5281/zenodo.3267315 (Nickols et al 2019) All versions available from http://doi.org/10.5281/zenodo.595460.

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REFERENCES

Allen, C. R., Fontaine, J. J., Pope, K. L., & Garmestani, A. S. (2011). Adaptive management for a turbulent future. *Journal of Environmental Management*, *92*, 1339–1345. https://doi.org/10.1016/j.jenvman.2010.11.019

Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., ... Russ, G. R. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 18256–18261. https://doi.org/10.1073/pnas.0908012107

Baskett, M. L., & Barnett, L. A. K. (2015). The ecological and evolutionary consequences of marine reserves. *Annual Review of Ecology Evolution and Systematics*, *46*, 49–73. https://doi.org/10.1146/annurev-ecolsys-112414-054424

Blowes, S. A., & Connolly, S. R. (2012). Risk spreading, connectivity, and optimal reserve spacing. *Ecological Applications*, *22*, 311–321. https://doi.org/10.1890/11-0952.1

Boettiger, C., & Hastings, A. (2012). Quantifying limits to detection of early warning for critical transitions. *Journal of the Royal Society, Interface*, *9*, 2527–2539. https://doi.org/10.1098/rsif.2012.0125

Botsford, L. W., White, J. W., Carr, M. H., & Caselle, J. E. (2014). Marine protected area networks in California, USA. In *Marine managed areas and fisheries*, *advances in marine biology* (pp. 205–251). Elsevier.

Brown, C. J., Abdullah, S., & Mumby, P. J. (2014). Minimizing the short-term impacts of marine reserves on fisheries while meeting long-term goals for recovery. *Conservation Letters*, *8*, 180–189. https://doi.org/10.1111/conl.12124

Brown, C. J., Parker, P., Ahmadia, G. N., Ardiwijaya, R., Purwanto, & Game, E. T. (2018). The coast of enforcing a marine protected area to achieve ecological targets for the recovery of fish biomass. *Biological Conservation*, *227*, 259–265.

Byers, J. E., & Noonburg, E. G. (2007). Poaching, enforcement, and the efficacy of marine reserves. *Ecological Applications*, *17*, 1851–1856. https://doi.org/10.1890/07-0067.1

California Department of Fish and Wildlife (CDFW). (2016). California marine life protection act master plan for marine protected areas. Retrieved from https://www.wildlife.ca.gov/Conservation/Marine/MPAs/Master-Plan

Carr, M. H., Robinson, S. P., Wahle, C., Davis, G., Kroll, S., Murray, S., ... Williams, M. (2017). The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*, 6–29. https://doi.org/10.1002/aqc.2800

Carr, M. H., & Syms, C. (2006). Chapter 15: Recruitment. In L. G. Allen, D. J. Pondella, & M. H. Horn (Eds.), *The ecology of marine fishes: California and adjacent waters* (pp. 411–427). Berkeley: University of California Press.

Caselle, J. E., Wilson, J. R., Carr, M. H., Malone, D. P., & Wendt, D. E. (2010). Can we predict interannual and regional variation in delivery of pelagic juveniles to nearshore populations of rockfishes (genus *Sebastes*) using simple proxies of ocean conditions? *CalCOFI Report*, *51*, 91–105.

Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.-A., Pérez-Ruzafa, Á., ... Planes, S. (2008). Marine reserves: Size and age do matter. *Ecology Letters*, *11*, 481–489. https://doi.org/10.1111/j.1461-0248.2008.01166.x

Cohen, J. E. (1979). Distance from an observed to a stable age structure. *SIAM Journal on Applied Mathematics*, *36*, 169–175.

De Leo, G. A., & Micheli, F. (2015). The good, the bad and the ugly of marine reserves for fishery yields. *Philosophical Transactions of the Royal Society B*, *370*, 20140276.

Dorn, M. W. (2002). Advice on west coast rockfish harvest rates from Bayesian meta-analysis of stock-recruit relationships. *North American Journal of Fisheries Management*, *22*, 280–300. https://doi.org/10.1577/1548-8675(2002)022<0280:AOWCRH>2.0.CO;2

Edgar, G. J., & Barrett, N. S. (2012). An assessment of population responses of common inshore fishes and invertebrates following declaration of five Australian marine protected areas. *Environmental Conservation*, *39*, 271–281. https://doi.org/10.1017/S0376892912000185

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., ... Thomson, R. J. (2014). Global conservation outcomes depend on marine protected areas with five key features. *Nature*, *506*, 216–220. https://doi.org/10.1038/nature13022

Ellner, S. P., Childs, D. Z., & Rees, M. (2016). *Data-driven modelling of structured populations: A practical guide to the Integral Projection Model*. Switzerland: Springer.

Freiwald, J. (2012). Movement of adult temperate reef fishes off the west coast of North America. *Canadian Journal of Fisheries and Aquatic Science*, *69*, 1362–1374. https://doi.org/10.1139/f2012-068

Giakoumi, S., Scianna, C., Plass-Johnson, J., Micheli, F., Grorud-Colvert, K., Thiriet, P., ... Guidetti, P. (2017). Ecological effects of full and partial protection in the crowded Mediterranean Sea: A regional meta-analysis. *Scientific Reports*, *7*, 1–12. https://doi.org/10.1038/s41598-017-08850-w

Grafton, R. Q., & Kompas, T. (2005). Uncertainty and the active adaptive management of marine reserves. *Mar. Pol.*, *29*, 471–479. https://doi.org/10.1016/j.marpol.2004.07.006

Halpern, B. S., Gaines, S. D., & Warner, R. R. (2004). Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecological Applications*, *14*, 1248–1256. https://doi.org/10.1890/03-5136

Hamilton, S. L., Wilson, J. R., Ben-Horin, T., & Caselle, J. E. (2011). Utilizing spatial demographic and life history variation to optimize sustainable yield of a temperate sex-changing fish. *PLoS ONE*, *6*, e24580. https://doi.org/10.1371/journal.pone.0024580

Hanley, J. A., & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Diagnostic Radiology*, *143*, 29–36. https://doi.org/10.1148/radiology.143.1.7063747

Hastings, A. (2016). Timescales and the management of ecological systems. *Proceedings of the National Academy of Sciences of the United*

States of America, *113*, 14568–14573. https://doi.org/10.1073/pnas.1604974113

Hopf, J. K., Jones, G. P., Williamson, D. H., & Connolly, S. R. (2016). Fishery consequences of marine reserves: Short-term pain for longer-term gain. *Ecological Applications*, *26*, 818–829. https://doi.org/10.1890/15-0348

Johnson, D. W. (2007). Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish. *Ecology*, *88*, 1716–1725. https://doi.org/10.1890/06-0591.1

Key, M., MacCall, A. D., Field, J., Aseltine-Nelson, D., & Lynn, K. (2008). *The 2007 assessment of blue rockfish (Sebastes mystinus) in California*. Santa Cruz: California Department of Fish and Game.

Kimbro, D. L., White, J. W., & Grosholz, E. D. (2018). The dynamics of open populations: Integration of top-down, bottom-up, and supply-side influences on intertidal oysters. *Oikos*, *128*, 584–595. https://doi.org/10.1111/oik.05892

Laidig, T., Pearson, D., & Sinclair, L. (2003). Age and growth of blue rockfish (*Sebastes mystinus*) from central and northern California. *Fishery Bulletin*, *101*, 800–808.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., … Warner, R. R. (2009). Biological effects within no-take marine reserves: A global synthesis. *Marine Ecology Progress Series*, *384*, 33–46. https://doi.org/10.3354/meps08029

Love, M. S., Yoklavich, M., & Thorsteinson, L. (2002). *The rockfishes of the Northeast Pacific*. Berkeley: University of California Press.

Mangel, M. (2000). Irreducible uncertainties, sustainable fisheries and marine reserves. *Evolutionary Ecology Research*, *2*, 547–557.

Micheli, F., Halpern, B., Botsford, L. W., & Warner, R. (2004). Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications*, *14*, 1709–1723.

Moffitt, E. A., White, J. W., & Botsford, L. W. (2013). Accurate assessment of marine protected area success depends on metric and spatiotemporal scale of monitoring. *Marine Ecology Progress Series*, *489*, 17–28.

Molloy, P. P., McLean, I. B., & Cote, I. M. (2009). Effects of marine reserve age on fish populations: A global meta-analysis. *Journal of Applied Ecology*, *46*, 743–751.

Morris, C. J., & Green, J. M. (2014). MPA regulations should incorporate adaptive management—The case of Gilbert Bay Labrador Atlantic cod (Gadus morhua). *Mar. Pol.*, *49*, 20–28.

Nickols, K. J., White, J. W., Malone, D., Carr, M. H., Starr, R. M., Baskett, M. L., … Botsford, L. W. (2019). Data from: Setting ecological expectations for adaptive management of marine protected areas. *Zenodo* https://doi.org/10.5281/zenodo.3267315

Rist, L., Campbell, B. M., & Frost, P. (2013). Adaptive management: Where are we now? *Environmental Conservation*, *40*, 5–18.

Russ, G. R., & Alcala, A. C. (2004). Marine reserves: Long-term protection is required for full recovery of predatory fish populations. *Oecologia*, *138*, 622–627.

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., et al. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, *20*, 74–80.

Schindler, D. E., & Hilborn, R. (2015). Prediction, precaution, and policy under global change. *Science*, *347*, 953–954.

Starr, R. M., Carr, M., Malone, D., & Greenley, A. (2010). Complementary sampling methods to Inform ecosystem-based management of nearshore fisheries. *Marine and Coastal Fisheries*, *2*, 159–179.

Starr, R. M., Wendt, D. E., Barnes, C. L., Marks, C. I., Malone, D., Waltz, G., et al. (2015). Variation in responses of fishes across multiple reserves within a network of marine protected areas in temperate waters. *PLoS ONE*, *10*, e0118502–e118524.

Walters, C. J. (1986). *Adaptive management of renewable resources*. New York, NY: MacMillan Publishing Company.

Walters, C. J., & Hilborn, R. (1978). Ecological optimization and adaptive management. *Annual Review of Ecology, Evolution, and Systematics*, *9*, 157–188.

Walters, C. J., & Holling, C. S. (1990). Large-scale management experiments and learning by doing. *Ecology*, *71*, 2060–2068.

Watson, J. E. M., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, *515*, 67–73.

Westgate, M. J., Likens, G. E., & Lindenmayer, D. B. (2013). Adaptive management of biological systems: A review. *Biological Conservation*, *158*, 128–139. https://doi.org/10.1016/j.biocon.2012.08.016

White, J. W., Botsford, L. W., Baskett, M. L., Barnett, L. A. K., Barr, R. J., & Hastings, A. (2011). Linking models with monitoring data for assessing performance of no-take marine reserves. *Frontiers in Ecology and the Environment*, *9*, 390–399. https://doi.org/10.1890/100138

White, J. W., Botsford, L. W., Hastings, A., Baskett, M. L., Kaplan, D. M., & Barnett, L. A. K. (2013). Transient responses of fished populations to marine reserve establishment. *Conservation Letters*, *6*, 180–191. https://doi.org/10.1111/j.1755-263X.2012.00295.x

White, J. W., Botsford, L. W., Moffitt, E. A., & Fischer, D. T. (2010). A decision-analysis approach to MPA network assessment under uncertainty regarding fishery status of multiple species. *Ecological Applications*, *20*, 1523–1541.

White, J. W., Nickols, K. J., Malone, D., Carr, M. H., Starr, R. M., Cordoleani, F., … Botsford, L. W. (2016). Fitting state-space integral projection models to size-structured time series data to estimate unknown parameters. *Ecological Applications*, *26*, 2677–2694. https://doi.org/10.1002/eap.1398

White, W. (2016). IPM_statespace: State-space IPM – White et al. 2016 (Version v1.0). *Zenodo*. https://doi.org/10.5281/zenodo.595460

Whiteman, L., Meyer, E., Freidenburg, T., Rindge, H., Meyer, R., Pribyl, A., et al. (2013). *State of the California Central Coast: Results from baseline monitoring of marine protected areas 2007–2012*. California, USA: California Ocean Science Trust and California Department of Fish and Wildlife.

Wilson, R. S., Hardisty, D. J., Epanchin-Niell, R. S., Runge, M. C., Cottingham, K. L., Urban, D. L., … Peters, D. P. C. (2016). A typology of time-scale mismatches and behavioral interventions to diagnose and solve conservation problems. *Conservation Biology*, *30*, 42–49. https://doi.org/10.1111/cobi.12632

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