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Integrating Marine Reserves into Data-poor Fisheries Management:
Challenges and Opportunities

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Environmental Science and Management

by

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December 2017

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Dec 2017

Integrating Marine Reserves into Data-poor Fisheries Management:
Challenges and Opportunities

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by

Sarah R. Valencia

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- Selden, RL, Valencia, SR, Cornejo-Donoso, J, TE, Larsen, AE., Wasserman, A.A. (2016) How sustainable are MSC-certified fisheries? *Marine Policy* 64: 102-115.
- Hordyk, A, Ono, K, Valencia, SR, Loneragan, N and Prince, JD. (2014) A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES Journal of Marine Science* 72(1): 217-231.
- Prince, JD, Hordyk, A, Valencia, SR, Loneragan, N, Sainsbury, K. (2014) Revisiting the concept of Beverton-Holt Life History Invariants with the aim of informing data-poor fisheries assessments. *ICES Journal of Marine Science* 72(1): 194-203.
- Wilson, JR, Valencia SR, Kay MC, & Lenihan HS. 2013. Integration of no-take marine reserves in the assessment of data-limited fisheries. *Conservation Letters*.
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ABSTRACT

Integrating Marine Reserves into Data-poor Fisheries Management: Challenges and Opportunities

by

Sarah R. Valencia

Recent studies have demonstrated that data from marine reserves can benefit fisheries management. Marine reserves may improve assessments by acting as a reference area when protected populations approach unfished conditions. This forms the theoretical basis for the recent development of assessment techniques that utilize data from inside marine reserves to assess fished populations out of reserves, and that better inform the selection of management control rules.

In this dissertation I examine how no-take marine reserves impact our ability to assess the status of data-poor fisheries. In my second chapter I review the evolution in scientific thinking on how reserves have been integrated into fisheries management, and describe the emerging research on how reserves may be used as reference areas for the assessment and management of fish stocks. I also examine how the characteristics of marine reserves designed for use as reference areas compare with those used to meet the more

traditional goals of conservation or fishery enhancement, and suggest some avenues of future research in this vein.

In my third chapter, I demonstrate how a recently developed data-poor stock assessment method, the Length-based Spawning Potential Ratio estimator relies heavily on correctly assuming biological parameters such as growth and natural mortality, and show how this method can be extended to include information from MPAs to estimate these parameters when this biological information is unavailable.

In my fourth chapter, I compare the performance of a suite of MPA-based data-poor methods, both in the short and long term under a range of different kinds of uncertainty. The results indicate that all assessment methods are sensitive to the time since MPA creation, historical fishing pressure, and movement, but that the methods that rely on length data are more robust to these conditions than those that rely on CPUE data. When paired with a control rule, all of the assessment methods performed reasonably well, suggesting that MPA-based assessment techniques may provide a viable option for the management of sedentary data-poor stocks.

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I. General Introduction

Fisheries science ultimately revolves around two questions: How many fish are in the ocean, and how many can we sustainably remove? In pursuit of the answers, fishery scientists have devised increasingly complex statistical models to better capture ecological systems (Cochrane 1999, Hilborn 2003). These models were primarily designed to address industrial scale fisheries, and rely on time series of catch and effort data collected both directly from the fishery and from independent survey programs. Yet up to 90% of the world's fisheries remain unassessed, and many are artisanal or small-scale in size, thus making the application of large-scale fishery strategies unrealistic (FAO 2012).

There are myriad obstacles to using traditional assessment approaches for small scale, data-deficient fisheries. Historical data required for conventional assessments are lacking in most small-scale fisheries. Furthermore, small-scale fisheries are also low-value, precluding the implementation of expensive data collection programs. Some fisheries violate the assumptions of homogeneity made by conventional stock assessments due to their multi-gear, multi-species, or spatially structured dynamics (Mahon 1997). Without necessary data there is no way to measure the impact of fishing on fish populations or set sustainable targets and limits for these data-poor fisheries.

Managers have historically taken two courses of action in dealing with fisheries that are incompatible with application of conventional stock assessments. First they have drastically reduced catches to a fraction of historically stable levels (Restrepo and Powers 1999). Although this may promote recovery in overfished stocks, there are generally socio-economic costs to these reductions due to lost catch and revenue. The second option has been to create no-take marine reserves as insurance against management failures caused by insufficient data (Lauck et al. 1998, Holland 2002, Roberts et al. 2005). Marine reserves represent an appealing option for managers because they are simple, straightforward to enforce, and can have both conservation and fisheries benefits (Guénette et al. 1998, Hastings 1999, Gerber et al. 2003). In response, more than 6,000 marine reserves, covering an estimated 3.27% of ocean waters, have been implemented around the world (Boonzaier and Pauly 2015).

Empirical studies have shown that both the abundance and biomass of fish increases within marine reserves (Halpern and Warner 2002, Halpern 2003, Lester et al. 2009), and spillover from marine reserves has been detected in catches of some fisheries (Goñi et al. 2006, 2010). However, marine reserves provide limited protection for highly mobile species, and do not protect fish in areas open to fishing (Walters et al. 2007), and thus must be paired with fisheries management measures outside of reserves (Hilborn et al. 2004). The shift towards spatial management via the creation of reserves complicates stock assessments because traditional stock assessment methods assume a homogeneously distributed population (Punt and Methot 2004). This dissertation explores these questions to provide

insights into the conditions under which reserves may provide otherwise unavailable information for use in assessing data-poor stocks.

This research relies on simulation modeling using a Management Strategy Evaluation (MSE) framework (Smith 1994, Lane and Stephenson 1998, Butterworth 2007, Butterworth et al. 2010). MSE is a simulation technique that models the entire adaptive management process. The framework consists of a) an operating model, which simulates the underlying biological and economic characteristics of the fishery and generates data from that fishery based on a sampling protocol, and b) a management model, composed of an assessment model to analyze the generated data and a control rule to set harvest or effort levels based on the assessment results. The procedure uses Monte Carlo simulation to explore tradeoffs between alternative management strategies under various uncertainties through time. First, I examine the accuracy of each assessment method to understand the ability of the reserve to act as a reference area under different conditions in Chapter 4. I then evaluate the ability of management strategies that include the tested assessment methods to a) maximize yield, b) maximize stability for the fishing industry, and c) achieve a target biomass while avoiding limit reference points over a 20-year period. This analysis provides insight into the value of optimized control rules, which can help to achieve management objectives even when the assessment method itself is inaccurate.

The use of marine reserves as a source of information for the assessment and management of small-scale or data-poor fisheries is an area in need of further research, as MPAs have important implications for small-scale fisheries management. This work

represents the first direct comparison of the ability of MPA-based assessment methods to achieve management objectives. By some accounts, these “small-scale” fisheries land half of the world’s catch and employ more than 90% of the world’s 35 million fishermen (FAO 2012). Given their characteristics it is unlikely that conventional assessments will ever be a viable option. With the projected human population increases over the next 100 years, these fisheries are likely to face even more pressure to meet seafood demand in developed countries and food security needs in developing ones (Smith et al. 2010). The development of effective monitoring and assessment methods for these fisheries remains one of the major challenges confronting fisheries management today (FAO 2012).

References

- Babcock, E.A., and MacCall, A.D. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? *Can J Fish and Aquat Sci* 68(2): 343–359.
- Bohnsack, J.A. 1999. Incorporating no-take marine reserves into precautionary management and stock assessment. In *Providing Scientific Advice to Implement Precautionary Approach Under the Magnuson-Stevens Fishery Conservation and Management Act*. NOAA Tech. Memorandum NMFS-F/SPO-40.
- Boonzaier, L., & Pauly, D. 2016. Marine protection targets: An updated assessment of global progress. *Oryx*, 50(1): 27-35.
- Butterworth, D.S. 2007. Why a management procedure approach? Some positives and negatives. *ICES J Mar Sci* 64(4): 613–617.
- Butterworth, D.S., Johnston, S.J., and Brandão, A. 2010. Pretesting the Likely Efficacy of Suggested Management Approaches to Data-Poor Fisheries. *Mar Coast Fish* 2(1): 131–145.
- Cochrane, K. 1999. Complexity in fisheries and limitations in the increasing complexity of fisheries management. *ICES J Mar Sci* 56(6): 917–926.
- FAO. 2012. *The State of World Fisheries and Aquaculture 2012*. In FAO Fisheries and Aquaculture Department. Food and Agriculture Organization of the United Nations, Rome. Available from <http://www.fao.org/docrep/016/i2727e/i2727e.pdf>.
- Gaines, S.D., Lester, S.E., Grorud-Colvert, K., Costello, C., and Pollnac, R. 2010. Evolving science of marine reserves: New developments and emerging research frontiers. *PNAS* 107(43): 18251–18255.
- Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., and Andelman, S. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol Appl* 13(1): 47–64.
- Goñi, R., Hilborn, R., Díaz, D., Mallol, S., and Adlerstein, S. 2010. Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Prog Ser* 400: 233–243.
- Goñi, R., Quetglas, A., and Renones, O. 2006. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar Ecol Prog Ser* 308: 207–219.
- Guénette, S., Lauck, T., and Clark, C. 1998. Marine reserves: from Beverton and Holt to the present. *Rev Fish Biol Fisher* 8(3): 251–272.
- Halpern, B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol Appl* 13(1): 117–137.

- Halpern, B.S., and Warner, R.R. 2002. Marine reserves have rapid and lasting effects. *Ecol Lett* 5(3): 361–366.
- Hastings, A. 1999. Equivalence in Yield from Marine Reserves and Traditional Fisheries Management. *Science* 284(5419): 1537–1538.
- Hilborn, R. 2003. The state of the art in stock assessment: Where we are and where we are going. *Sci Mar* 67(S1): 15–20.
- Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K.L., Garcia, S., Hall, S.J., Kirkwood, G.P., Sainsbury, K., Stefansson, G., and Walters, C. 2004. When can marine reserves improve fisheries management? *Ocean Coast Manage* 47(3-4): 197–205.
- Holland, D.S. 2002. Integrating marine protected areas into models for fishery assessment and management. *Nat Resour Model* 15(3): 369–386.
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., and Prince, J. 2015. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES J Mar Sci* 72(1): 217–231.
- Lane, D.E., and Stephenson, R.L. 1998. A framework for risk analysis in fisheries decision-making. *ICES J Mar Sci* 55(1): 1–13.
- Lauck, T., Clark, C.W., Mangel, M., and Munro, G.R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecol Appl* 8(1): S72–S78.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., and Warner, R.R. 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 384: 33–46.
- Mahon, R. 1997. Does fisheries science serve the needs of managers of small stocks in developing countries. *J Fish Res Board Can* 54(9): 2207–2213.
- McGilliard, C.R., Hilborn, R., MacCall, A., Punt, A.E., and Field, J.C. 2011. Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks? *ICES J Mar Sci* 68: 201–211.
- Punt, A.E., and Methot, R.D. 2004. Effects of marine protected areas on the assessment of marine fisheries. *American Fisheries Society Symposium* 42: 133–154.
- Restrepo, V.R., and Powers, J.E. 1999. Precautionary control rules in US fisheries management: specification and performance. *ICES J Mar Sci* 56(6): 846–852.
- Roberts, C.M., Hawkins, J.P., and Gell, F.R. 2005. The role of marine reserves in achieving sustainable fisheries. *Philos T R Soc B* 360(1453): 123–132.

- Smith, A. 1994. Management strategy evaluation: the light on the hill. In Population dynamics for fisheries management. Edited by D.A. Hancock. Australian Society for Fish Biology Workshop Proceedings, Perth, 24-25 August 1993, Perth. pp. 249–253.
- Smith, M.D., Roheim, C.A., Crowder, L.B., Halpern, B.S., Turnipseed, M., Anderson, J.L., Asche, F., Bourillon, L., Guttormsen, A.G., Khan, A., Liguori, L.A., McNevin, A., O'Connor, M.I., Squires, D., Tyedmers, P., Brownstein, C., Carden, K., Klinger, D.H., Sagarin, R., and Selkoe, K.A. 2010. Sustainability and Global Seafood. *Science* 327(5967): 784–786.
- Walters, C.J., Hilborn, R., and Parrish, R. 2007. An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. *J Fish Res Board Can* 64(7): 1009–1018.
- Wilson, J.R., Prince, J.D., and Lenihan, H.S. 2010. A Management Strategy for Sedentary Nearshore Species that Uses Marine Protected Areas as a Reference. *Mar Coast Fish* 2(1): 14–27.
- Wilson, J.R., Valencia, S.R., Kay, M.C., and Lenihan, H.S. 2013. Integration of no-take marine reserves in the assessment of data-limited fisheries. *Conserv Lett* 7: 451–458.

II. Integrating Marine Protected Areas into Fisheries Management: A new perspective

Abstract

Marine Protected Areas (MPA) can benefit fisheries, but also present a number of challenges for traditional fisheries management approaches. Here I review the theoretical benefits of MPAs to fisheries management and examine the empirical literature to assess when and under what conditions those benefits have materialized. I also discuss the challenges MPAs present to stock assessments and the emerging science surrounding the use of MPAs as reference areas in the assessment and management of fish stocks.

Recently MPAs have been suggested as a source of new information, which may prove useful in the assessment of the status of nearby fished stocks, especially in areas where conventional stock assessment methods are impossible due to a lack of historical data or high spatial heterogeneity in key stock metrics. Early research on this incipient topic indicates that the conditions that make MPAs most successful at meeting conservation goals may also make the best reference areas, suggesting that there may be less conflict than previously assumed associated with attempting to site MPAs to meet both conservation and fishery goals.

1. Introduction

The world's oceans face many threats, including loss of biodiversity, overfishing, habitat destruction, and climate change. While the threats are varied in nature, they are unified in their anthropogenic source. In response, there have been increased calls over the last three decades to create spaces in the ocean where human impacts are limited or removed to the extent possible. This movement has resulted in the establishment of >5,000 marine protected areas (MPAs) globally, many of them in connected networks of multiple reserves.

MPAs are usually created with two specific objectives: (1) biodiversity and habitat protection, either for conservation benefit or for recreational enjoyment, and (2) sustainable fisheries management (Gaines et al. 2010a). However, the conditions that enhance the capacity for an MPA to contribute to sustainable fisheries may cripple its capacity for meeting conservation objectives (Hastings and Botsford 2003, Edgar et al. 2014). This inherent tradeoff between meeting conservation and extractive goals has been a persistent challenge to designing effective MPAs and measuring their performance (Gaines et al. 2010b).

There is an extensive literature on the potential and realized benefits of MPAs to nearby fisheries. Early studies were based mostly on simulation models due to the lack of existing MPAs (see (Guénette et al. 1998) for a comprehensive review). Models predicted two main benefits of MPAs on nearby fisheries. First, as with any management strategy that increases the number of older fish in the population, MPAs can increase egg

production. Second, higher densities of fish accumulating within MPAs may increase competition for scarce resources, forcing fish to emigrate from the MPA and subsequently increasing catches for nearby fishermen. Empirical evidence of fishery enhancement by MPAs is equivocal (Hilborn et al. 2004b), and in areas where there has been enhancement (Murawski et al. 2005, Goñi et al. 2006) the underlying causal mechanisms are often poorly understood and unpredictable.

The use of MPAs as a fisheries management tool has been controversial despite potential benefits. The creation of MPAs has often resulted in less, rather than more, yield for fishermen in the short term (Hilborn et al. 2004a, Guenther 2010). Additionally, MPAs change the distribution of fishing effort (Murawski et al. 2005) and may condense fishing effort into a smaller area, causing crowding and increasing the race to fish (Greenstreet et al. 2009). MPAs may not protect against localized depletion outside their borders, and are likely to be ineffective at helping fisheries meet socio-economic goals.

A growing consensus indicates that MPAs alone are unable to solve the major problems confronting fisheries around the world (Hilborn et al. 2004b). Instead, some suggest that MPAs be integrated as part of existing management frameworks (Agardy et al. 2011, Mesnildrey et al. 2013). This presents a unique set of challenges to fisheries scientists and managers because the creation of MPAs complicates conventional stock assessment methods by decreasing the fishery-dependent data available for assessment models while also increasing spatial heterogeneity in stocks (Bohnsack 1999, Punt and Methot 2004, Field et al. 2006). By contrast, MPAs present new opportunities for

fisheries management by acting as reference areas and sources of biological information (Bohnsack 1999, Garrison et al. 2011). This provides a realistic and practical way that MPAs may benefit nearby fisheries, especially in areas where traditional reference data such as historical time series are lacking.

Research on the use of MPAs as sources of information for stock assessments and management decisions of nearby fisheries is incipient but the emerging science suggests a paradigm shift in the scientific community's thinking on how MPAs can benefit nearby fisheries. Here I summarize how the science on the integration of MPAs into fisheries management has evolved over the past three decades. There is a need to understand what design characteristics are necessary for MPAs to function effectively as sources of information for stock assessments if MPAs are to be used effectively in assessment and management of fish stocks. This review highlights what is currently known about designing MPAs for use as reference areas, and suggests avenues of future research on this topic.

2. The early years: Using MPAs to fuel nearby fisheries

The idea of closing areas to fishing as a means of fueling fishing grounds was first proposed in 1912, to little effect (Roberts 2012). Beverton and Holt (1957) explored spatial closures as a potential fishing mortality control using an equilibrium yield-per-recruit model, but found that closed areas only resulted in increased yields when the fishing mortality was very high. Due to the high cost of information necessary to properly site closed areas, Beverton and Holt favored other controls such as effort and gear restrictions for the management of fisheries (Beverton and Holt 1957). As our

understanding of the environmental and ecosystem impacts of fishing increased, however, there has been greater focus on how and when MPAs might be used as a management tool to mitigate these impacts.

Much of the early literature on the benefits of MPAs to nearby fisheries relied on evaluations of simulated MPAs. These models predicted that the elimination of fishing mortality in an area would lead to higher abundances and older, larger fish (Polacheck 1990, DeMartini 1993, Quinn et al. 1993, Attwood and Bennett 1995), which had the potential to boost yields in nearby areas through both density-dependent spillover of adults and the export of larvae (Russ 2002). These predictions helped to fuel the widespread adoption of MPAs as a spatial management tool in coastal areas.

The effects of removing fishing from an area can take many years to accumulate, and the majority of MPAs have been implemented within the last 15 years. Despite this, some rapid responses have been observed (Halpern and Warner 2002, Gell and Roberts 2003). Empirical studies have examined biomass changes within MPAs, mainly through increases in the size and/or density of fish, and assessed the effects through comparisons to a) reference areas outside MPAs, b) data collected prior to MPA implementation, or c) both, in a Before-After-Control-Impact (BACI) design (Alcala 1988, Attwood and Bennett 1995, Francini-Filho and Moura 2008, Kay et al. 2012). Studies using meta-analyses have found that the elimination of fishing in MPAs results in increased biomass, density, species richness, and size of some organisms within MPA borders, although

there has been considerable variation in responses across sites and taxonomic groups (Halpern 2003, Lester et al. 2009, Claudet et al. 2010).

These studies clearly demonstrate that removing fishing mortality results in more and/or larger fish. It has been much more difficult to ascertain whether higher biomasses inside MPAs translates to fisheries benefits outside their borders (Badalamenti et al. 2000, Willis et al. 2003). In this section I summarize the theory underpinning the three direct methods by which MPAs can benefit fisheries, and the empirical evidence for each.

2.1 Increased catches via spillover

Spillover of adult fish occurs when a population of fish protected in an MPA grows large enough to cause emigration to surrounding fished areas as fish compete for limited resources. Spillover is most likely when the rate of emigration from the MPA is low, but constant or occurs in pulses, such that the MPA provides some refuge from fishing but a certain proportion of the population exits the MPA. This may happen when a species exhibits home range behavior (Moffitt et al. 2009), or when high densities inside the MPA increase competition for scarce resources, causing some individuals to leave the MPA in search of food or shelter. Gell and Roberts (2003) reviewed a number of studies demonstrating dramatic increases in abundance within MPAs. There has been less evidence that these rapid biomass increases result in higher catches in nearby fisheries, but a few empirical studies have documented larger fish or higher catch rates (McClanahan and Mangi 2000, Roberts 2001, Murawski et al. 2005, Goñi et al. 2006). In one review, spillover was detected in 12 of the 14 studies included in the review, but primarily at distances less than 1km from the MPA border, suggesting that when spillover

does occur its effects are highly localized (Halpern et al. 2010). Spillover of most demersal or benthic species requires benthic habitat corridors extending from inside the MPAs to fished areas (Kay and Wilson 2012). Additionally, the ability of spillover to increase yields may be undermined by a density-dependent somatic growth reduction of fish within MPA borders (Gårdmark et al. 2005).

2.2 Increased productivity via larval export

The second way that MPAs can contribute directly to fisheries yields is through increased spawning biomass. Protection from fishing results in higher abundances and/or sizes of fish, which in turn results in higher egg production (Hastings 1999). The maintenance of unfished size and age structures in fish populations may also boost fecundity and subsequent recruitment because older, larger females can produce larvae that are more robust to starvation, increasing the probability of successful settlement in some species (Berkeley et al. 2004). In fact, some studies have predicted that the increased larval production may offset reductions in yields from MPA creation (Halpern et al. 2004). Modeled predictions indicate that fishery yields and profits are highest when MPAs are configured to maximize larval export to fished areas. This occurs when multiple, interconnected MPAs are as small as is practically possible to maximize the ratio of MPA borders to the area protected (Hastings and Botsford 2003), and assumes that local retention of larvae is sufficient to maintain MPA populations (Berumen et al. 2012) while still allowing for transport to other areas (Warner and Swearer 2000).

The models used in these studies assumed sedentary adults, post-dispersal density dependence, and a dispersal probability that was mediated by the distance from the release site. These simplifying assumptions have important implications for the results of these studies. If the species managed is sessile rather than sedentary, there will be no spillover across the MPA boundary, but highly mobile species will move outside the closed area and be exposed to fishing mortality. Also, larval dispersal patterns must transport larvae to areas where recruitment is less than the maximum possible, and prior to any density-dependent effects that might negate the benefits within the closed areas (Parrish 1998). Thus, marine reserves can increase yields only in fisheries in which fishing has reduced recruitment, and if the above conditions are met [14–17].

A large number of theoretical studies have predicted the conditions necessary for larval export from MPAs to enhance nearby fished populations. but empirical evidence of this phenomenon is limited, in part because the parentage of a fish recruiting to the fishery is difficult to establish (Bohnsack 1999). Additionally, the proportional increase in recruitment at each individual site outside an MPA is typically small, particularly for species with long larval dispersal distances, making it very difficult to detect in field studies (Pelc et al. 2010). Halpern and Warner (2003) attributed the lack of empirical evidence to a dearth of MPAs of sufficient size to see measurable results, but pointed to increases in scallop yields near the Georges Bank trawl closures as evidence of a fishery buoyed by larval export.

Most studies have examined the potential larval contributions of MPAs to nearby fisheries using a combination of age or size-based egg-per-recruit models and larval transport models (Tetreault and Ambrose 2007). Pelc et al. (2010) summarized studies of sessile, broadcast-spawning invertebrates from eight sites where recruitment increased or where gradients were observed near MPA borders, suggesting larval export from these MPAs. Additionally, Harrison et al. (2012) used spatially-specific genetic markers to assign juvenile fish as having been spawned within specific MPAs, and found that up to half of recruits in a fished area originated from a MPA covering 28% of the total habitat. Of course, reserves tend to be strategically placed to protect areas that are perceived to be valuable, often because they provide habitat for a wide variety of fish and invertebrate species, and it is possible that this higher than expected productivity was a feature of this area prior to the establishment of the reserve. Without a study that measured pre-MPA productivity, it is unknown whether the observed effect was due entirely to the closure.

2.3 Reduced fishing mortality

Spatial closures, whether temporary or permanent, have long been recognized as a mechanism to reduce overall fishing mortality (Beverton and Holt 1957). Spatial closures are functionally similar to raising the age at first capture or reducing effort (Botsford et al. 2003), although they may provide additional benefits over more traditional methods because they can prevent incidental habitat damage or the take of vulnerable bycatch species if strategically placed. The capacity for MPAs to reduce the effective fishing mortality depends on the mobility of the target stock as well as the placement of the MPA relative to the location of fishing effort. In fish stocks that are migratory or have large

home ranges relative to the MPA, but are targeted by spatially-distributed fishing effort, a strategically-placed MPA can provide a refuge from fishing for a portion of the fish's life history, which reduces mortality, enhances reproductive potential, or conserves the population through positive influence on another demographic process. However, if fishing effort is concentrated into a small space, even a large MPA will not reduce fishery mortality if it is not placed where the majority of catches occur. MPAs are generally assumed to effectively reduce the fishing effort on sedentary stocks, but may actually increase mortality outside of the MPA due to the concentration of existing fishing effort into the remaining space (Guenther 2010).

Large spatial closures have been used on both the east and west coasts of the U.S. to reduce the fishing mortality rate on valuable species and promote stock rebuilding (Holland 2000, Murawski et al. 2000, Field et al. 2006). MPAs may be a promising means of controlling fishing mortality in developing countries that lack the management structures necessary to enforce gear or effort restrictions. In fisheries with many landing sites spread out over a long coastline, one or more no-take zones are easier to enforce than conventional gear, effort, or catch restrictions. It has been suggested that even blue-water pelagic habitats can benefit from protection from fishing when placed in strategic areas to target areas of high biodiversity (such as seamounts) or demographic importance (such as spawning grounds; Norse et al. 2005). However, open ocean MPAs are unlikely to see the biomass accumulation normally associated with a successful MPA.

3. The indirect benefits of MPAs on fisheries

MPAs were gradually implemented in larger numbers during the late 1990s and early 2000s. During this time, scientists considered how MPAs, both individually and in networks, functioned as part of holistic marine systems (Bohnsack 1999, Gell and Roberts 2003, Bohnsack et al. 2004). Much of the literature in this vein examined the auxiliary benefits MPAs have on fisheries via the preservation of ecosystem function. This section summarizes these benefits.

3.1 Insurance against management failures

MPAs can provide a buffer against management miscalculations (Allison et al. 1998, Lauck et al. 1998). Because estimates of sustainable catch limits are based on predictions about the average productivity of a stock, there is always the potential to set limits too high during periods of environmental stress, which can reduce recruitment success or increase natural mortality (Roberts et al. 2005). In such cases, protected populations could potentially serve as recovery centers if they provide spillover. MPAs may also dampen variability in recruitment from year to year by keeping spawning biomass at higher levels, increasing population resilience to overfishing and buffering against decreases in reproductive success or increases in mortality (Gu nette et al. 1998). Theoretical studies suggest MPAs may also reduce year-to-year variation in catch size, an important economic benefit for fishing communities (Sladek Nowlis and Roberts 1999). Therefore MPAs offer a way for managers to be precautionary, especially in fisheries with little or no data available (Bohnsack 1999).

3.2 Protection of natural size and age structures

MPAs provide benefits that other types of conventional management such as catch limits or gear modifications do not, such as protecting the natural age structure of the stock (Bohnsack 1999, Roberts et al. 2005). Conventional management tends to require gear modifications that make fishing more, rather than less, selective because fishing mortality is focused intensively on specific age or size classes (frequently the largest fish, though not always (Reddy et al. 2013)). While successful gear modifications direct fishing towards mature rather than immature age classes, recent work has shown that highly selective fishing can have detrimental ecological impacts (Zhou et al. 2010, Rochet et al. 2011, Garcia et al. 2012, Worm and Lenihan 2014). Large or old female fish, such as those found in MPAs, may produce far more and often larger eggs than smaller mature females, and their larvae grow faster and appear better able to withstand starvation (Berkeley et al. 2004, Hixon et al. 2014). Evidence also suggests that a truncation in the size structure of a stock can decrease stability in population dynamics due to demographic changes (Berkeley et al. 2004, Hsieh et al. 2010). MPAs can provide protection against these impacts by extending the age structure of the protected portion of the stock to unfished levels.

3.3 Preserving genetic variation

Protecting natural age structures may also preserve genetic variation in fish stocks in addition to boosting the egg production of a population (Bohnsack 1999). A number of studies have documented the effects of intensive fishing on the selection of specific heritable traits in the population (Ricker 1981, Quinn and Adams 1996, Drake et al.

1997). In particular, size-selective fishing can select for faster growth rates, younger age at first maturity, smaller maximum sizes, and behavioral changes (Worm and Lenihan 2014). Over multiple generations of intensive fishing the alleles associated with other traits may be lost from the population. MPAs can help maintain the genetic diversity of a stock by providing refuges from fishing.

4. MPAs and integrated management systems: The challenges of implementation

Early studies lauded the benefits of MPAs to fisheries (Roberts and Polunin 1993), but by the mid-2000s there were calls for caution in applying MPAs as a panacea for the perceived failures of fisheries management (Sainsbury and Sumaila 2003, Willis et al. 2003, Hilborn et al. 2004b, Kaiser 2005). Multiple studies had shown that the ability of MPAs to benefit fisheries required 1) the presence of specific habitat and life history characteristics, 2) the source-sink dynamics between closed and open areas, and 3) properly siting MPAs to take advantage of these conditions, all of which were difficult to know with any certainty. In addition, MPAs that met all of these characteristics could provide little assistance in meeting the socio-economic goals of fisheries management (Smith and Wilen 2003).

There was an increased examination of the merits of MPAs within the context of existing fisheries management. For example, Hilborn et al. (2006) used a modeled MPA to demonstrate that the implementation of a MPA in a fishery already regulated by a catch limit required a reduction in the catch limit to avoid overexploitation of the resource outside the MPA borders, and McGilliard et al. (2008) extended this analysis to include the effects of larval dispersal distance. Botsford et al. (2009) expanded the theory

of MPAs to include not only movement of fish and larvae between areas but fishermen as well (Botsford et al. 2009). These studies considered MPAs as one potential action available in the fisheries management toolbox.

These papers marked a shift toward viewing MPAs as part of integrated fishery management systems (Agardy et al. 2003). The addition of MPAs to seascapes with existing regulatory procedures for fisheries management, however, highlighted the many challenges scientists faced when tasked when creating these integrated approaches. The next section provides an overview of the ways in which the addition of no take MPAs to seascapes has complicated existing fisheries management systems.

4.1 Reduction in fishery-dependent data available to stock assessments

Stock assessments have traditionally relied heavily on fishery-dependent data, which are collected directly from fishing activities. Fishery-independent data streams are also frequently incorporated into stock assessments, but fishery-dependent data have the advantage of being relatively inexpensive to collect, and directly measure the impact of fishing in terms of both location and age classes targeted. As a result, the creation of MPAs may result in less data available to stock assessment methods, or for large closed areas to go unsampled (Bohnsack 1999). The most commonly used type of fishery-dependent data in assessments is catch-per-unit-effort (CPUE) data. The fishery CPUE, which reflects abundance in fished areas, will not reflect any potential increasing abundance of sedentary species within MPAs, and may be lower after MPA creation due to the concentration of fishing effort in the remaining open space. For species with

limited mobility, spillover may result in a concentrated fishing effort along the border of the MPA as fishermen “fish the line” (Murawski et al. 2005; but see Guenther et al. [2015] for alternative fishing responses). If data are spatially aggregated over the entire management range, the inflated catch rates near the borders of MPAs may mask declines in catch rates in other areas (McGilliard et al. 2015), leading to biased assessments (Maunder et al. 2006).

Bohnsack et al. (1999) suggested interference with fishery-dependent data gathering might be alleviated through greater fishery-independent sampling. Traditional means of fishery-independent sampling, which often rely on trawl gear, may be destructive and thus disallowed inside MPAs. In these situations, MPAs will require a change in sampling design, making direct comparisons with historical data difficult or impossible. Sampling within the MPA, which can offer the best available method to obtain samples of age structure, age-length and age-weight relationships that are unbiased by years of selective fishing pressure, may also not be allowed in no-take zones as managers try to limit all anthropogenic sources of mortality. This may necessitate a move towards length-based sampling methods inside MPAs such as low mortality catch-and-release methods (Bartholomew and Bohnsack 2005), or the use of underwater stereo-video, as well as a shift towards length-based assessment models (Bohnsack 1999).

4.2 Spatial heterogeneity in stock assessments

Stock assessments traditionally assume that the stock in question is homogeneously distributed over the management area or targeted with uniform fishing intensity. MPAs

violate this assumption (Bohnsack 1999), creating patches of high biomass inside their borders, and potentially leading to stock depletion outside (Hilborn et al. 2006). As such, MPAs and their effects on the spatial distribution of both fish and fishermen may introduce biases in stock assessments, as in the case where the diffusion of older fish outside the boundaries of the reserve can cause underestimations of the fishing mortality rate and over estimations of the population size (Punt and Methot 2004, McGilliard et al. 2015). This can lead to misspecification of catch or effort limits.

Solutions include a greater use of spatially-specific modeling, but this may require data collection on a finer scale (Bohnsack 1999, Holland 2002). Punt and Methot (2004) showed that conducting a single assessment with fishery-dependent and fishery-independent CPUE data aggregated over a simulated stock's range resulted in underestimates of spawning stock biomass in the presence of a no take MPA. The magnitude of bias increased with the number of years since MPA implementation as biomass builds up inside the closed areas (Punt and Methot 2004). Conducting separate assessments of the open and closed areas resolved this underestimation, but required separate data streams for the fished and unfished areas (Punt and Methot 2004). The additional data required for spatial assessments increases the cost of monitoring and assessment programs. Spatial models also require an understanding of the connectivity between the various spatial patches, information that is rarely known with much certainty. Punt and Methot (2004) found that spatially-specific assessments overestimated biomass when movement rates between areas were high.

4.3 Accounting for populations inside MPAs

Field et al. (2006) raised the question of whether the populations within MPAs should be considered “on the table” or “off the table” when assessing depletion levels and setting harvest limits. Given the mandates to rebuild populations, there is an incentive for managers to count protected biomass in stock assessments to demonstrate increased stock health (Field et al. 2006). Many regulatory bodies have overcome opposition to MPAs via promises of healthier spawning stocks and increased yields, and so there may be pressure from the fishing industry to count the fraction of population in MPAs as part of the total stock when setting catches. Including protected fish when calculating catch limits based on the total vulnerable biomass can lead to unsustainable fishing mortality rates in the fish region because in reality only a portion of the stock is targeted (Hilborn et al. 2004b, 2006). This conflict was evident in a study modeling the effect of MPAs on the lobster fishery in Victoria, Australia, where catch rates (and thus profits) were predicted to remain low under the pre-MPA catch limits, despite the fact that MPAs would accelerate total stock recovery due to biomass increases inside the closure (Hobday et al. 2005). The effects of overfishing on the vulnerable stock biomass may negate the benefits of the MPA population because overfishing reduces the age structure of the population, impacting both the yield per recruit and the lifetime spawning output of each fish (Greenstreet et al. 2009). Conversely, not taking protected populations into account when determining stock status is likely to lead to a reduction in MSY and thus catch limits, as well as extend the time period until recovery targets are achieved, both of which may have severe economic impacts. Movement and larval dispersal between the closed and open populations can alter these predictions.

Recently, Lester et al. (2013) called for the use of projection models to predict a MPA's future conservation benefits as a means of "giving credit" to fisheries who are seeking sustainability certification. They argued that considering the populations protected within MPAs as part of the entire stock might provide incentives for stakeholders to support MPA creation and help overcome the barriers to certification experienced in many data-poor and developing world countries (Lester and Gaines 2013). However, the previously noted feedbacks between MPAs and the fisheries regulations outside them make predicting these benefits very difficult without complex spatial models. Wilson et al. (2013) proposed a simple mechanism for accounting for the spawning biomass within MPAs using spatial Spawning Potential Ratio (SPR) models to account for the increased egg production achieved by maintaining an older age structure in a proportion of the population. However, this study assumed a common larval pool between the closed and open areas, and that the population abundance was proportional to the area in the closed and open regions that prior to MPA establishment. Currently there are no clearly established rules of thumb for accounting for the contributions of MPAs to nearby fished areas.

4.4 Economic effects of MPAs on fisheries

Implementation of MPAs is likely to come with potential benefits balanced by costs (Sumaila and Charles 2002). While MPAs can buffer fish populations against decline, they are rarely able to address the socio-economic objectives that make up the other half of the definition of "sustainable fisheries". The creation of an MPA almost always results

in a decrease in catch unless the population is over-exploited prior to the MPA (Beverton and Holt 1957, Hannesson 2002). Yamazaki et al. (2015) examined the effects of combining a MPA with a harvest control rule to rebuild an overfished stock, and found that a small MPA (10% of fishing grounds) improved the rebuilding timeline, the net present value of the fishery, and average catches when paired with the optimal harvest control rule, but that tradeoffs between these performance statistics were introduced when either the MPA was larger or the harvest control rule was sub-optimal. However, model results suggest MPAs may produce more stable catches (Hannesson 2002, Sladek Nowlis and Roberts 1999), which is highly valued by many fishing communities.

Most MPA modeling has assumed open access conditions, but Lester et al. (2016) examined the impact of MPAs when combined with Territorial User Rights Fisheries (TURFS) and found that in this combination did not eliminate the tradeoff between conservation and fisheries goals unless the overfishing was occurring, echoing the findings seen in open access systems. However, Sanchirico and Wilen (2002) applied a spatial bioeconomic model to examine how MPAs affect fishermen in limited entry fisheries and found that both biomass and license price increased when the fishery was operating at or near open access effort levels prior to the creation of the MPA. In general, though, MPAs result in a decrease in the sustainable catch level (Hilborn et al. 2006, McGilliard and Hilborn 2008).

Over the short term, fishery profits may decline at a rate greater than the proportion of area removed from the fishery. Often the most biologically productive areas are set aside

for protection, but this can undermine performance if the goal is to simultaneously improve both the economic and biological conditions in the fishery (Sanchirico and Wilen 2002). MPAs can result in a concentration of effort into the remaining open areas, reducing catch rates and exacerbating competition. In addition, the catch rates may decrease in the short term due to fishermen having to relearn how and where to fish when they are displaced from favored fishing grounds (Guenther et al. 2015). Fishers may also have to travel farther to access fishing grounds with high catch rates, increasing their costs and altering the distribution of fishing effort (Smith and Wilen 2003). Such short-term losses present an obstacle to stakeholder support for MPAs as well as to managers looking to maximize the socio-economic benefits of fisheries.

4.5 Informational and management needs of MPAs

MPAs have generally been characterized as a management tool with low informational requirements relative to traditional fisheries management. As such, they have been suggested for use in fisheries with complex spatial structure, minimal centralized management, and/or low capacity for data collection. Such fisheries are difficult to assess using conventional methods because of spatial heterogeneity in stocks, lack of data, low economic value, or having an artisanal or otherwise diffuse social structure (Bohnsack 1999, Orensanz et al. 2005). MPAs have been suggested as a simple management solution in such fisheries because spatial closures protect spawning grounds (Roberts and Polunin 1993). In fact, the first MPAs implemented to meet fishery management goals were designed to support catches in places with complex, multi-species, and multi-gear fisheries with limited management capacity (Alcala 1988).

MPAs may appear to be a simple solution in data- or management-limited arenas, but their long-term efficacy may be undermined by the lack of information and enforcement capacity. The amount of information required to properly site an MPA to meet particular goals (whether fisheries enhancement or conservation) is high. Improper siting of MPAs can result in a lack of benefits to the surrounding area, undermining community support for the MPA (Agardy et al. 2011). In many places, particularly in developing countries, there is no top-down management entity to enforce a spatial closure, and MPAs often must depend on community support and self-policing to be effective. A lack of enforcement can further erode MPA benefits.

5. New opportunities for fisheries and MPAs: using reserves in stock assessments

A recent shift in the MPA literature suggests a new path for the integration of MPAs in to fisheries management. A nascent but growing body of research has explored the potential benefits of MPAs to fisheries management as a source of information that can be used to better assess and manage nearby fisheries. This section describes the work that has been done in this arena.

5.1 MPAs as fisheries reference areas

The addition of MPAs to the seascape adds a new class of ecological indicators that may be highly informative. As the stocks protected within MPA borders approach carrying capacity they may provide robust estimates of unfished stock density (Bohnsack et al. 2004), an important reference point in the assessment and management of fish stocks. Stock assessments estimate the size of a fish stock by looking for contrast

between data collected from a time when the stock was lightly fished and recently collected data. The larger the contrast between these two data streams, the easier it is to estimate the current stock size. However, many fisheries, especially small scale or artisanal fisheries in the developing world, lack historical time series necessary for this comparison. MPAs represent an opportunity for the assessment of data-poor fisheries by acting as a reference area with which to estimate unfished biomass (Bohnsack 1998). However, this is only true if MPAs are placed randomly on the seascape, which is rarely the case. Instead, MPAs are often placed in areas with high conservation value, and thus may have higher carrying capacities than unprotected areas. This may lead to an overestimate of unfished stock size. MPAs are subject to the same environmental fluctuations and non-fishing anthropogenic effects as nearby fished areas so represent contemporary rather than theoretical unfished conditions. Because of this, they provide important control sites that can provide both an understanding of anthropogenic versus natural disturbances as well as a buffer against the uncertainty caused by shifting baselines (Bohnsack 1999).

5.2 MPA-based control rules

Harvest control rules are used to set or update harvest levels in response to fishery performance. A few harvest control rules have been developed to use MPAs as reference areas in setting sustainable catch or effort limits (Wilson et al. 2010, Babcock and MacCall 2011, McGilliard et al. 2011, Wilson et al. 2013). The Density Ratio Control Rule (DRCR) uses a survey-based estimate of the ratio of the density of fish outside an MPA to that inside it (Babcock and MacCall 2011, McGilliard et al. 2011). It relies on

the assumption that the density inside the MPA is the best available representation of the stock at unfished conditions (McGilliard et al. 2011), and can be used to assess fisheries that lack estimates of virgin stock size. The DRCR is a proxy for overall depletion levels that incorporates contemporary environmental conditions and their potential effects on stock size (Babcock and MacCall 2011). It uses a linear control rule to determine magnitude of change in effort or catch in each year to reach the target ratio.

A MPA-based decision tree process developed by Wilson et al. (2010) extended a size- and CPUE-based decision tree used to identify catch limits (Prince et al. 2011) through the inclusion of MPA data rather than historical information to determine a target. This method provides a framework to compare a number of simple indicators, such as the magnitude and rates of change in the catch of small, medium, and large fish in the catch, against MPA-based indicators. Fishing pressure is then iteratively adjusted as needed to achieve predetermined target ratios between outside and inside the MPA (Wilson et al. 2010). An evaluation of this model using MSE found that it consistently improved total catches while meeting management objectives for biomass and spawning potential ratio (Wilson et al. 2010).

5.3 Estimation of biological parameters

MPAs may provide a way to estimate biological parameters that are unbiased by the effects of fishing (Bohnsack 1999). Fishing mortality that is very high, or consistent over many years, can bias estimates of biological parameters in manifold ways. Fishing can alter the age at first maturity by selecting for fish that mature prior to recruiting to the

fishery. Fishing frequently removes the largest individuals from the population, which can skew estimates of the maximum average size, the asymptotic parameter in the von Bertalanffy growth function. In fitting asymptotic growth functions to size-at-age data the growth rate will co-vary with the asymptotic length, so that an under-estimation of asymptotic length will result in an over-estimation of the growth rate (Knight 1968). MPAs remove the truncated age and size structures associated with heavy fishing pressure. This may provide an opportunity to estimate biological rates such as growth and natural mortality rates in unfished conditions.

Perhaps the arena in which MPAs can add the most value to the estimation of biological parameters is in the estimation of natural mortality, which is notoriously difficult to infer due to the fact that it is frequently confounded by fishing mortality (Jamieson and Levings 2001, Kenchington 2014). Garrison et al. (2011) showed that application of a statistical catch-at-age model (Methot and Wetzel 2013) to data from a MPA allowed for accurate estimation of natural mortality provided there was no movement between fished and unfished areas, or if movement rates were known. A recent study (Wilson et al. 2013) demonstrated the application of a bounded mortality estimator (Ehrhardt and Ault 1992) to length data inside and outside a MPA to estimate the total mortality experienced by the fish in each location. The mortality inside the MPA was assumed to be the natural mortality, and the difference between the mortalities was used to estimate the fishing mortality and SPR of the fished portion of the stock. Another size-based method, the Length-based spawning potential ratio estimator, which has been shown to be sensitive to assumed parameter values (Hordyk et al. 2015), has been

extended to include information from MPA monitoring in order to improve the accuracy of assumed parameter values (Chapter 3). MPAs provide an opportunity to obtain more accurate estimates of these parameters, especially in data poor systems that lack information dating back to the development of the fishery (Kay and Wilson 2012).

6. Designing MPAs for use in stock assessments: what we know and what we need to learn

There have been several studies providing guidelines on how to design MPAs that meet conservation vs. fishery enhancement goals (Roberts 2001, Allison et al. 2003, Gerber et al. 2003, Hastings and Botsford 2003, Halpern and Warner 2003, Gaines et al. 2010b). The advice provided differs based on the stated goal of the MPA. For example, Hastings and Botsford (2003) examined the optimal arrangement of MPAs and found that they should be placed in a network of small MPAs to maximize spillover and larval export if the goal is fisheries enhancement, but that MPAs should be as large as possible to maximize conservation objectives (i.e. increase adult biomass). Additionally, while Ballantine (1997a,b) suggested that MPAs should be designed with the entire ecosystem in mind, MPAs designed for fishery enhancement usually focus on maximizing responses in high value target species, such as in the case of the Georges Bank closures (Murawski et al. 2000). These conflicting guidelines exemplify the tradeoffs inherent in designing MPAs to meet conservation versus extractive objectives.

6.1 Resolving the conflict between fisheries enhancement and conservation goals

Some authors have attempted to overcome this conflict in design recommendations. Halpern and Warner (2003) suggested that a single general network design of moderate

size and variable spacing could balance within-reserve (conservation) and between-reserve (fishery) responses, meeting the goals of most stakeholders. Gaines et al. (2010) proposed guidelines to reduce or eliminate these tradeoffs across MPA networks by acknowledging the economic costs and benefits that various MPA designs have, and encouraging MPA designs to consider joint conservation and harvest goals via a network of MPAs. However, these recommendations still acknowledge direct tradeoffs.

With this in mind, the use of MPAs as reference areas (as summarized in section five) for fisheries management presents an appealing alternative. Early research on this topic suggests that many of the MPA characteristics necessary to support conservation goals also facilitate the creation of a suitable reference area for fisheries. The ability to use MPAs as a reference requires that 1) the MPA be in place for enough time for the population to reach approximate carrying capacity, 2) the population within is completely protected from fishing mortality, and 3) the protected area is representative of nearby fished areas in terms of productivity and habitat availability. MPA reference areas are most likely to perform well when the MPA has been in place for at least the mean generation time of the fish stock being assessed (Wilson et al. 2010, 2013). In addition, the MPA must be well enforced, be larger than the home range of the target species, and have limited connectivity between the fished and unfished areas, so that the fishing mortality experienced inside the MPA is minimized or eliminated. Finally, the MPA must be similar to nearby fished areas, ensuring that all fished habitats are adequately represented. Note that this may require the sites of MPAs to be chosen randomly so that they adequately reflect the spatial variation of the fishing grounds.

These characteristics are similar to those found to be crucial to the ability of MPAs to meet conservation goals in a recent meta-analysis of 87 existing MPAs from around the world. Edgar et al. (2014) found that the conservation benefits of MPAs, which they defined as significant increases in total biomass and diversity of fish species compared to fished reference sites, increased when the following five key factors were present: 1) no take allowed, 2) well enforced, 3) old 4) large, and 5) lacking continuous habitat along its borders resulting in isolation from fished populations. While the first three are important to the success of MPAs regardless of their stated purpose, characteristics four and five support the findings of Hastings and Botsford (2003), and highlight the direct tradeoff inherent between MPAs designed to fuel nearby fisheries and those designed for biomass build ups within its borders. However, new research on the utility of MPAs for the assessment of fish stocks may resolve this tradeoff between using MPAs to support conservation and fishery goals.

6.2 MPAs as reference sites: Assessing the knowledge gaps

While there are several lessons that can be gleaned from the existing literature on the design of MPAs to maximize conservation benefits, future research is needed to better understand the opportunities and limitations associated with using MPAs as reference areas for stock assessments. Table 1 is an extension of the table presented in Gaines et al. (2010) describing the differences in the design attributes of areas considered for inclusion in MPAs created with fisheries and conservation goals in mind, and includes a column describing what is known about the design attributes of MPAs used as fishery reference

sites, and what remains unknown. All MPAs must be persistent and self-sustaining, regardless of their intended goal. High population growth rates will decrease the time frame over which population responses occur under protection from fishing. While this is not a crucial determinant of success, it increases the speed with which benefits accrue, which is useful regardless of whether those benefits support population growth for conservation, increased spillover for fishery enhancement, or the achievement of local carrying capacity for assessment purposes. While high carrying capacity areas support conservation and fishery enhancement goals, it is unknown how the carrying capacity will affect performance as a reference area. Ideally the reference area should have a density at carrying capacity that is representative of the surrounding fished areas. While MPA sites should be larval sources to support both conservation and fishery enhancement goals, it is unknown whether being a larval source impacts an area's ability to act as a reference site.

Areas that are heavily exploited offer the most benefit for both conservation and fishery enhancement goals, but it is unknown how current exploitation rate impacts performance as a reference site. Heavy exploitation may increase the time required to reach carrying capacity, and may fundamentally alter ecological processes, making these areas unsuitable as proxies for unfished conditions. The cost of harvesting an area is also a consideration when deciding where to site MPAs. While the inclusion of costly areas in MPAs designed for fishery enhancement depend on whether the goal is to minimize cost or to maximize profit (Gaines et al. 2010b), costly areas are often targeted only after less costly areas have been fished out, or if the revenue gained from fishing is very high.

Gaines et al. (2010) suggested that high cost areas be considered for inclusion in conservation-oriented MPAs, despite the fact that these areas might be less exploited, as a way of lessening the economic impact on fishers. It is unknown whether high cost areas should be included in MPAs designed to be reference sites, and will likely depend on how representative they are of fished sites, as well as their accessibility for data collection. Additionally, areas that are high in cost to fish may also be high in cost to enforce (Halpern and Warner 2003). While all MPAs require consistent enforcement to be successful regardless of what they were designed for, any fishing mortality inside the reserve could be highly detrimental to a reserve's use as a proxy for unfished conditions, and could result in overly aggressive harvest targets and limits throughout the fishery.

MPAs designed for fishery enhancement must increase the value of the catch outside the reserves through larger and/or more abundant fish to be successful. This requires that the MPA be large enough relative to the home range of the fish such that the fish inside the MPA are protected from mortality, but have permeable borders with continuous habitat. However, while this may increase catches via spillover, the additional fishing mortality along the MPA border impacts the population structure inside the marine reserve, as was demonstrated by Kay et al. (2012) who found that fishing mortality on lobsters moving in and out of MPAs impacted lobster size structures within the MPA. As a result, many MPAs designed with conservation goals in mind have distinct habitat edges. Kay et al. (2012) advocated sampling in the middle of MPAs to avoid these edge effects, but any mortality from external sources experienced inside the reserve could bias stock assessments based on MPA data.

6.3 Future research needs

As demonstrated in Table 1, there is much we do not yet know about how the attributes of various marine spaces will influence their performance as reference sites. However, what is currently known suggests that MPAs designed for conservation may be compatible for use in stock assessments. In the following section I identify additional key issues relevant to the use of MPAs as reference sites that remain largely unexplored.

6.3.1 Movement

Movement of fish presents a challenge for the use of MPAs as reference areas. While Garrison et al. (2011) found that the ability to accurately estimate natural mortality rates was negatively influenced by movement across MPA borders, the bias was eliminated if the rate of movement was accurately known and accounted for in the model. However, movement rates are rarely known with any accuracy, especially in the data poor species that might benefit most from including reference MPAs in their management. Additionally, movement rates may vary between sexes and across life stages (Martell et al. 2000), or be facilitated by site-specific ecological characteristics (Kay and Wilson 2012). There is some evidence that MPAs may facilitate movement as stocks build up within closed areas, and the resulting competition for scarce resources drives individuals to seek less crowded habitat outside the MPA. More research is needed to quantify the sensitivity of stock assessment data from MPAs under different rates and types of movements.

6.3.2 Issues of scale and reserve spacing

The few studies that have examined the potential for use of MPAs as management reference areas have generally modeled single, large (~20% coverage) MPAs directly adjacent to fishing grounds (Wilson et al. 2010, McGilliard et al. 2011, Wilson et al. 2013). It is unknown over what distances MPAs can function as representative comparisons, and whether the current recommendations for size (10-20km), spacing (20km apart to allow for widely dispersing propagules to settle; (Shanks et al. 2003), and inclusion of biogeographic zones (20% or greater) will also apply for reserves designed for use in stock assessments. Additionally, while it is appealing to think about MPAs functioning as proxies for unfished biomass, current stock assessments are largely unequipped to deal with temporal or spatial variation in estimates of unfished conditions, which is likely to occur in a network of MPAs.

6.3.3 Trophic level, response to protection, and time to carrying capacity

Responses to protection under an MPA can be slow, complex and species-specific (Barrett et al. 2007). Large, long-lived species that require many years to reach maturity are likely to respond much less quickly than small, fast-growing species (Russ and Alcala 2004). The intensity of exploitation of the species before protection, as well as trophic level and species interactions, will also play a role in determining response (Polacheck 1990, Baskett et al. 2007). Additionally, while responses in terms of increased size and abundance may be rapid for some species (especially those heavily targeted by fishing prior to MPA creation) it will be difficult to know when unfished conditions (in terms of abundance or population age structure) have been sufficiently met, especially in the face

on temporal environmental fluctuations. Research is needed to determine the time frame over which MPAs become useful reference areas for different species, as well as to evaluate how using data from within MPAs prior to achievement of full carrying capacity impacts assessments and harvest recommendations.

6.3.4 Costs of data collection inside MPAs

The consideration of reserves as a reference area for the assessment of nearby fished stocks requires an understanding of the costs incurred in conducting fishery-independent sampling within MPAs, which is more costly than fishery-dependent sampling. These data streams will need to be paired with data collected using a similar protocol outside the reserves for comparison. The value of reserve-based reference points in stocks assessments needs to be evaluated, especially in comparison with iterative, data-driven fishery-dependent indicators, which have also been proposed for use in data-poor fisheries that lack reference points (Hilborn 2002).

7. Conclusion

Studies have shown that MPAs on their own are unlikely to result in productive, well-managed fisheries, and must be integrated into comprehensive marine management systems. New research suggests that MPAs may provide an informational opportunity for the improved management of stocks because they can be used as reference areas to measure the impacts of fishing when historical data are lacking. While the ability of MPAs to enhance fisheries relies on maximizing connectivity between the open and closed areas through many porous borders (Hastings and Botsford 2003), early research

suggests that MPAs provide the most reliable reference areas when MPAs are large, old, and isolated from nearby fished areas. Interestingly, this echoes the characteristics necessary for MPAs to maximize conservation benefits. More research is needed to further understanding along this exciting frontier, but this suggests that MPAs sited with conservation goals in mind can still be very valuable to fisheries management, especially to data poor fisheries that lack historical data streams.

References

- Agardy, T., Bridgewater, P., Crosby, M.P., Day, J., Dayton, P.K., Kenchington, R., Laffoley, D., McConney, P., Murray, P.A., Parks, J.E., and Peau, L. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquat Conserv* 13(4): 353–367. doi:10.1002/aqc.583.
- Agardy, T., di Sciara, G.N., and Christie, P. 2011. Mind the gap Addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Mar Policy* 35(2): 226–232. Elsevier. doi:10.1016/j.marpol.2010.10.006.
- Alcala, A.C. 1988. Effects of marine reserves on coral fish abundances and yields of Philippine coral reefs. *Ambio* 17(3): 194–199. doi:10.2307/4313453.
- Allison, G.W., Gaines, S.D., Lubchenco, J., and Possingham, H.P. 2003. Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecol Appl* 13(1): 8–24. Eco Soc America.
- Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol Appl* 8(1): S79–S92. Eco Soc America.
- Attwood, C.G., and Bennett, B.A. 1995. Modelling the effect of marine reserves on the recreational shore-fishery of the south-western Cape, South Africa. *S Afr J Marine Sci* 16(1): 227–240.
- Babcock, E.A., and MacCall, A.D. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? *Can J Fish and Aquat Sci* 68(2): 343–359. NRC Research Press. doi:10.1139/F10-146.
- Badalamenti, F., Ramos, A.A., Voultziadou, E., Sanchez Lizaso, J.L., D'Anna, G., Piptone, C., Ruiz Fernandez, J.A., Whitmarsh, D., and Riggio, S. 2000. Cultural and socio-economic impacts of Mediterranean marine protected areas. *Environ Conserv* 27(2): 110–125.
- Barrett, N.S., Edgar, G.J., Buxton, C.D., and Haddon, M. 2007. Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. *J Exp Mar Biol Ecol* 345: 141–157. doi:10.1016/j.jembe.2007.02.007.
- Bartholomew, A., and Bohnsack, J.A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Rev Fish Biol Fisher* 15: 129–154. doi:10.1007/s11160-005-2175-1.
- Baskett, M.L., Micheli, F., and Levin, S.A. 2007. Designing marine reserves for interacting species: Insights from theory. *Biol Conserv* 137(2): 163–179. doi:10.1016/j.biocon.2007.02.013.

- Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004. Fisheries Sustainability via Protection of Age Structure and Spatial Distribution of Fish Populations. *Fisheries* 29(8): 23–32. doi:10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2.
- Berumen, M.L., Almany, G.R., Planes, S., Jones, G.P., Saenz-Agudelo, P., and Thorrold, S.R. 2012. Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. *Ecol Evol* 2(2): 444–452. Blackwell Publishing Ltd. doi:10.1002/ece3.208.
- Beverton, R., and Holt, S.J. 1957. On the dynamics of exploited fish populations. *Fishery Investigations Series II Volume XIX*, Ministry of Agriculture.
- Bohnsack, J.A. 1998. Application of marine reserves to reef fisheries management. *Aust J Ecol* 23(3): 298–304. Wiley Online Library.
- Bohnsack, J.A. 1999. Incorporating no-take marine reserves into precautionary management and stock assessment. In *Providing Scientific Advice to Implement Precautionary Approach Under the Magnuson-Stevens Fishery Conservation and Management Act*. NOAA Tech. Memorandum NMFS-F/SPO-40.
- Bohnsack, J.A., Ault, J.S., and Causey, B. 2004. Why have no-take marine protected areas? *American Fisheries Society Symposium* 42: 185–193.
- Botsford, L.W., Brumbaugh, D.R., Grimes, C., Kellner, J.B., Largier, J., O'Farrell, M.R., Ralston, S., Soulanille, E., and Weststad, V. 2009. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Rev Fish Biol Fisher* 19(1): 69–95. doi:10.1007/s11160-008-9092-z.
- Botsford, L.W., Micheli, F., and Hastings, A. 2003. Principles for the design of marine reserves. *Ecol Appl* 13(1): 25–31. doi:10.1890/1051-0761(2003)013[0025:PFTDOM]2.0.CO;2.
- Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., Garcia-Charton, J.A., Goni, R., Borg, J.A., Forcada, A., De Lucia, G.A., Perez-Ruzafa, A., Alfonso, P., Brito, A., Le Direach, L., Sanchez-Jerez, P., Somerfield, P.J., and Planes, S. 2010. Marine reserves: fish life history and ecological traits matter. *Ecol Appl* 20(3): 830–839. doi:10.1890/08-2131.1.
- DeMartini, E.E. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fish B-NOAA* 91: 414–427.
- Drake, M.T., Claussen, J.E., Philipp, D.P., and Pereira, D.L. 1997. A Comparison of Bluegill Reproductive Strategies and Growth among Lakes with Different Fishing Intensities. *North Am J Fish Manage* 17(2): 496–507. doi:10.1577/1548-8675(1997)017<0496:ACOBRS>2.3.CO;2.

- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., and Thomson, R.J. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506(7487): 216–220. Nature Publishing Group. doi:10.1038/nature13022.
- Ehrhardt, N.M., and Ault, J.S. 1992. Analysis of two length-based mortality models applied to bounded catch length frequencies. *T Am Fish Soc* 121(1): 115–122. Taylor & Francis. doi:10.1577/1548-8659(1992)121<0115:AOTLMM>2.3.CO;2.
- Field, J.C., Punt, A.E., Methot, R.D., and Thomson, C.J. 2006. Does MPA mean ‘Major Problem for Assessments’? Considering the consequences of place-based management systems. *Fish Fish* 7(4): 284–302. Wiley Online Library. Available from http://scholar.google.com/scholar?cites=13350350392059245002&as_sdt=2005&scioldt=0,5&hl=en.
- Francini-Filho, R.B., and Moura, R.L. 2008. Evidence for spillover of reef fishes from a no-take marine reserve: An evaluation using the before-after control-impact (BACI) approach. *Fish Res* 93: 346–356. doi:10.1016/j.fishres.2008.06.011.
- Gaines, S.D., Lester, S.E., Grorud-Colvert, K., Costello, C., and Pollnac, R. 2010a. Evolving science of marine reserves: New developments and emerging research frontiers. *PNAS* 107(43): 18251–18255. doi:10.1073/pnas.1002098107.
- Gaines, S.D., White, C., Carr, M.H., and Palumbi, S.R. 2010b. Marine Reserves Special Feature: Designing marine reserve networks for both conservation and fisheries management. *PNAS* 107(43): 18286–18293. doi:10.1073/pnas.0906473107.
- Garcia, S.M., Kolding, J., Rice, J., Rochet, M.J., Zhou, S., Arimoto, T., Beyer, J.E., Borges, L., Bundy, A., Dunn, D., Fulton, E.A., Hall, M., Heino, M., Law, R., Makino, M., Rijnsdorp, A.D., Simard, F., and Smith, A.D.M. 2012. Reconsidering the Consequences of Selective Fisheries. *Science* 335(6072): 1045–1047. doi:10.1126/science.1214594.
- Garrison, T.M., Hamel, O.S., Punt, A.E., and Jonsson, B. 2011. Can data collected from marine protected areas improve estimates of life-history parameters? *Can J Fish and Aquat Sci* 68(10): 1761–1777. doi:10.1139/f2011-073.
- Gårdmark, A., Jonzén, N., and Mangel, M. 2005. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *J Appl Ecol* 43(1): 61–69. Blackwell Publishing Ltd. doi:10.1111/j.1365-2664.2005.01104.x.
- Gell, F.R., and Roberts, C.M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol Evol* 18(9): 448–455. Elsevier. doi:10.1016/S0169-5347(03)00189-7.

- Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., and Andelman, S. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol Appl* 13(1): 47–64. *Eco Soc America*.
- Goñi, R., Quetglas, A., and Renones, O. 2006. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar Ecol Prog Ser* 308: 207–219.
- Greenstreet, S.P., Fraser, H.M., and Piet, G.J. 2009. Using MPAs to address regional-scale ecological objectives in the North Sea: modelling the effects of fishing effort displacement. *ICES J Mar Sci* 66(1): 90–100. Oxford University Press.
- Guenther, C., Lopez-Carr, D., and Lenihan, H.S. 2015. Differences in lobster fishing effort before and after MPA establishment. *Applied Geography* 59(C): 78–87. Elsevier Ltd. doi:10.1016/j.apgeog.2014.12.016.
- Guenther, C.M. 2010. A socio-ecological analysis of marine protected areas and commercial lobster fishing in the Santa Barbara Channel, California.
- Guénette, S., Lauck, T., and Clark, C. 1998. Marine reserves: from Beverton and Holt to the present. *Rev Fish Biol Fisher* 8(3): 251–272. Springer.
- Halpern, B.S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol Appl* 13(1): 117–137. *Eco Soc America*.
- Halpern, B.S., and Warner, R.R. 2002. Marine reserves have rapid and lasting effects. *Ecol Lett* 5(3): 361–366. Wiley Online Library.
- Halpern, B.S., and Warner, R.R. 2003. Review Paper. Matching marine reserve design to reserve objectives. *P Roy Soc B-Biol Sci* 270(1527): 1871–1878. The Royal Society. doi:10.1098/rspb.2003.2405.
- Halpern, B.S., Gaines, S.D., and Warner, R.R. 2004. Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecol Appl* 14(4): 1248–1256. doi:10.1890/03-5136.
- Halpern, B.S., Lester, S.E., and Kellner, J.B. 2010. Spillover from marine reserves and the replenishment of fished stocks. *Environ Conserv* 36(04): 268–276. Cambridge University Press. doi:10.1017/S0376892910000032.
- Hannesson, R. 2002. The Economics of Marine Reserves. *Nat Resour Model* 15(3): 273–290. Blackwell Publishing Ltd. doi:10.1111/j.1939-7445.2002.tb00090.x.
- Hastings, A. 1999. Equivalence in Yield from Marine Reserves and Traditional Fisheries Management. *Science* 284(5419): 1537–1538. doi:10.1126/science.284.5419.1537.

- Hastings, A., and Botsford, L.W. 2003. Comparing designs of marine reserves for fisheries and for biodiversity. *Ecol Appl* 13(sp1): 65–70. Eco Soc America.
- Hilborn, R. 2002. The dark side of reference points. *B Mar Sci* 70(2): 403–408. University of Miami-Rosenstiel School of Marine and Atmospheric Science.
- Hilborn, R., Micheli, F., and De Leo, G.A. 2006. Integrating marine protected areas with catch regulation. *Can J Fish and Aquat Sci* 63(3): 642–649. doi:10.1139/f05-243.
- Hilborn, R., Punt, A.E., and Orensanz, J. 2004a. Beyond band-aids in fisheries management: fixing world fisheries. *B Mar Sci* 74(3): 493–507.
- Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K.L., Garcia, S., Hall, S.J., Kirkwood, G.P., Sainsbury, K., Stefansson, G., and Walters, C. 2004b. When can marine reserves improve fisheries management? *Ocean Coast Manage* 47(3-4): 197–205. doi:10.1016/j.ocecoaman.2004.04.001.
- Hixon, M.A., Johnson, D.W., and Sogard, S.M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J Mar Sci* 71(8): 2171–2185. Oxford University Press. doi:10.1093/icesjms/fst200.
- Hobday, D., Punt, A.E., and Smith, D.C. 2005. Modelling the effects of Marine Protected Areas (MPAs) on the southern rock lobster (*Jasus edwardsii*) fishery of Victoria, Australia. *New Zeal J Mar Fresh* 39(3): 675–686. doi:10.1080/00288330.2005.9517344.
- Holland, D.S. 2000. A bioeconomic model of marine sanctuaries on Georges Bank. *Can J Fish and Aquat Sci* 57: 1307–1319. NRC Research Press Ottawa, Canada.
- Holland, D.S. 2002. Integrating marine protected areas into models for fishery assessment and management. *Nat Resour Model* 15(3): 369–386. Wiley Online Library.
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., and Prince, J. 2015. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES J Mar Sci* 72(1): 217–231. doi:10.1093/icesjms/fsu004.
- Hsieh, C.H., Yamauchi, A., Nakazawa, T., and Wang, W.F. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences* 72(2): 165–178.
- Jamieson, G.S., and Levings, C.O. 2001. Marine protected areas in Canada — implications for both conservation and fisheries management. *Can J Fish and Aquat Sci* 58(1): 138–156. doi:10.1139/cjfas-58-1-138.

- Kaiser, M.J. 2005. Are marine protected areas a red herring or fisheries panacea? *J Fish Res Board Can* 62(5): 1194–1199. doi:10.1139/f05-056.
- Kay, M.C., and Wilson, J.R. 2012. Spatially explicit mortality of California spiny lobster (*Panulirus interruptus*) across a marine reserve network. *Environ Conserv* 39(03): 215–224. Cambridge University Press. doi:10.1017/S0376892911000695.
- Kay, M.C., Lenihan, H.S., Guenther, C.M., Wilson, J.R., Miller, C.J., and Shrout, S.W. 2012. Collaborative assessment of California spiny lobster population and fishery responses to a marine reserve network. *Ecol Appl* 22(1): 322–335. doi:10.1890/11-0155.1.
- Kenchington, T.J. 2014. Natural mortality estimators for information-limited fisheries. *Fish Fish* 14(4): 533–562. doi:10.1111/faf.12027.
- Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. *J Fish Res Board Can* 25(6): 1303–1307.
- Lauck, T., Clark, C.W., Mangel, M., and Munro, G.R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecol Appl* 8(1): S72–S78. Eco Soc America.
- Lester, S.E., and Gaines, S.D. 2013. Encourage Sustainability by Giving Credit for Marine Protected Areas in Seafood Certification. *PLoS Biology* 11(12): e1001730. Public Library of Science. doi:10.1371/journal.pbio.1001730.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., and Warner, R.R. 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 384: 33–46.
- Martell, S.J., Walters, C.J., and Wallace, S.S. 2000. The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). *B Mar Sci* 66(3): 729–743.
- Maunder, M., Sibert, J., Fonteneau, A., Hampton, J., Kleiber, P., and Harley, S. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. *ICES J Mar Sci* 63(8): 1373–1385. doi:10.1016/j.icesjms.2006.05.008.
- McClanahan, T.R., and Mangi, S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol Appl* 10(6): 1792–1805. Eco Soc America.
- McGilliard, C.R., and Hilborn, R. 2008. Modeling No-Take Marine Reserves in Regulated Fisheries: Assessing the Role of Larval Dispersal. *Can J Fish and Aquat Sci* 65: 2509–2523.

- McGilliard, C.R., Hilborn, R., MacCall, A., Punt, A.E., and Field, J.C. 2011. Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks? *ICES J Mar Sci* 68: 201–211.
- McGilliard, C.R., Punt, A.E., Methot, R.D., Jr, and Hilborn, R. 2015. Accounting for marine reserves using spatial stock assessments. *Can J Fish and Aquat Sci* 72(2): 262–280. doi:10.1139/cjfas-2013-0364.
- Mesnildrey, L., Gascuel, D., and Le Pape, O. 2013. Integrating Marine Protected Areas in fisheries management systems: some criteria for ecological efficiency. *Aquat Living Resour* 26(2): 159–170. doi:10.1051/alr/2013056.
- Methot, R.D., Jr, and Wetzel, C.R. 2013. Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. *Fish Res* 142: 86–99. Elsevier B.V. doi:10.1016/j.fishres.2012.10.012.
- Moffitt, E.A., Botsford, L.W., and Kaplan, D.M. 2009. Marine reserve networks for species that move within a home range. *Ecol Appl* 19(7): 1835–1847. doi:10.1890/08-1101.1.
- Murawski, S.A., Brown, R., Lai, H.L., Rago, P.J., and Hendrickson, L. 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience. *B Mar Sci* 66(3): 775–798. University of Miami-Rosenstiel School of Marine and Atmospheric Science.
- Murawski, S.A., Wigley, S., Fogarty, M., Rago, P., and Mountain, D. 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES J Mar Sci* 62: 115–1167. doi:10.1016/j.icesjms.2005.04.005.
- Norse, E.A., Crowder, L.B., Gjerde, K., Hyrenbach, D., Roberts, C., Safina, C., and Soule, M.E. 2005. Place-based ecosystem management in the open ocean. In *Marine Conservation Biology*. Edited by E.A. Norse and L.B. Crowder. Island Press, Washington, DC. pp. 302–327.
- Orensanz, J.M.L., Parma, A.M., Jerez, G., Barahona, N., Montecinos, M., and Elias, I. 2005. What are the Key Elements for the Sustainability of “S-Fisheries?” Insights from South America. *B Mar Sci* 76(2): 527–556. University of Miami - Rosenstiel School of Marine and Atmospheric Science.
- Parrish, R. 1999. Marine reserves for fisheries management: why not. Symposium of the CalCOFI Conference: a continuing dialogue on no-take reserves for resource management, Asilomar, CA, USA; 4 November 1998. California Cooperative Oceanic Fisheries Investigations Report, 40: 77-86.
- Pelc, R.A., Warner, R.R., Gaines, S.D., and Paris, C.B. 2010. Detecting larval export from marine reserves. *PNAS* 107(43): 18266–18271. National Acad Sciences. doi:10.1073/pnas.0907368107.

- Polacheck, T. 1990. Year around closed areas as a management tool. *Nat Resour Model* 4(3): 327–354. *Natural Resource Modeling* 4(3).
- Prince, J.D., Dowling, N.A., Davies, C.R., Campbell, R.A., and Kolody, D.S. 2011. A simple cost-effective and scale-less empirical approach to harvest strategies. *ICES J Mar Sci* 68(5): 947–960. doi:10.1093/icesjms/fsr029.
- Punt, A.E., and Methot, R.D. 2004. Effects of marine protected areas on the assessment of marine fisheries. *American Fisheries Society Symposium* 42: 133–154.
- Quinn, J.F., Wing, S.R., and Botsford, L.W. 1993. Harvest Refugia in Marine Invertebrate Fisheries: Models and Applications to the Red Sea Urchin, *Strongylocentrotus franciscanus*. *Amer Zool* 33(6): 537–550. Oxford University Press. doi:10.1093/icb/33.6.537.
- Quinn, T.P., and Adams, D.J. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecol* 77(4): 1151. doi:10.2307/2265584.
- Reddy, S.M., Wentz, A., Aburto-Oropeza, O., Maxey, M., Nagavarapu, S., and Leslie, H.M. 2013. Evidence of market-driven size-selective fishing and the mediating effects of biological and institutional factors. *Ecol Appl* 23(4): 726–741. *Eco Soc America*.
- Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. *Can J Fish and Aquat Sci* 38(12): 1636–1656. doi:10.1139/f81-213.
- Roberts, C. 2012. Marine Ecology: Reserves Do Have a Key Role in Fisheries. *Curr Biol* 22(11): R444–R446. Elsevier Ltd. doi:10.1016/j.cub.2012.04.030.
- Roberts, C.M. 2001. Effects of Marine Reserves on Adjacent Fisheries. *Science* 294(5548): 1920–1923. doi:10.1126/science.294.5548.1920.
- Roberts, C.M., and Polunin, N.V. 1993. Marine reserves: simple solutions to managing complex fisheries? *Ambio* 22: 363–368. JSTOR.
- Roberts, C.M., Hawkins, J.P., and Gell, F.R. 2005. The role of marine reserves in achieving sustainable fisheries. *Philos T R Soc B* 360(1453): 123–132. doi:10.1098/rstb.2004.1578.
- Rochet, M.-J., Collie, J.S., Jennings, S., and Hall, S.J. 2011. Does selective fishing conserve community biodiversity? Predictions from a length-based multispecies model. *Can J Fish and Aquat Sci* 68: 469–486.
- Russ, G.R. 2002. Yet another review of marine reserves as reef fishery management tools. In *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York. pp. 421–444.

- Russ, G.R., and Alcala, A.C. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138(4): 622–627. Springer-Verlag. doi:10.1007/s00442-003-1456-4.
- Sainsbury, K., and Sumaila, U.R. 2003. Incorporating Ecosystem Objectives into Management of Sustainable Marine Fisheries, Including “Best Practice” Reference Points and Use of Marine Protected Areas. In *Responsible Fisheries in the Marine Ecosystem*. Edited by M. Sinclair and G. Valdimarsson. FAO, Rome. pp. 343–361.
- Sanchirico, J.N., and Wilen, J.E. 2002. The Impacts of Marine Reserves on Limited-Entry Fisheries. *Nat Resour Model* 15(3): 291–310. Blackwell Publishing Ltd. doi:10.1111/j.1939-7445.2002.tb00091.x.
- Shanks, A.L., Grantham, B.A., and Carr, M.H. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13(1): 159–169. doi:10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2.
- Sladek Nowlis, J., and Roberts, C.M. 1999. Fisheries benefits and optimal design of marine reserves. *Fish B-NOAA* 97(3): 604–116. *Fishery Bulletin*.
- Smith, M.D., and Wilen, J.E. 2003. Economic impacts of marine reserves: the importance of spatial behavior. *J Environ Econ Manag* 46(2): 183–206. doi:10.1016/S0095-0696(03)00024-X.
- Sumaila, U.R., and Charles, A.T. 2002. Economic models of marine protected areas: an introduction. *Nat Resour Model* 15(3): 261–272.
- Tetreault, I., and Ambrose, R.F. 2007. Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. *Ecol Appl* 17(8): 2251–2267. *Eco Soc America*.
- Walters, C. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? *B Mar Sci* 66(3): 745–757. University of Miami-Rosenstiel School of Marine and Atmospheric Science.
- Warner, R.R., and Swearer, S.E. 2000. Larval accumulation and retention: implications for the design of marine reserves and essential habitat. *B Mar Sci* 66(3): 821–830.
- Willis, T.J., Millar, R.B., Babcock, R.C., and Tolimieri, N. 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environ Conserv* 30(2): 97–103. doi:10.1017/S0376892903000092.
- Wilson, J.R., Prince, J.D., and Lenihan, H.S. 2010. A Management Strategy for Sedentary Nearshore Species that Uses Marine Protected Areas as a Reference. *Mar Coast Fish* 2(1): 14–27. doi:10.1577/C08-026.1.

- Wilson, J.R., Valencia, S.R., Kay, M.C., and Lenihan, H.S. 2013. Integration of no-take marine reserves in the assessment of data-limited fisheries. *Conserv Lett* 7: 451–458. doi:10.1111/conl.12073.
- Worm, B., and Lenihan, H.S. 2014. 20. Threats to marine ecosystems: overfishing and habitat degradation. In *Marine Community Ecology and Conservation*. Edited by M.R. Bertness, B.J. Silliman, and J.J. Stachowicz. pp. 449–476.
- Yamazaki, S., Jennings, S., Grafton, R.Q., and Kompas, T. 2015. Are marine reserves and harvest control rules substitutes or complements for rebuilding fisheries? *Resour. Energy Econ.* 40: 1–18. Elsevier B.V. doi:10.1016/j.reseneeco.2015.01.001.
- Zhou, S., Smith, A.D.M., Punt, A.E., Richardson, A.J., Gibbs, M., Fulton, E.A., Pascoe, S., Bulman, C., Bayliss, P., and Sainsbury, K. 2010. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *PNAS* 107(21): 9485–9489. doi:10.1073/pnas.0912771107.

Tables

Table 1. Attributes of the area in question, and the decision to protect it within a reserve, given the objective of conservation, fishery enhancement, of use as a stock assessment reference area. “Y” means yes, “N” means no, and “U” means unknown.

Area Attribute	Include Area In MPA?		
	Conservation	Fishery Enhancement	Fishery Reference Area
Persistent	Y	Y	Y
High population growth rate	Y	Y	Y
High carrying capacity	Y	Y	U
Larval source	Y	Y	U
Heavily exploited prior to implementation	Y	Y	U
Costly to Harvest	Y	Depends	U
Has distinct habitat edge	N	Y	N

III. Evaluating the contribution of biological information from marine protected areas to data-limited stock assessments

Abstract

Data-limited assessment methods have been proposed for the management of fisheries that lack the historical catch and survey information needed for conventional stock-assessment-based management. Many data-limited assessment methods rely heavily on biological parameter estimates, which may be biased by heavy fishing and constrained by the lack of historical data. No-take Marine Protected Areas (MPAs), which are closed to all types of fishing, can restore fished populations to their unfished size and age structures. It has been suggested that MPAs can improve stock assessment methods by providing low-cost estimates of necessary biological parameters in fisheries that lack these data, but methods incorporating MPA-based estimates into assessments and management have not been implemented. I simulated fisheries for three model nearshore finfish species: gopher rockfish, blue rockfish, and lingcod, to evaluate the effect of incorporating information obtained from a no-take MPA on biological processes into a data-limited stock assessment. The MPA-based estimation procedure returned robust results even when key biological parameter values were incorrectly assumed. In a simulated case study, in which all of the necessary parameters were unknown, the MPA-based assessment method provided robust estimates of fishing mortality and spawning potential ratio, and outperformed the status-quo data-limited assessment method for species with low to moderate variability in length-at-age. Results of this study have important implications for the use of MPAs as reference areas for fisheries management.

1. Introduction

Successful fisheries management requires an understanding of how much reproductive capacity must be protected to sustain long-term catches. Stock assessment models often require a substantial amount of biological and fisheries data that can only be acquired with adequate financial investment, stable monitoring programs, and scientific expertise. As such, data-rich stock assessments are out of reach for most of the world's fisheries, which in fact are cash strapped and data-limited, making it difficult to implement management strategies (Berkes 2003).

Data-limited fisheries present a significant challenge to achieving goals of sustainable management. The FAO Code of Conduct for Responsible Fisheries emphasizes that a lack of data should not prevent the immediate adoption of management measures (FAO 2012). The need to calculate sustainable yields for data-limited fisheries has been heightened in first world countries as well: recent legislation in the U.S.A. requires the determination of annual catch limits, whether adequate supporting data exists or not (MacCall 2009). Therefore, efforts have increased to develop assessment methods that require less data, rely on data-based indicators rather than model-derived reference points, and that link the intensity of exploitation to the level of uncertainty (Essington 2001, Hilborn 2002).

Assessment strategies have been developed in recent years to utilize what little information is available in data-limited fisheries including historical time series of catches (MacCall 2009, Dick and MacCall 2011, Martell and Froese 2012, Costello et al.

2012, Kleisner et al. 2013), information borrowed from data-rich stocks (Jensen 1996, Punt et al. 2011, Jiao et al. 2011), or catch-composition data (Froese 2004, Cope and Punt 2009, Wilson et al. 2010). Size-based methods may be the most promising for fisheries that have no historical data available. The size composition of a catch is relatively inexpensive to collect and can be obtained from sampling during a single fishing season. Size-based assessment methods for fisheries are not new (Beverton and Holt 1956, Pauly and Morgan 1987, Ehrhardt and Ault 1992), but recent emphasis on the role of unassessed or unmanaged stocks in global overfishing (Patrick et al. 2010, Le Quesne and Jennings 2011, Worm and Branch 2012, Hilborn and Ovando 2014) has spurred development of data-limited stock assessment methods that utilize size-related data (Froese 2004, Klaer et al. 2012, Babcock et al. 2013, Wilson et al. 2013, Hordyk et al. 2015).

Size-based methods have relatively few data requirements, but rely heavily on underlying assumptions about the biology of the species. For example, size-based methods often use information about basic biological processes to convert observed length compositions to theoretical age compositions. Thus, they are sensitive to assumed values of growth rates, maximum sizes, and natural mortality (Cope and Punt 2009, Babcock et al. 2013, Hordyk et al. 2015). Tag-and-recapture methods can be used to estimate both growth and natural mortality, but such studies require lightly fished stocks, large sample sizes, and multiple years of data collection (Hoenig et al. 1998, Pine et al. 2003). Otoliths can be collected for length-at-age information, but the truncation of age-structures by heavy fishing can bias both growth and natural mortality estimates

(Mulligan and Leaman 1992). More frequently, assessment scientists rely on analytically or empirically derived relationships to estimate unknown parameters from known ones (Jensen 1996). Sometimes biological parameters are borrowed from a well-studied stock, either of the same species or a closely related congener. The uncertainty associated with these parameter estimates is rarely accounted for in data-limited assessments.

Assumptions about biological processes are also used to set the target and limit reference points necessary to implement stock assessment outcomes (Brooks et al. 2010, Edwards et al. 2012, Moore et al. 2013). Status evaluations can range from susceptibility analyses based on life history traits (Patrick et al. 2010, Le Quesne and Jennings 2011) to more formal biological representations of a population. One of the most commonly used reference points is the Spawning Potential Ratio (SPR) of a stock. SPR describes the proportion of unfished egg production retained at a given fishing level, providing a prediction of how the reproductive capacity of a stock might respond to harvest (Sissenwine and Shepherd 1987, Goodyear 1993). SPR models require estimates of natural mortality, fishing mortality, maturity, and fecundity (Goodyear 1990). Fecundity and maturity ogives are relatively simple to obtain via biological studies, but natural mortality is notoriously difficult to estimate, even in data-rich stocks, because it is often confounded with fishing mortality (Vetter 1988, Pascual and Iribarne 1993). Weight is often used as a proxy for fecundity (Myers et al. 1999), and so a growth function is also required. Biased biological parameters may compromise the ability to calculate meaningful reference points and to accurately measure the performance of stocks against these reference points.

No-take marine protected areas (MPAs) provide an opportunity to improve the assessment of stocks that lack accurate estimates of these important biological parameters (Wilson et al. 2013). MPAs have been implemented around the world to conserve biodiversity and provide a buffer against management failures for marine resources (Gaines et al. 2010). Some have suggested that MPAs provide unfished reference areas that increase our understanding of fishing impacts via contrast (Edwards et al. 2012), and a few assessment methods have been based on this principle (Wilson et al. 2010, Babcock and MacCall 2011, McGilliard et al. 2011). Additionally, MPAs provide an opportunity to better estimate life-history parameters (Field et al. 2006). Well-enforced MPAs can help return protected portions of populations to unfished size and age structures, which can improve precision in estimates of maximum or asymptotic size. Additionally, MPAs show promise for improving empirical estimates of natural mortality (Garrison et al. 2011, Kay and Wilson 2012, Wilson et al. 2013).

Here I test whether MPA-derived estimates of biological parameters, specifically growth and natural mortality, improve the accuracy of a size-based assessment method for three model fisheries that lack historical data. I show that incorporation of MPA data increases the precision and accuracy of stock status estimates relative to traditional data poor approaches for sedentary target species with low to moderate variation in growth, and provides equivalent performance in species with high variation in growth. This work illustrates the potential for MPAs to improve the management of fisheries that lack historical data, and lends support for the experimental use of MPAs in fisheries assessment.

2. Methods

I assessed the performance of a recently developed length-based, data-limited assessment method known as the Length-based Spawning Potential Ratio, or LBSPR (Hordyk et al. 2015), both with and without biological estimates from MPA data. In common with many size-based methods, the LBSPR requires information about growth and natural mortality, and thus provides a vehicle for exploring the contributions of information from a single year of data from MPAs to the assessment of data-limited fisheries. To assess performance of the LBSPR both with and without MPA-derived estimates of biological parameters under a wide spectrum of realistic conditions and constraints, I simulated fisheries of three model species that represented a broad range of life history types found in nearshore temperate environments. I assessed the status of each fishery across seven uncertainty scenarios. In each scenario, I used two procedures to estimate biological parameters (Table 1), and compared the accuracy and precision of the estimates of fishing mortality (F) and Spawning Potential Ratio (SPR) between the two. The specific details of LBSPR, fish species, two procedures for estimating biological parameters, and seven uncertainty scenarios are provided in the following sections.

2.1 LBSPR estimator

The LBSPR estimation procedure centers on the fact that, when scaled to the average maximum size, the theoretical unfished size distribution is determined by the ratio of the natural mortality (M) to the von Bertalanffy growth rate (k). The LBSPR model requires assumptions about the M/k ratio, the average maximum size (L_∞), and the variability in

the maximum size (CV_{L_∞}), as well as length-composition data from a fishery. The third parameter in the von Bertalanffy growth function, t_0 , was assumed to equal zero, following (Hordyk et al. 2015). The estimation procedure converts the observed and predicted length compositions to age compositions, and uses the maximum likelihood to estimate the fishing mortality (F) and Spawning Potential Ratio (SPR) of the stock, as well as the two parameters of a logistic function that describes the selectivity (Hordyk et al. 2015).

2.2 Model fish species

I used an operating model to simulate the population dynamics of three fish populations resembling species commonly found in California's nearshore groundfish fishery, specifically gopher rockfish (*Sebastes carnatus*), blue rockfish (*Sebastes mystinus*) and lingcod (*Ophiodon elongatus*). The equations used in the operating and sampling models can be found in the Appendix. Parameters used to describe the biology of each species are found in Table 1. Because of their differences in productivity, M/k ratios, and variation in both length-at-age and recruitment, the three species represent distinct life history strategies. Blue rockfish is a low productivity species with a relatively large size at first maturity (72% of L_∞), and so is vulnerable to overfishing (Key et al. 2008). Lingcod is a highly productive species that achieves a relatively large maximum size (126.7 cm) and exhibits high variation in length-at-age. The home ranges of adult blue rockfish, gopher rockfish, and lingcod differ in scale, but all are non-migratory species that inhabit nearshore rocky reefs (Key et al. 2005, 2008, Jagielo and Wallace 2005). I assumed no movement relative to the size of the MPA for the analyses. The

model did not specifically capture ontogenetic movement patterns, such as the offshore movement exhibited by lingcod (Martell et al. 2000), but does account for the relative differences in emigration probability between species (Walters et al. 2007). Recruitment followed a Beverton-Holt stock recruitment function. I assumed larval movement follows a common pool dispersal model for all three species. The effects of these assumptions are discussed later.

2.3 Simulation Procedures

A semi-realistic nearshore groundfish fishery with 25 consecutive habitat patches was simulated for each species to examine the contributions of MPA information to the performance of data-limited assessment techniques. The entire population began at an unfished equilibrium, and fishing was simulated for 30 years at a low ($F = M$) fishing pressure. A second high fishing pressure situation ($F=3M$) was also modeled to explore how performance depends on historical fishing pressure. In year 31, a MPA was created in 20% of the habitat (i.e., five consecutive habitat patches). I assumed the MPA to be no-take and well enforced, with no illegal fishing. The total fishing effort remained unchanged, and was concentrated within all non-MPA patches.

Simulated data collection was initiated 20 years after the MPA was created, in which 1,000 lengths were sampled from the catch (see Appendix). Mortality estimates from MPAs have been shown to be biased in the years immediately following the creation of the an MPA (Wilson et al. 2013), because mortality estimators assume constant mortality rates over a cohort's lifetime and the sudden cessation of fishing mortality violates that

assumption. In theory, it is necessary to allow the fish inside the MPA to achieve an unfished age structure before sampling to ensure accurate mortality estimates (but see Wilson et al. 2013). The time required to achieve unfished conditions will vary depending on the life history of the species. To avoid this potential bias the simulated populations were sampled and assessed 20 years after the MPA was established.

The biological parameters necessary to fit the LBSPR model (L_∞ , k , M , and CV_{L_∞}) must be estimated externally and provided to the model. I compared how different procedures for obtaining these parameters affected the performance of the LBSPR assessment across seven different uncertainty scenarios (Table 2; described below). In situations where no biological studies exist for a particular stock, parameters values are frequently borrowed from well-studied stocks of the same species or genus. To recreate this method, the LBSPR model was fit to the fishery-dependent length composition data using assumed values of L_∞ , k , and M , and estimates of F and SPR were produced. I refer to this assessment procedure as the Data Limited-LBSPR (DL-LBSPR).

In the second assessment procedure, an additional fishery-independent data collection protocol was simulated, in which the 1,000 lengths were sampled from inside the MPA. 400 of these lengths were aged in the simulated sampling protocol to provide length-at-age data (see Appendix). A von Bertalanffy growth function was fit to the length-at-age data, and L_∞ , k , and t_0 were estimated. An age-length key was also created from these data, and was used to convert the remaining length composition data from inside the MPA to age composition data. A catch curve was fit to the logged age frequency data to

estimate the total mortality inside the MPA, which I assumed equaled M (sensu Kay et al. 2012). Only those cohorts that had been protected from fishing throughout their entire lives were included, thus eliminating older age classes that experienced fishing mortality prior to MPA protection. The LBSPR model was then fit to the fishery-dependent length composition using the estimated values of M and the von Bertalanffy growth parameters to produce estimates of F and SPR. I refer to this MPA-based assessment procedure as the MPA-LBSPR.

I assumed the CV_{L_∞} was known without error for all the assessment procedures. An exploration of sensitivities of the LB-SPR showed that while the estimate of F is somewhat sensitive to this CV_{L_∞} for low M/k species, the estimate of SPR is insensitive to this parameter. Accuracy of the LBSPR can be improved by knowledge of the size at first maturity (Hordyk et al. 2015). While biological parameters are never known exactly, maturity-at-length studies are one of the easiest and least expensive studies to conduct, and so I assumed that the lengths at 50% and 95% maturity were available for all three model species.

2.4 Seven Uncertainty Scenarios

The accuracy and precision of F and SPR estimates from both assessment procedures were examined across six uncertainty scenarios (Table 2). Each scenario consisted of 100 trials; in each simulated trial the population was fished for 30 years before an MPA was established, data were collected 20 years after MPA implementation, and both assessment

procedures were applied for each species. Each species was subjected to the same randomly generated sampling error across scenarios.

In scenario 1, all of the parameters were assumed correctly and recruitment was deterministic to explore the performance of each assessment procedure under ideal (although non-realistic) conditions. The assumed parameters were passed to the DL-LBSPR, and the MPA-LBSPR used the length and age data from the MPA to estimate these parameters. As a result, I expected the DL-LBSPR to outperform the MPA-LBSPR under ideal conditions. In scenarios 2-4, the values of L_∞ , k , and M were misspecified. For each trial the assumed value of the parameter of interest was randomly drawn from a uniform distribution centered around the true parameter value used in the operating model (Table 2). The assumed values of M and k were distributed within $\pm 30\%$ of the true value. This range of uncertainty was somewhat arbitrary, but illustrated a situation where biological information was borrowed from a related species, and so was similar to the true value. A smaller uncertainty range of $\pm 20\%$ was used for the assumed values of L_∞ because extremely low assumed values of L_∞ may be smaller than the estimated length of selectivity, resulting in high rates of non-convergence of the LBSPR fitting routine. Recruitment was deterministic for scenarios 2, 3, and 4.

Scenarios 5 and 6 provided an opportunity to quantify how non-equilibrium conditions affected the performance of both procedures. The LBSPR estimation model fits a logistic selectivity curve to a length composition, and recruitment pulses might interfere with the assessment model's ability to fit accurate selectivity curves (Hordyk et

al 2014). All parameters in scenario 5 were known correctly (however, these parameters were still estimated in the MPA-LBSPR procedure), but recruitment was stochastic with log-normally distributed recruitment deviations. Scenario 6 was similar except that recruitment deviations were autocorrelated.

2.5 Simulated case study: assessing the contribution of MPA data

Scenario 7 was intended to mimic a real world situation for a data-limited fishery in which multiple kinds of uncertainty operate in concert (stochastic recruitment and unknown biological parameters). No borrowed parameter values were available for the DL-LBSPR, and so it was necessary to modify the DL-LBSPR by creating a simulated parameter estimation procedure that mimics the approach commonly taken when life history parameters must be estimated but no MPA data is available. In scenario 7, I modeled identical fishery-independent sampling protocols to collect 1,000 length and 400 age samples from both inside and outside the MPA. The MPA-LBSPR method was applied as previously described, with growth parameters and natural mortality estimated from length-at-age data from inside the MPA. The parameters used in the DL-LBSPR method were estimated from the data collected outside the MPA as follows: a von Bertalanffy growth function was fit to the age-at-length data, and M was estimated by assuming the Beverton-Holt Life History Invariant M/k to be equal to 1.5 (Jensen 1996), a commonly used relationship for estimating natural mortality (Kenchington 2014). Note that, of the three species tested here, this assumption is closest to the true value for lingcod, which has a M/k ratio of 1.63 (Table 1). F and SPR were then estimated following the usual LBSPR fitting procedure.

2.6 Performance metrics

For each trial in each scenario, I computed the relative error in the parameters of management interest, namely, F and expected equilibrium SPR at that F . Relative error (RE) is defined as the standardized difference between the estimated ($\hat{\theta}$) and the true (θ) values of a given parameter:

$$RE = \frac{\hat{\theta} - \theta}{\theta}$$

I examined the distribution of RE for both F and SPR for each species in each scenario, with positive mean relative error (MRE) values indicating an overestimation of the quantity of interest, and negative values indicating an underestimation. The RE was also used to calculate the mean absolute relative error (MARE) by averaging the absolute value of the RE from each trial for a given scenario. The MARE described the total deviation of the estimated parameter from the true value in terms of both bias and variance, regardless of direction, providing an overall measure of estimation performance. An increase in MARE indicated decreasing estimation ability for given procedure and scenario combination.

3. Results

3.1 Scenario 1: Perfect information

Scenario 1 tested the performance of the MPA-LBSPR and DL-LBSPR procedures under ideal conditions (correctly assumed biological parameters and deterministic recruitment). Both procedures estimated F with similar levels of bias for gopher and blue rockfish when perfect biological information was used. The MRE in F for both

procedures was $<3\%$ for both species (Table 3). For lingcod the MRE in F was 3.1% when the DL-LBSPR was used, and 12.9% when the MPA-LBSPR was used. This consistent overestimation of F in lingcod, the species with the highest variation in length at age (Table 1), led to an underestimation of SPR. The MARE in F was higher for the MPA-LBSPR than for the DL-LBSPR for all three species when the biological parameters were provided to the DL-LBSPR without error.

Conditions modeled in scenario 1 (perfect information, no recruitment variability) are unlikely to be encountered in the real world, yet this scenario provided a useful standard against which to compare the performance of each procedure when additional types of error were added. In the following sections, scenario 1 is included as benchmark to illustrate the change in performance when misspecification of error (scenarios 2-4) or recruitment variability (scenarios 5 and 6) is added.

3.2 Scenarios 2-4: Misspecification of Biological Parameters

Figure 1 shows the RE in F resulting from misspecification of the parameters M , L_∞ and k for both the DL-LBSPR procedure and the MPA-LBSPR procedure. The RE was smoothed using non-parametric local regression (LOESS). Misspecification in M (scenario 2) was negatively related to the RE in the DL-LBSPR estimates of F (Figure 2a), while misspecification in L_∞ and k were both positively related to the DL-LBSPR procedure's estimates of F (Figure 2b and 2c). Thus, assuming that M is lower than the true value results in an underestimation of F , but assuming that L_∞ or k is lower than the true value results in an overestimation of F . This trend was reversed in gopher rockfish when L_∞ was severely underestimated because gopher rockfish has a low true L_∞ relative

to its size at selectivity (Table 1). When L_{∞} was assumed to be very low, the LBSPR model interpreted the large number of fish near the assumed maximum size as the product of an F near or equal to zero, as seen in the bend of the solid trend line in Figure 2b. As expected, the MPA-LBSPR was insensitive to the assumed error in all three parameters (Figure 1d-f). The MARE associated with the MPA-LBSPR estimates remained constant across Scenarios 1-4, while it increased substantially for the DL-LBSPR.

The assumed parameters were used in both the assessment model to estimate F and the spawning biomass per recruit model used to calculate the SPR retained at that F . Figure 2 shows the distribution of SPR estimates from both assessment procedures for all three species when the biological parameters were known perfectly (scenario 1) and when M , L_{∞} or k were assumed with error (scenarios 2-4). When the biological parameters were assumed correctly, unbiased and extremely precise estimates of SPR were generated by the DL-LBSPR procedure for all three species (Figure 2a-c, scenario 1). However, misspecification in the biological parameters increased the variance in SPR estimates substantially (Figure 2a-c, scenarios 2-4). Error in the assumed value of L_{∞} had a larger effect on the estimated SPR for blue and gopher rockfish than for lingcod at both low and high fishing pressures. Error in the assumed value of M had the smallest effect on error in the estimated SPR.

The error in the empirically obtained estimates of M , L_{∞} and k contributed to the higher variance observed in the MPA-LBSPR than the DL-LBSPR in scenario 1 (Figure

2a and 2d). Because the same data was generated for each trial across scenarios the variance in estimated SPR remained constant regardless of the error in assumed parameters. The MPA-LBSPR yielded more precise estimates of SPR across scenarios 2-4 than the DL-LBSPR.

3.3 Scenarios 5 and 6: Non-equilibrium conditions

Figure 3 shows how the addition of stochastic (scenario 5) and autocorrelated (scenario 6) recruitment variability affected the performance of both the DL-LBSPR and MPA-LBSPR. In the deterministic model (scenario 1; Figure 3a-c) the estimated size at full selectivity (sel_{95}) is underestimated for all three species using the MPA-LBSPR method. However, there was little bias in the estimation of F and SPR using both procedures for gopher and blue rockfish, though the variance in both parameters was lower when the DL-LBSPR had perfect biological information available (Table 3). The MPA-LBSPR method overestimated F and underestimated SPR for lingcod when the fishing pressure was low.

When stochastic recruitment was introduced (scenario 5; Figure 3d-f), both assessment procedures showed the same patterns in their estimates of selectivity parameters as in the deterministic scenario. The MARE in F increased for both procedures, achieving similar values for all three species scenario 5 (Table 3). The estimates of both F and SPR were unbiased for gopher and blue rockfish, but the MPA-LBSPR overestimated F and underestimated SPR for lingcod under low F conditions. The MARE in F increased when autocorrelation was present (Table 3), however, SPR

estimates remained unbiased with low variance for gopher and blue rockfish. The MARE for lingcod more than doubled when autocorrelation was present, suggesting that autocorrelation severely impacts the precision of the estimator.

3.4 Scenario 7: Simulated case study

When all of the parameters were unknown, the modified DL-LBSPR estimates of growth parameters were relatively accurate for gopher and blue rockfish, despite being fit to data from a moderately fished site (Figure 4a-b). However, estimates varied more for lingcod (Figure 4c). The DL-LBSPR consistently overestimated M for both gopher and blue rockfish, though estimates for lingcod were more accurate (Figure 4a-c). This was due to the fact that the true M/k ratio used in the underlying operating model for lingcod was 1.63, compared to 0.8 for gopher rockfish and 1.07 for blue rockfish. Thus the DL-LBSPR approach of estimating M by assuming M/k to equal 1.5 resulted in a (coincidentally) more accurate estimate of M for lingcod than for the other two species. For both gopher and blue rockfish, the modified DL-LBSPR procedure resulted in an extreme underestimation of F and an overestimation of SPR (Figure 4). Despite relatively accurate estimations of M , L_∞ and k for lingcod, F was overestimated and SPR was underestimated due to the high variation in length-at-age in larger individuals. By contrast, the MPA-LBSPR method returned unbiased estimates of F and SPR for gopher and blue rockfish, with equal or lower error than the modified DL-LBSPR (Figure 4). Both the DL-LBSPR and the MPA-LBSPR procedures displayed similar levels of accuracy for lingcod in the low fishing pressure scenarios.

3.5 High Fishing Mortality

The performance of the DL-LBSPR and MPA-LBSPR procedures across all seven scenarios followed the same general patterns described in the preceding sections when gopher and blue rockfish were fished at high fishing mortalities (Table 4; Figures 5-8). In general, both assessment procedures underestimate F for gopher rockfish and overestimate F for blue rockfish and lingcod (Figures 1 and 5). However, the bias seen in estimated F and SPR when lingcod was fished at $F=M$ disappeared at high fishing mortalities. This is due to the fact that the largest fish in the population, which exhibit the highest variation in length-at-age, have been effectively eliminated from the size structure when $F=3M$. As a result, the MPA-LBSPR was much more accurate for lingcod under high F conditions. While the error in estimated F is distributed around zero for all of the misspecification scenarios, the $MARE$ is large for all three species in scenario 3 (Table 4).

Figure 6 shows the RE in SPR for scenarios 1-4 when F is high. As in the low F set, the DL-LBSPR performs better when provided perfect information (scenario 1), but the MPA-LBSPR consistently performs better when biological parameters are misspecified (scenarios 2-4). While in the low F scenarios lingcod's estimates of SPR were equally affected by error in L_∞ and k , k has a larger effect in the high F scenarios (Figure 6). Under deterministic conditions (scenarios 1-4) the MPA-LBSPR estimates F with a MRE of $\leq 5\%$ of the true F for all three species, indicating that at higher fishing mortalities the variability in length at age, which increases with size, may be less problematic for the LBSPR fitting routine (Table 4).

Model performance under variable recruitment was similar for gopher and blue rockfish in the high F set (Figure 7) as it was in the low F set (Figure 3). Stochastic recruitment results in very little bias in estimates of F by the MPA-LBSPR, with $MRE < 5\%$ for all three species in scenario 5 (Table 4). Estimates of SPR produced by the MPA-LBSPR procedure are substantially less variable than those produced by the DL-LBSPR in scenario 5 (Figure 7). However, autocorrelated recruitment has a larger effect on the performance of the MPA-LBSPR than on the DL-LBSPR, especially for lingcod.

The performance of both procedures in the simulated case study at high F is shown in Figure 4. The performance of the modified DL-LBSPR in the simulated case study (scenario 7) was similar at both low and high F for gopher and blue rockfish, but the biological parameter estimates were substantially more variable for lingcod under the high F conditions. There was an increased tendency for the modified DL-LBSPR procedure to over estimate L_∞ and under estimate k across all three species. The MPA-LBSPR was able to estimate L_∞ and k accurately and consistently at high F for all species. The MPA-LBSPR had lower bias than in the low F scenarios while maintaining similar levels of variance for gopher and blue rockfish. The MPA-LBSPR was both more accurate and more precise for lingcod at high F .

4. Discussion

MPA-derived estimates of biological parameters improved the accuracy of SPR estimates when these parameters were unknown or misspecified. The MPA-LBSPR produced more accurate estimates for gopher and blue rockfish than for lingcod when

fished at a low F because the higher CV_{L_∞} value in lingcod introduced greater error when lengths were converted to ages. There was a tendency for both the DL-LBSPR and the MPA-LBSPR methods to overestimate fishing mortality and underestimate the SPR for lingcod at low fishing pressures indicating that this method, regardless of how the biological parameters were estimated, may be less appropriate for species with highly variable growth. However, the bias present for this species was both moderately low (SPR is underestimated by an average of 12% in scenarios 1-4, and 26% in scenario 7) and precautionary, and would therefore generate more conservative management decisions. The bias was reduced when fishing mortality was high due to the elimination of the largest (and most variable in terms of length at age) from the population.

The analysis conducted in scenario 7 tested the MPA-LBSPR under realistic conditions for data-limited fisheries. The method performed as well as the DL-LBSPR procedure for lingcod at low fishing levels, and outperformed the DL-LBSPR procedure for all other combinations of species and fishing pressures. The DL-LBSPR procedure likely performed well for lingcod because the assumption that $M=1.5k$ is close to the true underlying M/k ratio of 1.63 for this species. In a review of 29 natural mortality estimators that have been proposed for data limited fisheries, Kenchington (2014) found that Jensen's relationship yielded inaccurate mortality estimates both for species that exhibit deterministic growth (low M relative to k) and for those that never reach their asymptotic lengths (high M relative to k). Prince et al. (2014) came to a similar conclusion based on a meta-analysis of empirically-estimated M/k ratios across 123 marine species. The use of relationships to derive natural mortality estimates for fish

species has probably led to undetected biases in a wide range of assessment models, both data-rich and data-limited. Had another mortality estimator been chosen the modified DL-LBSPR method might have performed poorly for lingcod.

MPAs appear useful for improving natural mortality estimates for both data-limited and data-rich stocks of nearshore, sedentary species, but that value may depend on the amount of movement a target species exhibits. This study assumed negligible movement between closed and open patches for illustrative purposes. However, increased movement rates between fished and protected areas compromises the ability of populations inside MPAs to reach unfished size structures. As a result, low movement between patches, especially in the face of high fishing pressure, may cause assessors to overestimate stock status. This would impact an MPA-based assessment for lingcod which, despite having relatively small mean home ranges, occasionally move >20km, compared with observed movements of <0.2km for blue rockfish and <2km for gopher rockfish (Lea et al. 1999, Jorgensen et al. 2006). The size of the MPA relative the scale of movement will determine the effectiveness of MPAs as reference areas. While few fish species are completely sedentary, Kay and Wilson (2012) showed that it was possible to limit the biasing effects of movement on mortality estimates for lobster by sampling as far from the edges of the MPA as possible. Further research is needed to understand how movement between closed and open areas affects both the utility of information from inside MPAs to accurately estimate biological parameters and the LBSPR method's ability to estimate F .

I assumed that MPAs were a) completely no-take and well enforced, b) large relative to the adult home range of the species in question, and c) established long enough to allow the population inside the MPA to approach its unfished size and age structure. Real world MPAs are most likely to meet this criteria in developed countries (Edgar et al. 2014). However, the potential for MPAs to improve fisheries management via the estimation of biological parameters may provide an incentive for the creation of new MPAs and the maintenance of existing ones. Incorporation of MPAs into data-limited assessments may be particularly applicable in settings such as California, where a number of nearshore species remain unassessed. The presence of a network of no-take MPAs there may allow for the rapid assessment of these species that lack historical data . However, this analysis assumed that data collection began 20 years after the MPA was established in order to allow the age and size structure to approach unfished conditions. Many MPAs worldwide have only been established in the last few years, which suggests that methods that rely on MPAs as reference areas, while promising, may not be applicable for some time.

These results contribute to the nascent field of MPA-based fisheries management, specifically for small-scale, data-limited fisheries which, by some estimates, land up to 50% of the worlds catch (FAO 2012). It is likely that the cost of data required to assess these fisheries using conventional methods exceeds the value of these fisheries (Orensanz et al. 2005). Unfortunately, fishery-independent sampling is generally costly, even for a study with limited sample sizes such as is described here, and aging data is even more difficult to obtain. It may not be cost-effective to integrate MPAs into the management of

species that are considered low value or at low risk of overfishing (Johannes 1998). For higher value fisheries, however, pairing life history parameters estimated from MPAs with data-limited assessment such as the LBSPR method has the potential to improve estimates of fishing mortality using data that can be collected in a single fishing year. Of course, using an SPR-based estimation model assumes that the stock meets equilibrium conditions. While stocks are never in equilibrium, this method is most applicable to stocks with relatively stable dynamics from year to year. Basing management on single year snap-shots of data is always risky, but if such a method is required, the MPA-LBSPR provides a fairly robust option.

References

- Babcock, E.A., and MacCall, A.D. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? *Can J Fish and Aquat Sci* 68(2): 343–359.
- Babcock, E.A., Coleman, R., Karnauskas, M., and Gibson, J. 2013. Length-based indicators of fishery and ecosystem status: Glover's Reef Marine Reserve, Belize. *147*: 434–445.
- Berkes, F. 2003. Alternatives to conventional management: Lessons from small-scale fisheries. *Environments* 31: 5–20.
- Beverton, R., and Holt, S.J. 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *Rapp P-v Réunion - Cons Int Explor Mer* 154.
- Brooks, E.N., Powers, J.E., and Cortés, E. 2010. Analytical reference points for age-structured models: application to data-poor fisheries. *ICES J Mar Sci* 67(1): 165–175.
- Cope, J.M., and Punt, A.E. 2009. Length-Based Reference Points for Data-Limited Situations: Applications and Restrictions. *Mar Coast Fish* 1(1): 169–186.
- Costello, C., Ovando, D., Hilborn, R., Gaines, S.D., Deschenes, O., and Lester, S.E. 2012. Status and Solutions for the World's Unassessed Fisheries. *Science* 338(6106): 517–520.
- Dick, E.J., and MacCall, A.D. 2011. Depletion-based stock reduction analysis: a catch-based method for determining sustainable yields for data-poor fish stocks. *110*(2): 331–341.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., and Thomson, R.J. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506(7487): 216–220.
- Edwards, C.T.T., Hillary, R.M., Levontin, P., Blanchard, J.L., and Lorenzen, K. 2012. Fisheries Assessment and Management: A Synthesis of Common Approaches with Special Reference to Deepwater and Data-Poor Stocks. *Reviews in Fisheries Science* 20(3): 136–153.
- Ehrhardt, N.M., and Ault, J.S. 1992. Analysis of two length-based mortality models applied to bounded catch length frequencies. *T Am Fish Soc* 121(1): 115–122.

- Essington, T.E. 2001. The Precautionary Approach in Fisheries Management: the Devil Is in the Details. *Trends Ecol Evol* 16(3): 121–122.
- FAO. 2012. Fishery and Aquaculture Statistics. Global Fisheries commodities production and trade 1976-2009 (FishstatJ). FAO Fisheries and Aquaculture Department.
- Field, J.C., Punt, A.E., Methot, R.D., and Thomson, C.J. 2006. Does MPA mean ‘Major Problem for Assessments’? Considering the consequences of place-based management systems. *Fish Fish* 7(4): 284–302.
- Froese, R. 2004. Keep it simple: three indicators to deal with overfishing. *Fish Fish* 5(1): 86–91.
- Gaines, S.D., Lester, S.E., Grorud-Colvert, K., Costello, C., and Pollnac, R. 2010. Evolving science of marine reserves: New developments and emerging research frontiers. *PNAS* 107(43): 18251–18255.
- Garrison, T.M., Hamel, O.S., Punt, A.E., and Jonsson, B. 2011. Can data collected from marine protected areas improve estimates of life-history parameters? *Can J Fish and Aquat Sci* 68(10): 1761–1777.
- Goodyear, C.P. 1990. Spawning stock biomass per recruit: the biological basis for a fisheries management tool. In ICCAT Working Document SCRS/89/92. Miami, Florida.
- Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. In Risk evaluation and biological reference points for fisheries management. Edited by S.J. Smith, J.J. Hunt, and D. Rivard. *Can. Spec. Publ. Fish. Aquat. Sci.* 120. pp. 67–82.
- Hilborn, R. 2002. The dark side of reference points. *B Mar Sci* 70(2): 403–408.
- Hilborn, R., and Ovando, D. 2014. Reflections on the success of traditional fisheries management. *ICES J Mar Sci* 71: 1040–1046.
- Hoenig, J.M., Barrowman, N.J., Hearn, W.S., and Pollock, K.H. 1998. Multiyear tagging studies incorporating fishing effort data. *ICES J Mar Sci* 55(6): 1466–1476.
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., and Prince, J. 2015. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES J Mar Sci* 72(1): 217–231.
- Jagiello, T.H., and Wallace, F.R. 2005. Assessment of Lingcod (*Ophiodon elongatus*) for the Pacific Fishery Management Council in 2005.
- Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can J Fish and Aquat Sci* 53(4): 820–822.

- Jiao, Y., Cortés, E., Andrews, K., and Guo, F. 2011. Poor-data and data-poor species stock assessment using a Bayesian hierarchical approach. *Ecol Appl* 21(7): 2691–2708.
- Johannes, R.E. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol Evol* 13(6): 243–246.
- Jorgensen, S.J., Kaplan, D.M., Klimley, A.P., Morgan, S.G., O'Farrell, M.R., and Botsford, L.W. 2006. Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home range. *Mar Ecol Prog Ser* 327: 157–170.
- Kay, M.C., and Wilson, J.R. 2012. Spatially explicit mortality of California spiny lobster (*Panulirus interruptus*) across a marine reserve network. *Environ Conserv* 39(03): 215–224.
- Kenchington, T.J. 2014. Natural mortality estimators for information-limited fisheries. *Fish Fish* 14(4): 533–562.
- Key, M., MacCall, A.D., Bishop, T., and Leos, B. 2005. Stock assessment of the gopher rockfish (*Sebastes carnatus*). California Department of Fish & Game.
- Key, M., MacCall, A.D., Field, J.C., Aseltine-Neilson, D., and Lynn, K. 2008. The 2007 assessment of blue rockfish (*Sebastes mystinus*) in California. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center.
- Klaer, N.L., Wayte, S.E., and Fay, G. 2012. *Fisheries Research*. 134-136: 42–51.
- Kleisner, K., Zeller, D., Froese, R., and Pauly, D. 2013. Using global catch data for inferences on the world's marine fisheries. *Fish Fish* 14: 293–311.
- Le Quesne, W.J.F., and Jennings, S. 2011. Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity. *J Appl Ecol* 49(1): 20–28.
- Lea, R.N., McAllister, R.D., and VenTresca, D.A. 1999. Biological aspects of nearshore rockfishes of the genus *Sebastes* from central California: with notes on ecologically related sport fishes. State of California, The Resources Agency, Department of Fish and Game.
- MacCall, A.D. 2009. Depletion-corrected average catch: a simple formula for estimating sustainable yields in data-poor situations. *ICES J Mar Sci* 66(10): 2267–2271.
- Martell, S., and Froese, R. 2012. A simple method for estimating MSY from catch and resilience. *Fish Fish* 14(4): 504–514.
- Martell, S.J., Walters, C.J., and Wallace, S.S. 2000. The use of marine protected areas for conservation of lingcod (*Ophiodon elongatus*). *B Mar Sci* 66(3): 729–743.

- McGilliard, C.R., Hilborn, R., MacCall, A., Punt, A.E., and Field, J.C. 2011. Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks? *ICES J Mar Sci* 68: 201–211.
- Moore, J.E., Curtis, K.A., Lewison, R.L., Dillingham, P.W., Cope, J.M., Fordham, S.V., Heppell, S.S., Pardo, S.A., Simpfendorfer, C.A., TUCK, G.N., and Zhou, S. 2013. Evaluating sustainability of fisheries bycatch mortality for marine megafauna : a review of conservation reference points for data-limited populations. *Environ Conserv* 40(04): 329–344.
- Mulligan, T.J., and Leaman, B.M. 1992. Length-at-age analysis: can you get what you see? *J Fish Res Board Can* 49(4): 632–643. NRC Research Press.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can J Fish and Aquat Sci* 56: 2404-2419.
- Orensanz, J.M.L., Parma, A.M., Jerez, G., Barahona, N., Montecinos, M., and Elias, I. 2005. What are the Key Elements for the Sustainability of “S-Fisheries?” Insights from South America. *B Mar Sci* 76(2): 527–556.
- Pascual, M.A., and Iribarne, O.O. 1993. How good are empirical predictions of natural mortality? *16(1): 17–24.*
- Patrick, W.S., Spencer, P., Link, J., Cope, J., Field, J., Kobayashi, D., Lawson, P., Gedamke, T., Cortés, E., and Ormseth, O. 2010. Using productivity and susceptibility indices to assess the vulnerability of United States fish stocks to overfishing. *Fish B-NOAA* 108(3): 305–322.
- Pauly, D., and Morgan, G.R. (Editors). 1987. Length-based methods in fisheries research. ICLARM Conference Proceedings.
- Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J., and Rice, J.A. 2003. A Review of Tagging Methods for Estimating Fish Population Size and Components of Mortality. *Fisheries* 28(10): 10–23.
- Prince, J., Hordyk, A., Valencia, S.R., Loneragan, N., and Sainsbury, K. 2014. Revisiting the concept of Beverton-Holt life-history invariants with the aim of informing data-poor fisheries assessment. *ICES J Mar Sci* 72: 194-203.
- Punt, A.E., Smith, D.C., and Smith, A.D.M. 2011. Among-stock comparisons for improving stock assessments of data-poor stocks: the “Robin Hood” approach. *ICES J Mar Sci* 68(5): 972–981.
- Sissenwine, M.P., and Shepherd, J.G. 1987. An alternative perspective on recruitment overfishing and biological reference points. *J Fish Res Board Can* 44(4): 913–918.

- Vetter, E.F. 1988. Estimation of natural mortality in fish stocks. *Fish B-NOAA* 86(1): 25–43.
- Walters, C.J., Hilborn, R., and Parrish, R. 2007. An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. *Can J Fish and Aquat Sci* 64(7): 1009–1018.
- Wilson, J.R., Prince, J.D., and Lenihan, H.S. 2010. A Management Strategy for Sedentary Nearshore Species that Uses Marine Protected Areas as a Reference. *Mar Coast Fish* 2(1): 14–27.
- Wilson, J.R., Valencia, S.R., Kay, M.C., and Lenihan, H.S. 2013. Integration of no-take marine reserves in the assessment of data-limited fisheries. *Conserv Lett* 7: 451–458.
- Worm, B., and Branch, T.A. 2012. The future of fish. *Trends Ecol Evol* 27(11): 594–599.

Tables

Table 1. Biological parameters used in operating model for each species.

Category	Symbol	Gopher rockfish	Blue rockfish	Lingcod
Natural	M	0.2	0.12	0.18
Mortality				
Growth	L_{∞}	31.2 cm	40.02 cm	126.6 cm
	k	0.186	0.15	0.11
	t_0	0	0	0
	$CV_{L_{\infty}}$	0.05	0.1	0.15
Weight	w_a	$1.299e^{-5}$	0.0158	$1.76e^{-3}$
	w_b	3.077	2.988	3.3978
Fecundity	f_a	1.559	1.559	$3.026e^{-4}$
	f_b	3.179	3.179	3
Maturity	ma_{50}	17.7 cm	29 cm	55.7 cm
	ma_{95}	21 cm	35 cm	75 cm
Steepness	h	0.65	0.58	0.8
Recruitment variation	σ_r	0.5	0.7	0.8
Autocorrelation	ρ	0.5	0.5	0.7
Selectivity	v_{50}	20 cm	18 cm	40 cm
	v_{95}	24 cm	22 cm	50 cm
M/k Ratio	--	1.07	0.8	1.63

Table 2. Uncertainty scenarios explored in simulation.

Scenario	Parameter Assumptions	Recruitment
(1) Perfect Information	All parameters are assumed to be known correctly	Deterministic
(2) Error in assumed M	$M_{assumed}$ is uniformly distributed to be within $\pm 30\% M_{true}$	Deterministic
(3) Error in assumed L_{∞}	$L_{\infty assumed}$ is uniformly distributed to be within $\pm 20\% L_{\infty true}$	Deterministic
(4) Error in assumed k	$k_{assumed}$ is uniformly distributed to be within $\pm 30\% k_{true}$	Deterministic
(5) Stochastic recruitment	All parameters are assumed to be known correctly	Stochastic
(6) Auto-correlated recruitment	All parameters are assumed to be known correctly	Auto-correlated
(7) Simulated Case Study	M , L_{∞} , and k are estimated according to procedure outlined in methods	Stochastic

Table 3. Mean relative error (MRE) and mean absolute relative error (MARE) in estimated F/M when fishing pressure is low ($F=M$).

Scenario	Gopher rockfish		Blue rockfish		Lingcod	
	MRE	MARE	MRE	MARE	MRE	MARE
<i>(1) Perfect Information</i>						
DL-LBSPR	-0.023	0.059	-0.002	0.040	0.031	0.041
MPA-LBSPR	-0.022	0.122	-0.027	0.100	0.129	0.164
<i>(2) Error in assumed M</i>						
DL-LBSPR	0.005	0.302	0.013	0.246	0.073	0.243
MPA-LBSPR	-0.022	0.122	-0.027	0.100	0.129	0.164
<i>(3) Error in assumed L_{∞}</i>						
DL-LBSPR	-0.101	0.960	-0.054	0.743	0.012	0.327
MPA-LBSPR	-0.022	0.122	-0.027	0.100	0.129	0.164
<i>(4) Error in assumed k</i>						
DL-LBSPR	-0.025	0.263	-0.054	0.247	-0.023	0.250
MPA-LBSPR	-0.022	0.122	-0.027	0.100	0.129	0.164
<i>(5) Stochastic Recruitment</i>						
DL-LBSPR	-0.086	0.264	-0.042	0.150	0.111	0.295
MPA-LBSPR	0.040	0.287	-0.075	0.182	0.378	0.530
<i>(6) Auto-correlated Recruitment</i>						
DL-LBSPR	0.264	0.526	0.082	0.328	0.302	0.507
MPA-LBSPR	0.098	0.573	-0.025	0.429	0.150	0.964
<i>(7) Case Study</i>						
DL-LBSPR	-0.636	0.663	-0.898	0.898	0.577	0.639
MPA-LBSPR	0.040	0.287	-0.075	0.182	0.378	0.530

Table 4. Mean relative error (MRE) and mean absolute relative error (MARE) in estimated F/M when fishing pressure is high ($F=3M$).

Scenario	Gopher rockfish		Blue rockfish		Lingcod	
	MRE	MARE	MRE	MARE	MRE	MARE
<i>(1) Perfect Information</i>						
DL-LBSPR	-0.023	0.058	0.053	0.054	0.106	0.106
MPA-LBSPR	-0.039	0.107	0.025	0.069	0.046	0.096
<i>(2) Error in assumed M</i>						
DL-LBSPR	0.002	0.165	0.065	0.184	0.142	0.175
MPA-LBSPR	-0.039	0.107	0.025	0.069	0.046	0.096
<i>(3) Error in assumed L_∞</i>						
DL-LBSPR	-0.075	0.489	-0.012	0.409	0.082	0.197
MPA-LBSPR	-0.039	0.107	0.025	0.069	0.046	0.096
<i>(4) Error in assumed k</i>						
DL-LBSPR	-0.060	0.204	0.017	0.163	0.073	0.205
MPA-LBSPR	-0.039	0.107	0.025	0.069	0.046	0.096
<i>(5) Stochastic Recruitment</i>						
DL-LBSPR	-0.020	0.261	0.025	0.151	0.252	0.290
MPA-LBSPR	-0.002	0.315	-0.041	0.193	-0.025	0.302
<i>(6) Auto-correlated Recruitment</i>						
DL-LBSPR	0.075	0.350	0.107	0.254	0.212	0.340
MPA-LBSPR	0.108	0.464	0.084	0.349	-0.193	0.636
<i>(7) Case Study</i>						
DL-LBSPR	-0.249	0.380	-0.394	0.428	0.670	0.900
MPA-LBSPR	-0.002	0.315	-0.041	0.193	-0.025	0.302

Figures

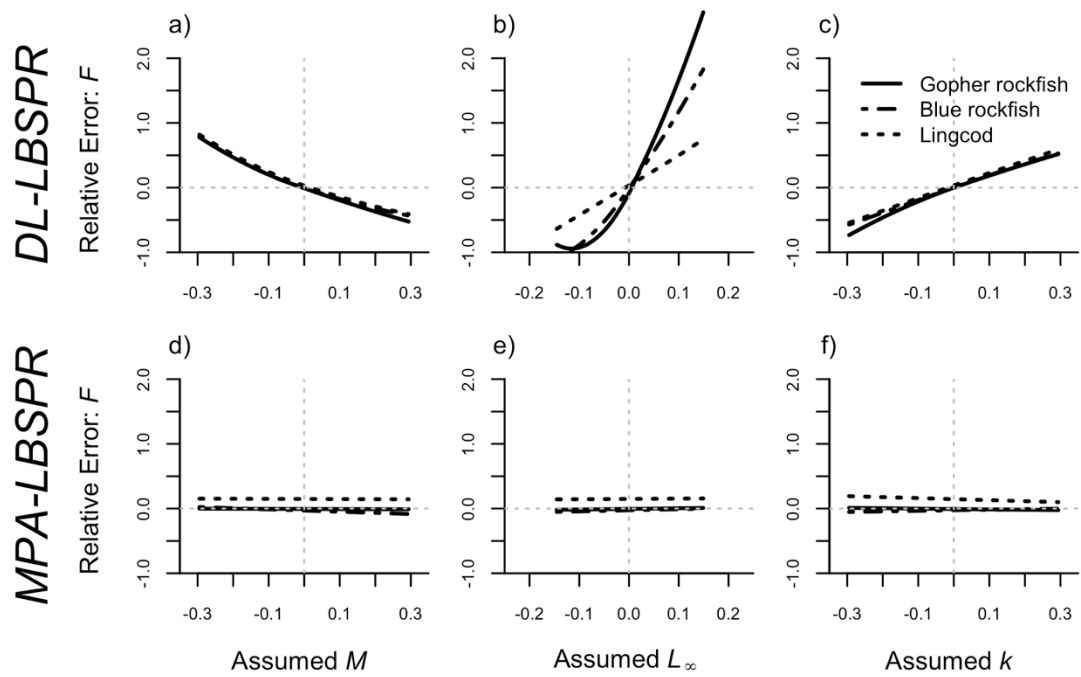


Figure 1. Relative error in F/M estimate for each species in response to assumed parameter values at low fishing pressure ($F=M$) when assessed using the DL-LBSPR (top, panels a-c) and MPA-LBSPR (bottom; panels d-f) procedures.

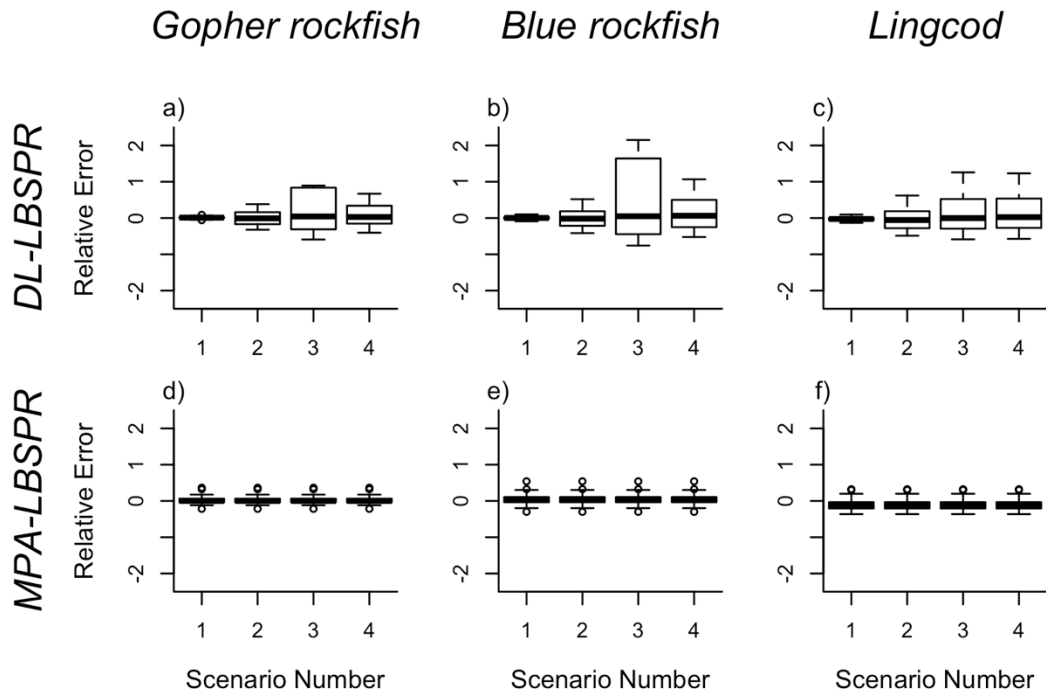


Figure 2. Relative error in estimated SPR for scenarios 1-4 at low fishing pressure ($F=M$) when assessed using the DL-LBSPR (top; panels a-c) and MPA-LBSPR (bottom; panels d-f) procedures.

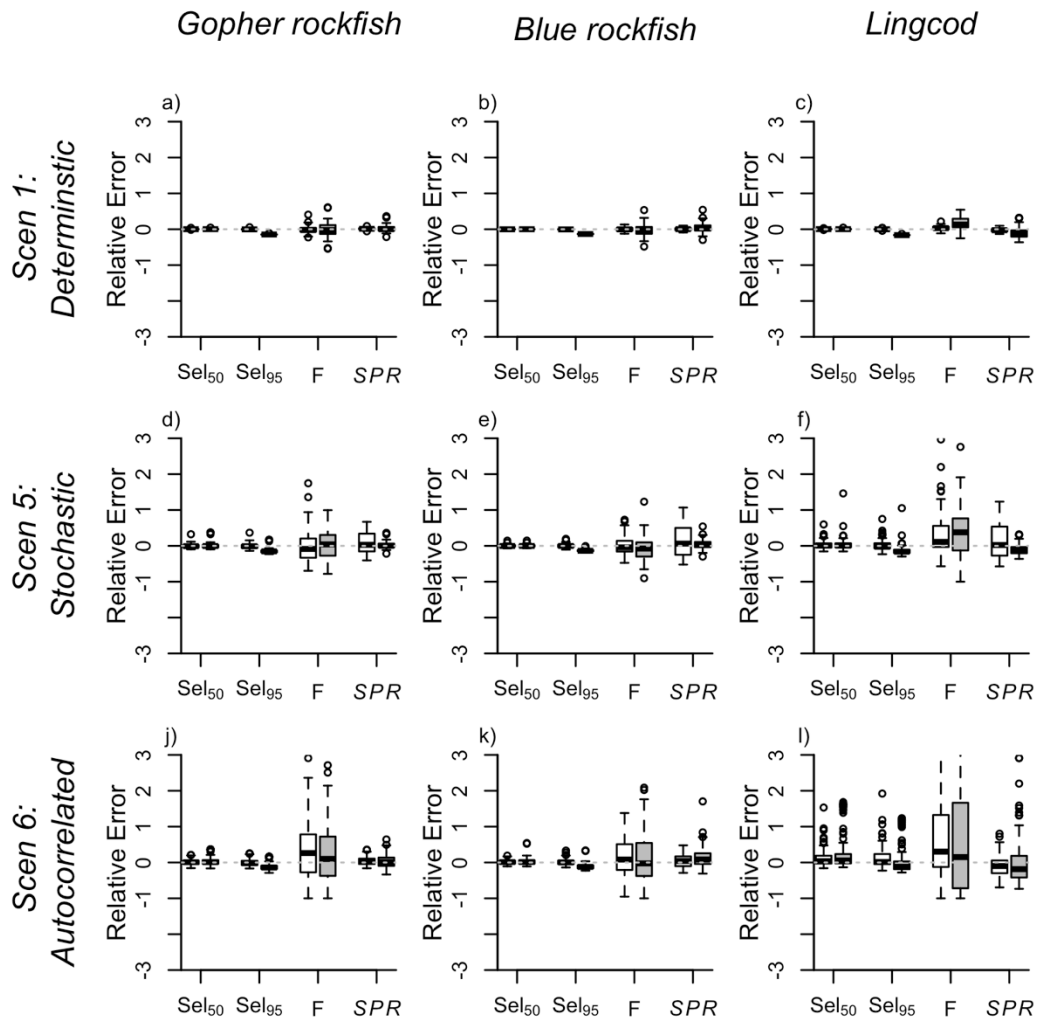


Figure 3. A comparison of accuracy and precision in the DL-LBSPR method (in white) and the MPA-LBSPR method (in grey) for each species under scenarios 1 (no stochasticity), 5 (stochastic recruitment) and 6 (auto-correlated recruitment) when fishing pressure is low ($F=M$).

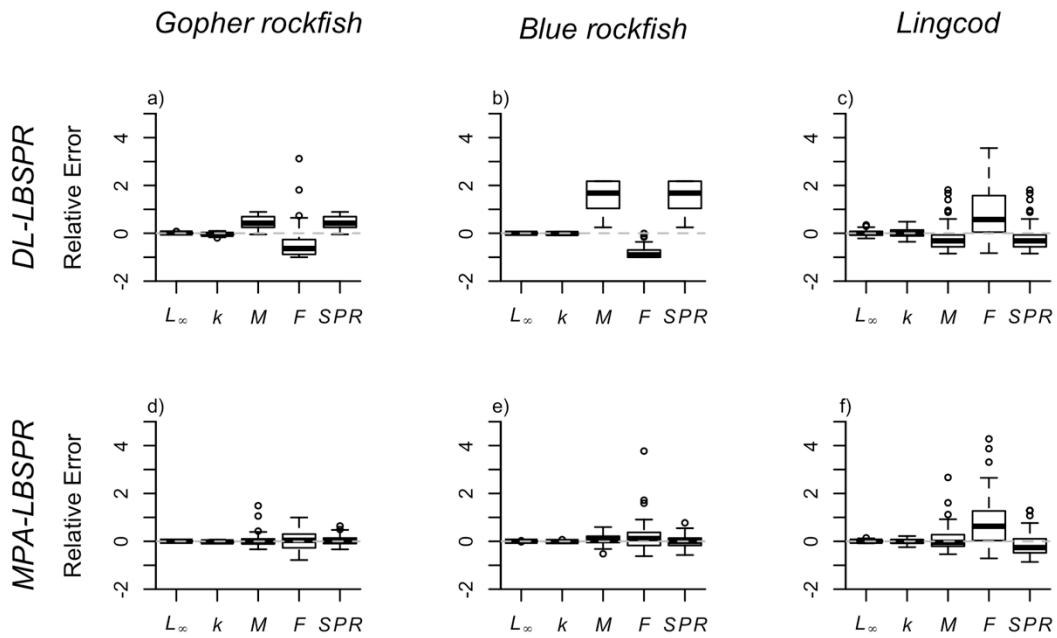


Figure 4. The estimated parameters resulting from the simulated case study under low fishing pressure ($F=M$). In the top panel (a-c), growth parameters are estimated using length-at-age data sampled from a fished site, M is assumed to equal $1.5k$, and F and SPR are estimated using the DL-LBSPR method. In the bottom panel (d-f), growth parameters are estimated using length-at-age data sampled from a no-take MPA, and M , F and SPR are estimated using the MPA-LBSPR procedure.

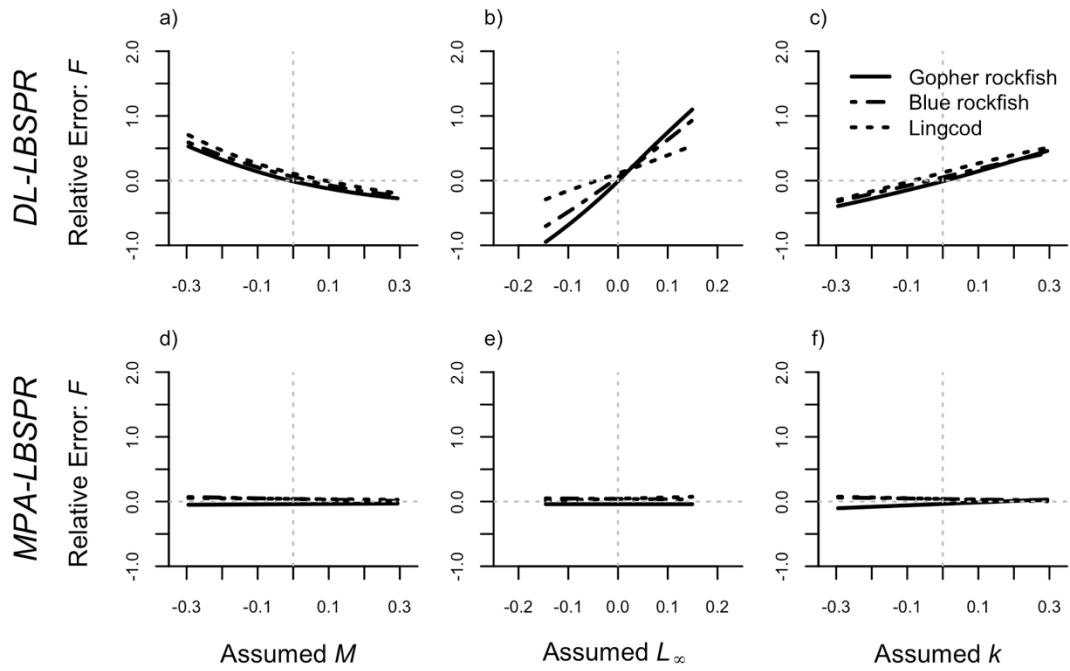


Figure 5. Relative error in F/M estimate for each species in response to assumed parameter values at high fishing pressure ($F=3M$) when assessed using the DL-LBSPR (top, panels a-c) and MPA-LBSPR (bottom; panels d-f) procedures.

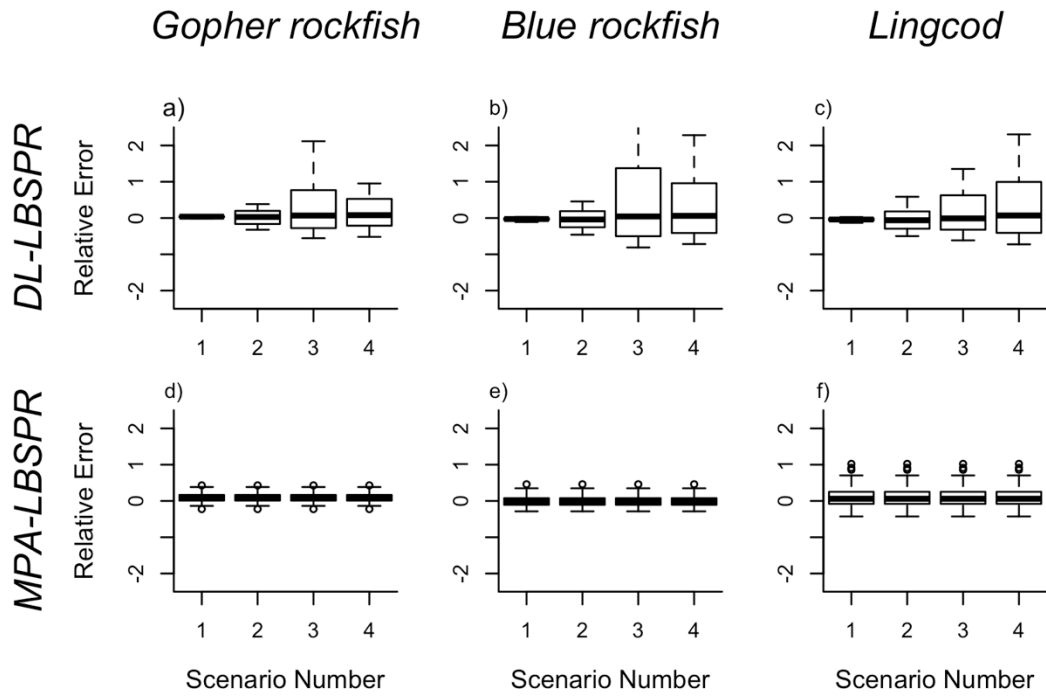


Figure 6. Relative error in estimated SPR for scenarios 1-4 at high fishing pressure ($F=3M$) when assessed using the DL-LBSPR (top; panels a-c) and MPA-LBSPR (bottom; panels d-f) procedures.

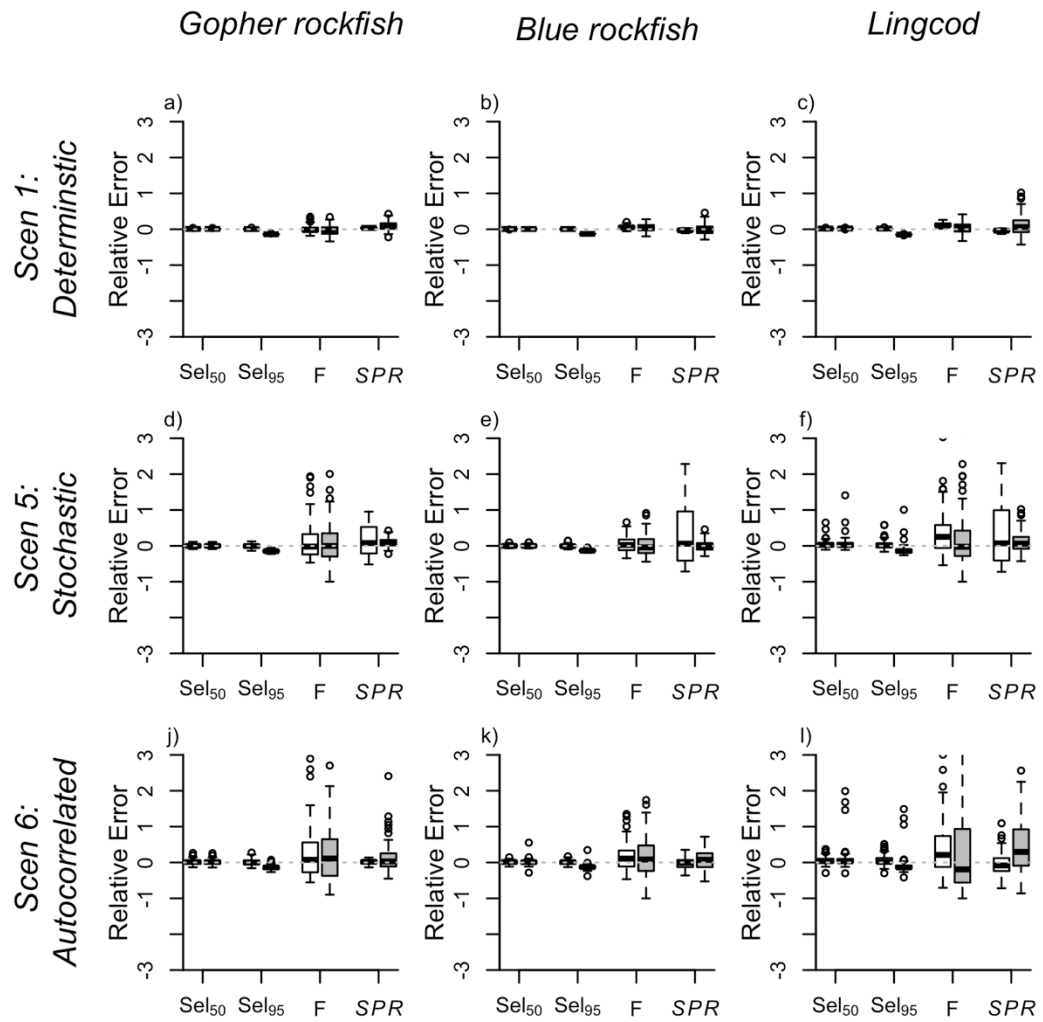


Figure 7. A comparison of accuracy and precision in the DL-LBSPR method (in white) and the MPA-LBSPR method (in grey) for each species under scenarios 1 (no stochasticity), 5 (stochastic recruitment) and 6 (auto-correlated recruitment) when fishing pressure is high ($F=3M$).

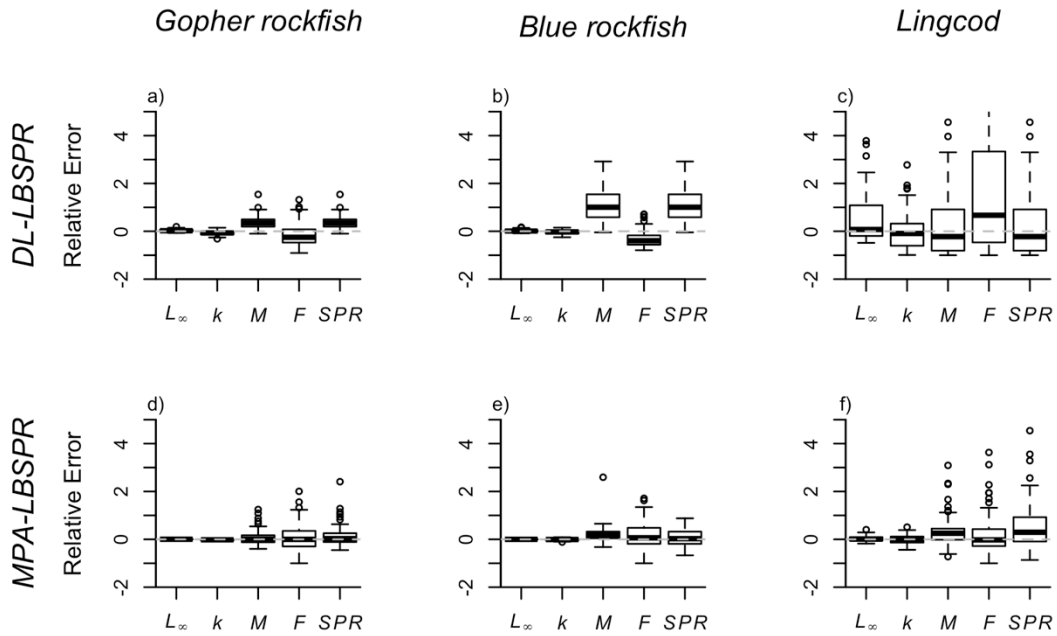


Figure 8. The estimated parameters resulting from the simulated case study under high fishing pressure ($F=3M$). In the top panel (a-c), growth parameters are estimated using length-at-age data sampled from a fished site, M is assumed to equal $1.5k$, and F and SPR are estimated using the DL-LBSPR method. In the bottom panel (d-f), growth parameters are estimated using length-at-age data sampled from a no-take MPA, and M , F and SPR are estimated using the MPA-LBSPR procedure.

IV. Integrating marine reserves into data-poor fisheries management: a comparison of reserve-based harvest strategies

Abstract

While MPAs can complicate conventional fisheries management by increasing the spatial heterogeneity in stock dynamics, recently developed harvest strategies take advantage of this heterogeneity by using MPAs as reference areas to better understand stock status. However, the accuracy of MPA-based harvest strategies, their capacity to safeguard against overfishing, and their general utility in fishery management has not been adequately tested. I examined the performance of four harvest strategies that require data from inside and outside MPAs for both short (<5 yrs) and long (20 yrs) temporal scales. For three model species, I ran six scenarios combining different levels of historical exploitation and movement behavior, with the objective of assessing the ability of MPA-based harvest strategies to prevent overfishing while maintaining high harvest levels under commonly occurring uncertainties in nearshore, spatially-explicit fisheries. All assessment methods were highly sensitive to time since MPA creation, historical fishing pressure, and movement. The size-based methods were generally more robust than the CPUE-based methods. When paired with a realistic control rule, all methods performed reasonably well for all three species. Results suggest that MPAs may improve the management of sedentary data-poor stocks, but that past fishing pressure and time since MPA implementation must be considered when using MPAs as reference areas.

1. Introduction

Up to 50% of the world's catch is landed by what Orensanz et al. (2005) labeled S-fisheries, those that target small-scale, spatially-structured, and sedentary stocks (FAO 2012). S-fisheries are usually data-poor and frequently the cost of data required to assess stock status using conventional data-rich methods exceeds their value. The majority of S-fisheries are artisanal and located in the southern hemisphere, where they play a major role in the economies and food security of developing countries (Berkes 2003). The set of factors described here present serious challenges for setting sustainable catch levels for half the world's fisheries.

No take marine protected areas (MPAs) have been proposed as a solution to manage or rebuild S-fisheries and buffer against perceived management failures. However, the creation of large MPAs introduce or increase spatial and temporal heterogeneity in stock size, abundance, and distribution, factors that create significant problems for traditional stock assessment-based management (Holland 2002), which aggregate data across space and assume homogeneity in fish distributions and population dynamics (Field et al. 2006). Additionally, traditional assessment approaches assume evenly distributed fishing mortality, an assumption that is hard to support in seascapes with MPAs, where empirical studies indicate that mortality is often clustered near reserve borders as fishermen "fish the line" (Murawski et al. 2005). The establishment of MPAs may also mean less abundant fishery-dependent data, upon which conventional stock assessments rely heavily (Bohnsack 1999). These factors interact to substantially complicate the integration of MPAs into existing stock assessment modeling and management (Punt and Methot 2004, Field et al. 2006).

Recently developed harvest strategies take advantage of spatio-temporal heterogeneity by using MPAs as reference areas with which to compare the impacts of fishing. These include a reserve-based decision tree (Wilson et al. 2010), a density ratio control rule (Babcock and MacCall 2011, McGilliard et al. 2011), a length-based spawning potential ratio estimator that uses MPA data to estimate critical biological parameters (Chapter 3), and a bounded catch curve estimator that compares mortality inside and outside MPAs (Wilson et al. 2013). This body of research suggests that MPAs provide information that can improve the management of small-scale or data-poor fisheries that lack the historical data required in stock assessments. Nevertheless, MPA-based approaches require different data inputs and estimate different reference points, so it is not yet clear which method may be most appropriate for a given fishery. To date, no formal evaluation of their performance under a standardized suite of commonly encountered uncertainties has been conducted.

In the last 10 years a network of MPAs have been established in California's waters, and the state is currently exploring the utility using of MPA-based harvest strategies to make management decisions for some of its near-shore data-poor fish stocks (e.g., Wilson et al. 2013). Here I use a bio-economic simulation model based on three species commonly landed in recreational and commercial fisheries in central California, to assess the ability of four MPA-based assessment methods to meet common management goals for data-poor stocks. In California, the current method of managing data-poor fisheries is to set catches at 50% of historically stable catch levels (Restrepo et al. 1998). As such, I compare the performance of the MPA-based methods to the Restrepo method, which requires no other data besides recent historical catches but severely reduces catches. The objective of this research is to provide

quantitative advice to managers about the tradeoffs between alternative methods under various conditions, as well as to further our understanding of MPAs as tools in the management of S-Fisheries.

2. Methods

A simulation model was used to evaluate how historical fishing pressure, stochastic recruitment, movement between fished and unfished areas, and time since reserve creation affected the performance of MPA-based stock harvest strategies. Harvest strategies include a data collection protocol, an assessment method to determine current stock status, and a control rule. A control rule is a function that describes the relationship between a stock status variable (usually abundance, depletion, or fishing mortality) and a management variable (usually fishing effort or catch) that will achieve predefined management objectives (Restrepo et al. 1998). Control rules represent agreed-upon actions in response to a given set of data, thus allowing managers to rapidly respond to changes as they arise.

I evaluated two aspects of harvest strategy performance. First, I assessed their ability to accurately estimate either fishing mortality or depletion level, depending on the assessment tested (Table 1), all under a constant effort harvest policy. Sometimes well-designed harvest strategies can achieve management objectives when estimates of stock status variables are inaccurate or imprecise (Dowling et al. 2015). This occurs when the estimated value falls within a range that triggers the control rule to adjust fishing intensity in the necessary direction. Therefore, in a second approach, I assessed the capacity of each harvest strategy to maximize catches while preventing stock declines, regardless of their accuracy in estimating stock status.

2.1 Simulation framework

Management Strategy Evaluation (MSE) is a commonly used and robust method for testing harvest strategies. Although there is no guarantee that a given strategy will perform in nature as it does virtually, simulation can identify strategies that do not perform well under probable uncertainties. MSE requires the specification of an operating model and a management model. The operating model used here consisted of a spatially-explicit population model that was used to represent the “true” underlying system. Data were generated using the operating model and provided to the management model, where the data were assessed and compared against targets, and a control rule was applied to determine harvest levels in the following time step (Figure 1). Each model run consisted of three phases. After a 100-year “burn in” period to allow the population to achieve unfished equilibrium, a 30-year historical fishing period was executed in which the stock was targeted at a constant fishing effort. After 30 years, a MPA was established in 20% of the available habitat. Twenty percent was used because it is often the lower bound of recommended target proportions of coastal area set aside in MPAs to prevent overfishing or preserve marine biodiversity (Gaines et al. 2010, Fox et al. 2011, Toonen et al. 2013). The fishery was then managed for 25 years under a data-poor scenario in which one of the candidate data-poor harvest strategies was applied every five years (Figure 2). Each run was repeated 100 times to explore how recruitment variation and sampling error impacts harvest strategy performance.

Two types of test procedures were run. The first was an analysis that gauged the accuracy of the stock status estimate returned by each assessment method and the second was a dynamic

analysis that examined management performance (i.e., maximizing harvest while preventing stock decline; Table 2). In the accuracy analysis, data were collected and assessed every five years but fishing effort remained constant for the entire 25-year assessment period, and stock status estimates from each assessment model were compared with the true values generated in the underlying operating model. In the dynamic analysis, each of the candidate harvest strategies (defined as a data collection protocol, assessment method, and control rule to update fishing pressure) was applied every five years. The long-term performance of each harvest strategy was evaluated based on its ability achieve a target biomass, prevent declines below a critical threshold, maximize catches, and maintain stable catches. Each simulation was composed of a test procedure, species, assessment type, and simulation scenario (Table 2), each of which is described in further detail below.

2.2 Operating model

The operating model consisted of an age-structured population model occupying 25 consecutive habitat patches. The equations governing the population dynamics are shown in the Appendix. I simulated the population dynamics of three demersal species commonly found in central California's nearshore groundfish fishery, specifically blue rockfish (*Sebastes mystinus*), gopher rockfish (*Sebastes carnatus*), and lingcod (*Ophiodon elongatus*). These three species were chosen to represent a slow (blue rockfish), medium (gopher rockfish), and fast (lingcod) life history type. That is, blue rockfish demonstrate slow growth, late maturation, and low productivity relative to the other two species, while lingcod display rapid growth, early maturation, and relatively high productivity. Gopher rockfish display intermediate values for these three life history parameters. The parameter values used to represent the life histories were

obtained from the most recent stock assessments for each species (Key et al. 2005, 2008, Jagielo and Wallace 2005), and are shown in Table 3.

The home ranges of adult blue rockfish, gopher rockfish, and lingcod differ in scale, but all are non-migratory species that inhabit nearshore rocky reefs (Key et al. 2005, 2008, Jagielo and Wallace 2005). The performance of reserves is highly sensitive to the movement of adult fish relative to the size of the reserve, because reserves provide less protection from fishing to species with higher movement rates (Grüss et al. 2011). Reserve-based assessment methods that rely on contrasts between fished and unfished areas to estimate stock status are also likely to be impacted by movement rates. I parameterized fish movement so that individuals had a 95% probability of staying within the specified number of consecutive patches during each time step (Table 2). In other words, a fish with a range of 3 patches had a 5% probability of moving 2 patches or more in either direction in a single time step. In the assessment accuracy test procedure, I ran simulations with and without movement to understand how movement affected the ability of each method to estimate quantities of interest. For the management strategy test procedures, I simulated movement for each species to understand how these procedures were likely to perform under real world conditions.

Recruitment followed a stochastic Beverton-Holt stock recruitment function, in which recruitment deviations were parameterized using a log-normally distributed error term (σ_r). Gopher rockfish was assumed to have the lowest variability in year-to-year recruitment, while lingcod was assumed to be the most variable (Jagiello and Wallace 2005). Larval movement followed a common pool dispersal model for all three species. Fishing effort was allocated in

proportion to the vulnerable biomass available in each patch in each year, conditional of the patch being open to fishing. The effects of these assumptions are discussed later.

2.3 Model starting conditions

It was necessary to a priori choose the number of recruits produced by each simulated unfished population (defined as R_0) because the number of recruits produced at all other population sizes is a function of R_0 and the steepness (h) of the population. Steepness is defined as the proportion of R_0 produced when the population is at 20% of unfished spawning stock biomass, and is a metric that describes the productivity of the stock in response to fishing, with higher steepness values indicating a higher number of recruits produced at 20% of the unfished biomass (B_0). Steepness values for the each species were extracted from their most recent stock assessments (Key et al. 2005, 2008, Jagielo and Wallace 2005), but the number of recruits produced at unfished levels is unknown. I chose a value of R_0 that would result in a catch level (i.e., landings) in years 30-35 of the model run that was similar to the average landings produced in the central coast region of California between 2002 and 2007 (based on commercial landings data, CPFV vessel logs, and the California Recreation Fisheries Survey; Table 3). While the performance of each assessment method and harvest strategy is not dependent on the value of R_0 , this allowed the results to be comparable to real world data.

2.4 Simulated data collection

A simulated yearly fishery-independent sampling program was initiated five years after the creation of the MPA to generate the size frequency and/or CPUE data required to run each assessment model (see Appendix). The survey employed the same selectivity as the fishery. One

patch in the center of the MPA was sampled to minimize the edge effects related to movement across the reserve borders (Kay and Wilson 2012), and the data from this patch was classified as “inside” the MPA. One patch at a distance of 10 patches from the MPA border was sampled to represent the conditions “outside” the reserve. The model was set up such that the all 25 patches formed a closed loop, with the patch number 1 being adjacent to both patch number 2 and patch number 25. Because of this, it did not matter on which side of the MPA the sampling occurred. The survey was simulated using a survey effort level that was <2% of the fishing effort (actual percentages varied because fishing effort was scaled in each scenario to keep F equal to either natural mortality or three times natural mortality for each species). I assumed that the survey catch weight was sampled without observation error, while the ages and lengths were sampled following the procedure in the Appendix.

The MPA-LBSPR and bounded mortality estimators also required additional sampling with a gear that sampled juvenile fish. Fish were sampled using this simulated protocol, in which the selectivity of the gear allowed for uniform sampling of the population above a very small size (such as a net with a very small mesh). These fish were aged and sized following the procedure describes in the Appendix, and for the rest age data was sampled from a probabilistic age-length key (Hilborn and Walters 1992). A von Bertalanffy growth function was also fit to the length-at-age data, and L_{∞} , k , and t_0 were estimated. A regression-based catch curve was fit to the logged age frequency data to estimate the total mortality inside the MPA, which I assumed equaled natural mortality (sensu Kay and Wilson 2012). Only those cohorts that had been protected from fishing throughout their entire lives were included, thus eliminating older age classes that

experienced fishing mortality prior to MPA protection. The estimates of these biological parameters were provided to the MPA-LBSPR and Bounded mortality methods (Table 2).

2.5 Data-poor harvest strategies tested

Five data-poor harvest strategies were chosen to be tested in both the accuracy and management performance simulations, including four reserve-based assessment models/control rules and the Restrepo et al. (1998) rule of setting catches at 50% of historical averages. The data requirements of each are shown in Table 4. Harvest control rules adjusted fishing effort every five years after MPA implementation. In comparing the long-term performance of these methods, it is necessary to ensure that the yearly and cumulative performance of each harvest strategy is not driven solely by the choice of unresponsive (or overly responsive) control rules. While truly optimal values for control rule parameters are always unknown due to fundamental environmental uncertainties (Lauck et al. 1998), for each control rule I determined parameterizations that would maximize catches over the 20 year time horizon while minimizing the probability of stock collapse ($SB_{curr} < 0.1SSB_0$). The parameters optimized in each harvest strategy are described in detail in the following sections.

2.5.1. MPA-Length based spawning potential ratio (MPA-LBSPR)

The first harvest strategy tested was the MPA-LBSPR. This method was adapted from the Hordyk et al.'s (2014) Length-Based Spawning Potential Ratio, which estimates the ratio of the fishing mortality (F) to the natural mortality (M) using size frequency data and estimates of biological parameters. The MPA-LBSPR uses size and age data collected from within a MPA to estimate the necessary biological parameters (see Chapter 3). A von Bertalanffy growth function

was fit to 1,000 simulated samples of paired size and age frequency data to estimate the maximum asymptotic size and growth rate, as well as to create a probabilistic age-length key to convert the size data collected inside the MPA to an age frequency. The CV of the length at age was assumed to be known. A linear regression catch curve was then fit to the logged age frequency to estimate the total mortality inside the MPA (assumed to be M). The estimates of M and k were then used to fit the LBSPR model to the length frequency data collected outside the MPA to estimate the F/M , and with estimates of M and the growth parameters, it was possible to calculate F as well as the spawning potential ratio (SPR) of the stock. I compared the estimated F with the true F in the operating model to assess the accuracy of this assessment method.

The MPA-LBSPR assessment method was paired with a simple slope to target control rule of the following form:

$$E_{next} = E_{curr}(1 + V) \quad (1)$$

where the current fishing effort (E_{curr}) was adjusted by V to determine the fishing effort in the following year (E_{next}). V is calculated in the following manner:

$$V = \zeta_{min} \leq A\phi_1 + B\phi_2 \leq \zeta_{max} \quad (2)$$

where A is the magnitude of change in the mean SPR (\overline{SPR}) over the last five years, and B is the distance between the SPR in the current year and the target SPR. ϕ_1 and ϕ_2 describe the responsiveness of the control rule to A and B , and were optimized to maximize the catch over 20

years while minimizing the probability that the population fell below $0.1B_0$. V was constrained between a minimum change of 2.5% and a maximum change of 20%. This means that if the recommended change in fishing effort was These constraints were present in all of the control rules tested to limit the quantity and magnitude of the prescribed changes in effort during each harvest strategy time step.

2.5.2. MPA-based bounded mortality estimator

The second method tested was a bounded MPA-based mortality estimator (Wilson et al. 2013). This method uses a similar process as described above to develop an age-length key to convert lengths to ages, and to fit a regression-based catch curve to logged age frequency data from both inside and outside the MPA. The age frequency from inside the reserve was bounded to reflect the time since the MPA was created, ensuring that the individuals included in the data set have never been subjected to fishing mortality. The mortality estimate inside the MPA was assumed to be M , while the mortality estimate outside was assumed to be composed of both F and M . F was then estimated by subtracting the mortality estimate obtained from inside the MPA from the mortality estimate obtained outside the MPA. This was used, along with M and growth parameters, to estimate the current SPR of the stock. I compared the estimated F with the true F to assess the performance of this assessment model in the accuracy analyses.

In the management performance analyses, the MPA-based bounded mortality estimator was paired with control rule of the same functional form as that used for the MPA-LBSPR. The responsiveness parameters (ϕ_1 and ϕ_2) were optimized in the same manner as the MPA-LBSPR but have different values because of the different assessment method.

2.5.3 Density Ratio

The density ratio (DR) provides an estimate of the abundance of fish outside the MPA relative to the abundance inside (Babcock and MacCall 2011, McGilliard et al. 2011). Traditionally, stock assessments estimate unfished abundance using data extending back to the early development of the fishery as a means of assessing the current depletion level of the stock. However, many data-poor stocks lack the necessary historical data. The density ratio provides an indicator of stock status by assuming that the density inside an MPA is the best available representation of unfished abundance (McGilliard et al. 2011). In addition, the density inside an MPA is subject to the same fluctuations in environmental conditions as the fished portion of the stock, making it potentially more useful under climate change than comparisons to historical abundances. The density ratio was calculated using the survey CPUE (in kg). To assess the accuracy of this metric, I compared the observed density ratio to the true ratio between the current and unfished abundance (also known as the depletion level). The closed patches were excluded from this calculation to better measure fishing impacts.

In the management performance analysis, I used a modified version of the control rule described in (McGilliard et al. 2011), which was a linear slope-to-target function of the form:

$$E_{next} = E_{curr}(1 + V) \quad (3)$$

$$V = \pi(\rho - \rho_{targ}) \quad (4)$$

where ρ was the weighted density ratio in the last five years, ρ_{targ} was the target density, and π was the slope of the control rule. The weighted density ratio was calculated in the following way:

$$\rho = \frac{\sum_{y-4}^y \rho_y (\omega^y)}{\sum_{y-4}^y \omega^y} \quad (5)$$

where π and ω were optimized to maximize the catch over 20 years under limited uncertainty while minimizing the probability that the population fell below $0.1SSB_0$.

2.5.4 MPA-based Decision Tree

The MPA-based decision tree (Dtree) uses size structure and CPUE as a proxy for the SPR of the stock (Wilson et al. 2010). Information derived from the size structure of the catch outside relative to the size structure inside the MPA was used to adjust catch iteratively over time to meet a target SPR. The idea is based on the suggestion that sustainable management requires adequate representation of three size-classes in the harvest: recently recruited small fish, medium or prime sized fish, and large fish of advanced age. The MPA was used as a proxy for the unfished composition of these size groups, allowing for the use of dynamic rather than static reference points that can incorporate spatial and temporal variation. While the decision tree has multiple levels, it is designed to maintain the stock at a target level of SPR, in which the MPA stands as a proxy for unfished conditions. In practice, this involves calculating the proportion of prime fish outside the MPA necessary to achieve a percentage of the spawning potential inside the reserve. The Dtree assesses size-based catch rates and compares them to the expected catch composition if the stock was at a target level of SPR. In the model, this is done by using size-at-age information, fecundity ogives, and an estimate of M to calculate the expected size distribution of the stock at the target SPR. This was used to estimate the size-based catch rates corresponding with the target SPR level. In the accuracy analysis, I compared the estimated SPR from the observed ratio with the $CPUE_{\text{prime}}$ with the true SPR of the stock.

Harvest levels were set using the control rule as described in (Wilson et al. 2010), which takes the following form:

$$V = \frac{CPUE_{out} - \lambda_{targ}CPUE_{in}}{d} \quad (6)$$

$$E_{init} = E_{curr}(1 + \Lambda V) \quad (7)$$

where E_{init} was the initial effort prescribed in level 1, E_{curr} was the fishing effort expended in the current year, λ_{targ} was the target ratio between the CPUE of prime individuals inside and out necessary to achieve the desired SPR , d was the desired time period over which the target should be achieved, and Λ was the responsiveness factor. The decision tree control rule allows for a phase-in period that modifies the target ratio if less than the mean generation time (MGT) has passed since MPA implementation such that V becomes:

$$V = 1 - \left(\frac{1 - \lambda_{targ}}{MGT} \right) (y_{curr} - y_{reserve}) \quad (8)$$

The initial effort was then modified by the subsequent levels of the decision tree as described in Wilson et al. (2010) to determine E_{next} , subject to the minimum and maximum change allowed in each year. The MGT for each species was estimated using FishBase in order to simulate real world management conditions. Λ and d were optimized to maximize the catch over 20 years under limited uncertainty while minimizing the probability that the population fell below $0.1SSB_0$.

2.6 Uncertainty Scenarios

I examined the assessment accuracy under six uncertainty scenarios. In the base scenario historical fishing pressure was low ($F=M$), recruitment was deterministic, and there was no movement of adult fish relative to the reserve. The alternative uncertainty scenarios tested assessment method accuracy under various combinations of fish movement, high historical fishing pressure ($F=3M$), and stochastic recruitment (Table 5).

2.7 Performance metrics

2.7.1 Accuracy of assessment methods

Each assessment model makes different assumptions about the system, and estimates different summary statistics to describe the current status of the stock, making direct comparisons of accuracy across models difficult. While the density ratio is a proxy for the ratio of the current spawning stock biomass to the unfished spawning stock biomass, the other three MPA-based methods are used to estimate the static SPR, which is defined as the equilibrium spawning biomass per recruit given a particular F and selectivity ogive, divided by the spawning biomass per recruit that would be obtained in an unexploited stock. To create a standardized error statistic across the four models I calculated the relative error (RE), which is defined as the standardized difference between the estimated ($\hat{\theta}$) and the true (θ) values of a given parameter:

$$RE = \frac{\hat{\theta} - \theta}{\theta} \quad (9)$$

The relative error was used to compare the accuracy and precision of each method across the different species and uncertainty scenarios.

2.7.2 Achievement of management objectives

In the management performance tests each management strategy was evaluated based on five metrics that reflect common management goals in fisheries. These were the: 1) median spawning stock biomass (SSB) in the final year of the simulation relative to the target SSB, 2) the probability that the population dropped below its overfished limit reference point between the first year the management strategies were implemented and the last year of the simulations (a 20-year time horizon), 3) the probability that the population dropped below a collapse reference point of 10% of unfished SSB, 4) the average catch over the 20 years the management strategies were employed, and 5) the average coefficient of variation in the catch, which reflects the stability in catches from year to year.

All of the MPA-based control rules adjusted fishing effort in relation to the distance of the current estimates from a target (SPR_{targ} or SSB_{targ}). Targets for SSB, as well as the overfished limit, were taken from the most recent stock assessments. For comparison it was necessary to set consistent targets across all methods. I used the steepness of each species to calculate the equilibrium SSB that would yield a $SPR = 0.45$ for lingcod and $SPR=0.5$ for gopher and blue rockfish for use as a target in the density ratio (Key et al. 2005, 2008, Jagielo and Wallace 2005).

3. Results

3.1. Evaluating accuracy of assessment methods under a constant effort harvest policy

This section details the accuracy of MPA-based assessments under constant fishing pressure over a 25-year time horizon. At five year intervals after MPA implementation, each assessment

method was evaluated based on whether it accurately estimated the current stock status in terms of either the SPR or depletion of the stock.

3.1.1 Accuracy under deterministic conditions (Uncertainty Scenarios 1 and 2)

I evaluated the ability of MPA-based assessment methods to accurately estimate stock status metrics under minimal uncertainty (deterministic recruitment, no movement) to understand their performance under ideal conditions. Figure 3 shows the results of these accuracy evaluations at 5, 10, 15, 20, and 25 years after MPA creation under low (left panels) or high (right panels) fishing mortality. The relative error illustrates each method's ability to estimate a specific status indicator: namely, the size-based methods' (MPA-LBSPR and Bounded) abilities to estimate F , the DR's ability to estimate stock depletion, and the Dtree's ability to estimate SPR. The estimation error across all assessment methods was greatest within 10-15 years of the creation of the MPA regardless of species, but decreased substantially as the population inside the MPA approached unfished abundance and age structure. Under a low fishing pressure (Figure 3; left panels), the two size-based methods underestimated the fishing mortality for all three species in the years soon after MPA creation. The MPA-LBSPR used age and size data from inside the MPA to estimate growth and natural mortality parameters. The lack of large fish in the early years of the MPA resulted in an overestimation of the natural mortality and a bias in the growth parameters (Valencia et al. in prep), and so F was underestimated in the 10 years after the MPA was established (Figure 3). The Bounded method estimated the difference in mortality inside and outside the MPA as a proxy for F . Despite bounding the data inside the MPA to account for the time since MPA implementation, M was overestimated inside the MPA soon after MPA

establishment, resulting in a negative bias in F . This negative bias was eliminated within 10 years for lingcod and within 15 years for gopher and blue rockfish.

Conversely, the two CPUE-based methods (DR and Dtree) overestimated the SPR and depletion levels in the early years of the MPA. During those years the population inside the MPA has not yet recovered to unfished conditions, and catch rates inside and outside were similar. The DR had a consistently higher RE. The DR uses the CPUE as a proxy for the spawning stock depletion level (McGilliard et al. 2011), while the Dtree uses the CPUE of prime-sized fish only in its first level as a proxy for SPR (Prince et al. 2011). While the MPA was still recovering from the effects of fishing, the largest fish, which contributed the most weight per fish to the CPUE, were the last to recover to unfished levels. Therefore the Dtree's use of the prime CPUE reduced the bias seen in the early years of the MPA. The bias in both methods declined over time, and the RE for each approached zero.

Blue rockfish are more susceptible to fishing than both gopher rockfish and lingcod due to a lower productivity (Key et al. 2008). The resulting bias in the CPUE-based methods was higher for blue rockfish soon after MPA implementation than for the two other species, was exacerbated by high historical fishing, and took longer to resolve. The bias associated with the DR under high historical fishing remained high even 25 years after MPA implementation. This was in part due to the slow life history of the blue rockfish, but also to the DR's implicit assumption that the fish selected by the survey gear were mature. Blue rockfish mature at a relatively large size, and thus many immature fish were included in the CPUE indicator, resulting in an overestimation of the true spawning stock biomass level relative to unfished.

The RE was extremely high in the early years of the MPA under a high historical F (Figure 3; right panel). In general, all of the methods followed the same patterns described in the low fishing scenario, although a longer time frame was required before the methods returned accurate results. The CPUE-based methods were especially sensitive to a high historical fishing pressure, with the DR and Dtree exhibiting a relative bias 2-6 times higher than in the low fishing scenario. This suggests that these methods are not suitable for use in the early years after MPA creation under high historical fishing pressure. While the bias associated with the size-based methods at five years post-MPA was 1-2 times greater in the high fishing scenario than in the low one, the bias was the same for both fishing scenarios after 15 years.

3.1.2 Accuracy under stochastic recruitment (Uncertainty Scenarios 3 and 4)

I examined the relative error in depletion (DR) and SPR (all other methods) over 100 stochastic simulations (Figure 4). SPR was used in this analysis rather than F because the transition from a fished to an unfished state after MPA implementation biases F and depletion in different directions, making cross comparison difficult. An underestimation of F causes an overestimation of SPR, and SPR is a more comprehensive measure of overall stock health than F alone because it accounts for the biology of the species.

With stochastic recruitment, similar trends are seen in the accuracy of each MPA-based assessment method (Figure 4). At five years after MPA creation, all of the methods were highly biased with wide distributions, but improved in accuracy and precision over time, with the median RE decreasing towards zero. The high fishing scenario (Figure 4; grey boxes) returned

estimates with a wide distribution after 5 years but trended towards a median RE of zero over time.

At 5 years post-MPA, both the MPA-LBSPR and the Bounded estimator were very unstable, frequently converging to an SPR estimate of 1 due to the limited data available and skewing the SPR distributions (Figure 4). However, both estimation routines stabilized after 15 years. The MPA-LBSPR performed better under high F , with more accurate median estimates and an increase in precision for all three species as more time passed.

The CPUE-based methods were extremely biased at 5 years post-MPA (Figure 4) just as they were in the deterministic scenarios. High fishing exacerbated this, with the DR returning depletion estimates up to 19 times higher than the true depletion level for blue rockfish and up to 14 times higher for the other species. This bias was largely eliminated after 25 years for gopher rockfish and lingcod. The distribution of error for both methods was wider for lingcod than for gopher rockfish due to lingcod's higher recruitment variability (Table 2). The bias seen in the deterministic scenarios when the DR was applied to blue rockfish persisted after 25 years under stochastic recruitment, and was higher in the high fishing scenario.

3.1.3 Effects of movement on accuracy (Uncertainty scenarios 5 and 6)

Figure 5 shows the RE for uncertainty scenarios 5 and 6, which included stochastic recruitment, as well as the movement of fish between patches. In the simulation model, blue rockfish was parameterized to have the lowest movement rate, while lingcod had the highest (Table 2). For blue rockfish, movement had minimal impact on the accuracy and precision of the

both the size-based methods the low fishing scenario (Figure 5; top row, white boxes) but resulted in a positive bias in the median SPR estimate, as well as a wider distribution of estimates in the high fishing scenario (Figure 5; top row, grey boxes), even after 25 years. The movement rate in the blue rockfish simulations had a negligible performance of the DR, which was already heavily biased, but did have a slight impact on the Dtree performance. This impact was most notable in the high fishing scenario, in which the Dtree's estimates of SPR had a higher variability than in the scenarios with no movement. These trends were magnified in the results for gopher rockfish (Figure 5; middle row) and lingcod (Figure 5; bottom row). For both species, biases caused by movement were evident in both the low and high fishing scenarios. The size-based methods were more sensitive to movement than the CPUE-based methods, and movement combined with high fishing resulted in broader distributions of RE. This suggests that as the movement rate between fished and unfished area increase, both the accuracy and the precision of the reserve-based methods declines, and an overestimation of stock status is likely.

3.2 Assessing the long-term performance of MPA-based harvest strategies.

This section details the performance of MPA-based assessments when they were combined with dynamic harvest control rules to update fishing effort every five years over a 20-year time horizon. For comparison, the MPA-based assessments were evaluated against a status quo data poor management approach of setting catches at 50% of recent historical averages (referred to as the Restrepo approach). The robustness of each harvest strategy was tested under four uncertainty scenarios (scenarios 2-6 in Table 5) for each of the three species. Performance was evaluated against five criteria of management importance, including their ability to reach a target

biomass, their ability to avoid becoming overfished or collapsed, their ability to maximize catches, and the stability of those catches, and is described in the following sections.

3.2.1 Ability to achieve target biomass

The median trajectories for each species over the evaluation time period are shown in Figures 6-8. After being fished for 50 years at $F=M$, the three species had median depletion levels ranging from 28-33%SSB₀ (Figures 6-8; left panels), while after being fished at $F=3M$ the median depletion levels ranged from 4-6%SSB₀ (Figures 6-8; right panels). In year 50 an MPA was implemented in 20% of the available habitat, spurring an increase in median spawning biomass across all three species. At year 55, and every 5 years until year 75, each of the candidate harvest control rules was implemented, and effects on the median biomass under each uncertainty scenario was quantified (Figures 6-8). In all of the scenarios, the Restrepo rule resulted in a rapid increase in biomass, regardless of movement rates. When historical fishing was low, the resulting increase surpassed the target biomass within a few years, and increased to a final median SSB of all three stocks at 74-90% of unfished biomass. When historical fishing was high, stocks recovered to median SSBs at 34-77% of unfished biomass.

For blue rockfish under low historical fishing pressure with no movement between patches (Figure 6a), the MPA-LBSPR and Bounded estimator came closer to the target over the simulated time period than the DR and Dtree. The size-based methods continued to approach the target biomass over the simulation time horizon, although neither achieved the target, while the CPUE-based methods resulted in a slight decline in the SSB. Similar trends were observed under low historical fishing pressure and movement (Figure 6c), with the CPUE-based methods resulting in a small decline in SSB. Under high historical fishing pressure, all four MPA-based

methods saw minimal population growth over the first 10 years, but increased in the second 10 years. The stock experienced the most recovery when managed using the Dtree harvest strategy, both with and without movement present (Figure 6b, d).

For gopher rockfish under low historical fishing pressure with no movement between patches (Figure 7a), all of the MPA-based methods achieved the target SSB within the simulation time horizon. The median SSB remained close to the target SSB under both the MPA-LBSPR and the DR, while both the Bounded and Dtree overshot the target. Movement delayed the time until each harvest strategy achieved the target (Figure 7c). The CPUE-based methods resulted in the most robust stock recovery in the high historical fishing scenarios, both with and without movement, although recover was faster in the scenario without movement (Figure 7b, d).

For lingcod under low historical fishing pressure with no movement between patches (Figure 8a), only the Bounded estimator achieved the target SSB. Under the Dtree the median SSB flattened out in the final years of the simulation time horizon while both the DR and MPA-LBSPR approached the target. When fish moved between patches, all of the harvest strategies caused the stock to begin to decline prior to reaching the target SSB, although the bounded estimator came the closest (Figure 8c). Under high historical fishing effort and no movement, the CPUE-based methods resulted in rapid biomass increases, while the size-based methods increased more slowly (Figure 8b). With movement, the recovery trajectories were dampened, and both the MPA-LBSPR and Bounded estimators resulted in stagnation (Figure 8d).

3.2.2 Probability of triggering limit reference points

In addition to achieving target reference points, successful harvest strategies should minimize the probability of triggering limit reference points. I examined the probability of each stock

dipping below either the overfished threshold or the collapse threshold in any given year when managed under each harvest strategy. Under low historical fishing, all five harvest strategies had <10% probability of the stock being overfished, regardless of the presence of movement (Table 6). However, the risk of each stock being overfished increased because under high historical fishing pressure all three species were at 4-6% of unfished SSB after 55 years of fishing. Only the Restrepo rule had a moderate (25-75%) risk of being overfished across all three species. Lingcod, with its higher productivity, had a moderate risk of being overfished under all harvest strategies when no movement between patches was present, but the risk increased substantially (>75%) for the MPA-LBSPR, Bounded, and DR when movement was present. The risk of being overfished was high for both blue and gopher rockfish under all of the MPA-based harvest strategies.

The probability of each stock being classified as “collapsed” ($SSB_{curr} < 10\%SSB_0$) is shown in Table 7. Under low historical fishing pressure, all of the stocks had zero probability of being collapsed, with and without movement. The risk of collapse was substantially higher under high historical fishing pressure, which is not surprising given that all three species started the testing time period in a collapsed state. However, the risk of being in a collapsed state was low under the Restrepo rule for all three species despite the history of high fishing mortality, and for lingcod when there was no movement present. The risk of collapse was moderate for blue and gopher rockfish when managed under the MPA-based harvest strategies.

3.2.4 Average catch and variability in catches

Figure 9 shows the distribution of the average catches over the final 10 years of the simulation time horizon for each species and each uncertainty scenario. I chose to examine the

final 10 years so that methods that promoted stock growth in the early years of the simulation time horizon via foregone catches would not be penalized. The Restrepo method resulted in the lowest catch levels across all species. Catches in the low historical fishing scenarios were higher than those in the high historical fishing scenarios (Figure 9). While the movement rates of blue rockfish were too low to increase catches, the movement scenarios generally resulted in higher catches for the gopher rockfish and lingcod stocks as spillover propelled fish across the MPA border. The harvest strategies that increased stock size the most generally resulted in the high median catches in each uncertainty scenario.

The mean CV provides a metric of how stable catches were from year to year, and are shown in Table 8. In general, higher historical fishing pressure increased the variation in catches, while the movement dampened the year-to-year variation. Lingcod had high variation in catches than either blue or gopher rockfish, probably due to its higher recruitment variability.

4. Discussion

This is the first direct comparison of a suite of data-poor harvest strategies that use MPAs as reference areas for the management of nearby fisheries. While other studies have developed and tested assessment methods or harvest strategies that rely on MPA data (Wilson et al. 2010, McGilliard et al. 2011, Babcock et al. 2011, Kay et al. 2012, Hordyk et al. 2015), these studies have not looked at how the differences in the data they rely on and the assumptions they make about the dynamics impact estimation performance under a suite of different conditions. The results presented here provide a greater understanding of which factors have the greatest impact on the ability of MPAs to accurately function as reference areas for use in stock assessments.

The accuracy of the MPA-based assessments was highly sensitive to the amount of time elapsed since MPA implementation. In the early years after MPA creation, the population inside the MPA is transitioning to an unfished state, which can take many years depending on the life span and productivity of the stock. In the early years of this transition, MPA-based assessment methods can return highly biased estimates of stock status. CPUE-based methods were more sensitive to this bias than size-based methods, suggesting that size recovers faster than abundance after MPA implementation. As a result, methods that rely on MPA size composition data as a reference may be more reliable while the MPA population is still in transition to an unfished state. All of the species modeled in this study were moderately long-lived, but the size-based assessment methods were accurate by 15 years after MPA establishment under a low fishing pressure, indicating that MPAs need not reach a completely unfished state before they can be used as reference areas. High historical fishing pressure increased both the bias in the early years after MPA implementation, as well as the time until the MPA provided a reference area to accurately assess stock status.

Movement increased the error in assessments, a result that was exacerbated under high fishing pressure. While animals with minimal movement levels, such as those whose home range occasionally carries individuals across MPA borders, are unlikely to heavily bias MPA-based stock assessments, moderate movement resulted in an overestimation of stock status. This suggests that reference area MPAs are best suited for species with small home ranges. By contrast, MPAs should be either very large or sited in such a way as to minimize movement across borders for fish with moderate to large home ranges.

Movement, recruitment variation, and high fishing pressure all extended the time it took for each assessment method to approach an accurate result (Figures 3-5). This is to be expected, because all three of those factors have the same effect on the MPA reference data, which is to lengthen the time it takes for the population inside the MPA to reach an approximate unfished size structure or density. With high historical fishing pressure, this is due to the initial size and age structure being more truncated and the initial biomass being lower, and thus the population takes longer to recover. With high recruitment variability, low recruitment years delay increases in density for the population inside the reserve, and thus the assessment methods that rely on density are more affected by this variability than the size-based methods. With movement, some fraction of the population is likely to be exposed to fishing mortality in a given time step, This suggests an interesting avenue of future research.

It is likely that the bias in estimation under these conditions scales in a predictable way, and this could be tested through further simulation work. Secondly, if there is a general result that describes the delayed accuracy in estimation performance when using MPA data as a reference for unfished conditions, this suggests that there may be some way to correct for the bias introduced by these conditions, which might allow for the use of MPAs as a reference are under a wider range of conditions. Additionally, it would be useful to determine which conditions can not be corrected for.

While time after MPA implementation, high historical fishing pressure, and movement all compromised the MPA's ability to act as a reference for stock status, in the management performance analysis the harvest strategies were generally able to achieve target and avoid limit

reference points, except in the case with both high historical fishing and movement, despite being applied just five years post-MPA. It is likely that the harvest strategies would have performed better they were first applied 15 years post-MPA. The control rule parameters used were optimized under limited uncertainty so were able to compensate for the poor performance of the assessment methods. This suggests that highly accurate assessments may provide less benefit to management than a responsive and well-calibrated control rule. However, optimizing control rule parameters is likely to be very difficult in a real world scenario because of the vast number of irreducible uncertainties.

The results for this work suggest that, for many species, MPAs can not be reliably used in as reference areas in stock assessments until 15+ years have passed. As mentioned previously, the size-based methods were accurate faster than the density-based ones, and the time period might be shorter for stocks with shorter life spans (however, the methods that make equilibrium assumptions are unlikely to be applicable to short lived species, which often exhibit highly variable dynamics from year to year). In many areas, MPAs have only been implemented in the last 5 or so years, so this presents an obstacle to managers who are looking for a data poor solution now. Additionally, management agencies might be reluctant to do any kind of sampling within MPAs that might result in mortality, This might be a viable option for nearshore MPAs in shallow waters where discards have a high chance of survival.

This analysis of reserve-based control rules indicated that no single harvest strategy performed best across all of the scenarios I explored. This suggests that managers have many options when considering implementing a harvest strategy based on one of the four MPA-based

data poor methods tested in this study, and that the best choice will likely depend on the life history characteristics of the stock, time since MPA creation, and the monitoring resources of the managing agency.

The Restrepo method is a commonly employed management strategy in data poor stocks but requires a) data on recent historical catches during a stable period, and b) an ability to collect timely data on total catches to know when to close the fishery each season if the TAC is reached. In addition, while catches are stable from year to year, they frequently are very low relative to maximum sustainable yields. Alternative harvest strategies such as the MPA-based methods explored here may be more appropriate for use in data poor fisheries that lack historical data, or that do not land catches in a centralized and easily accessible area. MPAs may provide higher yields in these cases. However, the Restrepo rule does have the advantage of requiring no fishery-independent monitoring to collect size compositions or indices of abundance inside the reserve, which can be costly for management agencies. Future research is needed to examine whether the increased costs associated with obtaining data from inside MPAs is warranted by gains in management objectives.

References

- Babcock, E.A., and MacCall, A.D. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? *Can J Fish and Aquat Sci* 68: 343–359.
- Berkes, F. 2003. Alternatives to conventional management: Lessons from small-scale fisheries. *Environments* 31: 5–20.
- Bohnsack, J.A. 1999. Incorporating no-take marine reserves into precautionary management and stock assessment. In *Providing Scientific Advice to Implement Precautionary Approach Under the Magnuson-Stevens Fishery Conservation and Management Act*. NOAA Tech. Memorandum NMFS-F/SPO-40.
- Dowling, N.A., Dichmont, C.M., Haddon, M., Smith, D.C., Smith, A.D.M., and Sainsbury, K. 2015. Empirical harvest strategies for data-poor fisheries: A review of the literature. *Fish Res*: 1–13.
- FAO. 2012. *The State of World Fisheries and Aquaculture 2012*. In FAO Fisheries and Aquaculture Department. Food and Agriculture Organization of the United Nations, Rome.
- Field, J.C., Punt, A.E., Methot, R.D., and Thomson, C.J. 2006. Does MPA mean ‘Major Problem for Assessments’? Considering the consequences of place-based management systems. *Fish Fish* 7(4): 284–302.
- Fox, H.E., Mascia, M.B., Basurto, X., Costa, A., Glew, L., Heinemann, D., Karrer, L.B., Lester, S.E., Lombana, A.V., Pomeroy, R.S., Recchia, C.A., Roberts, C.M., Sanchirico, J.N., Pet-Soede, L., and White, A.T. 2011. Reexamining the science of marine protected areas: linking knowledge to action. *Conserv Lett* 5(1): 1–10.
- Gaines, S.D., Lester, S.E., Grorud-Colvert, K., Costello, C., and Pollnac, R. 2010. Evolving science of marine reserves: New developments and emerging research frontiers. *PNAS* 107(43): 18251–18255.
- Grüss, A., Kaplan, D.M., and Hart, D.R. 2011. Relative Impacts of Adult Movement, Larval Dispersal and Harvester Movement on the Effectiveness of Reserve Networks. *PLoS ONE* 6(5): e19960.
- Hilborn, R., and Walters, C. 1992. *Quantitative fisheries stock assessment: Choice, dynamics and uncertainty*. Chapman and Hall, London.
- Holland, D.S. 2002. Integrating marine protected areas into models for fishery assessment and management. *Nat Resour Model* 15(3): 369–386.
- Jagiello, T.H., and Wallace, F.R. 2005. Assessment of Lingcod (*Ophiodon elongatus*) for the Pacific Fishery Management Council in 2005.

- Kay, M.C., and Wilson, J.R. 2012. Spatially explicit mortality of California spiny lobster (*Panulirus interruptus*) across a marine reserve network. *Environ Conserv* 39(03): 215–224.
- Key, M., MacCall, A.D., Bishop, T., and Leos, B. 2005. Stock assessment of the gopher rockfish (*Sebastes carnatus*). California Department of Fish & Game.
- Key, M., MacCall, A.D., Field, J.C., Aseltine-Neilson, D., and Lynn, K. 2008. The 2007 assessment of blue rockfish (*Sebastes mystinus*) in California. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center.
- Lauck, T., Clark, C.W., Mangel, M., and Munro, G.R. 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecol Appl* 8(1): S72–S78.
- McGilliard, C.R., Hilborn, R., MacCall, A., Punt, A.E., and Field, J.C. 2011. Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks? *ICES J Mar Sci* 68: 201–211.
- Murawski, S.A., Wigley, S., Fogarty, M., Rago, P., and Mountain, D. 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES J Mar Sci* 62: 115–1167.
- Prince, J.D., Dowling, N.A., Davies, C.R., Campbell, R.A., and Kolody, D.S. 2011. A simple cost-effective and scale-less empirical approach to harvest strategies. *ICES J Mar Sci* 68(5): 947–960.
- Punt, A.E., and Methot, R.D. 2004. Effects of marine protected areas on the assessment of marine fisheries. *American Fisheries Society Symposium* 42: 133–154.
- Restrepo, V.R., Thompson, G.G., Mace, P.M., Gabriel, W.L., Low, L.L., MacCall, A.D., Methot, R.D., Powers, J.E., Taylor, B.L., Wade, P.R., and Witzig, J.F. 1998. Technical Guidance On the Use of Precautionary Approaches to Implementing National Standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum NMFS-F/SPO-##.
- Toonen, R.J., Wilhelm, T.A., Maxwell, S.M., Wagner, D., Bowen, B.W., Sheppard, C.R.C., Taei, S.M., Teroroko, T., Moffitt, R., Gaymer, C.F., Morgan, L., Lewis, N.A., Sheppard, A.L.S., Parks, J., Friedlander, A.M., and Tank, T.B.O.T. 2013. One size does not fit all: The emerging frontier in large-scale marine conservation. *Marine Pollution Bulletin* 77(1-2): 7–10.
- Wilson, J.R., Prince, J.D., and Lenihan, H.S. 2010. A Management Strategy for Sedentary Nearshore Species that Uses Marine Protected Areas as a Reference. *Mar Coast Fish* 2(1): 14–27.
- Wilson, J.R., Valencia, S.R., Kay, M.C., and Lenihan, H.S. 2013. Integration of no-take marine reserves in the assessment of data-limited fisheries. *Conserv Lett* 7: 451–458.

Tables

Table 1. Data requirements and estimated status indicators for each of the data-poor methods assessed.

Harvest Strategy	Data Requirements				Biological Inputs					Estimated Status Indicators		
	Catch history	Size Freq.	Age Freq.	CPUE	Growth	Natural Mortality	Fecundity	Maturity	Variation in Length	Fishing Mortality	SPR	Depletion
Restrepo	Last 10 years											
MPA-LBSPR	Inside and outside		Inside					X	X	X	X	
Bounded	Inside and outside		Inside					X		X	X	
Density Ratio				Inside and outside								X
DTREE	Inside and outside		Inside and outside		X	X	X	X			X	

Table 2. List of all simulation combinations run. Each simulation was composed of one test procedure, species, assessment, and scenario. (*) denotes assessment method that was only used in Management Performance tests.

Test Procedure	Species	Assessment	Scenarios	Number of simulation combinations
Accuracy	Gopher rockfish	MPA-LBSPR	Base scenario	Accuracy: 72
Management Performance	Blue Rockfish	Bounded	High fishing pressure	Management Performance: 90
		Lingcod	Density Ratio	
	Decision Tree		Stochastic + high fishing	
	Restrepo*	Movement	Movement + high fishing	
Total				162

Table 3. Biological parameters used in operating model for each species.

Category	Symbol	Blue rockfish	Gopher rockfish	Lingcod
Natural Mortality	M	0.12	0.2	0.18
Growth	L_{∞}	40.02 cm	31.2 cm	126.6 cm
	k	0.15	0.186	0.11
	t_0	0	0	0
	$CV_{L_{\infty}}$	0.1	0.08	0.15
Weight	w_a	0.0158	$1.299e^{-5}$	$1.76e^{-3}$
	w_b	2.988	3.077	3.3978
Fecundity	f_a	1.559	1.559	$3.026e^{-4}$
	f_b	3.179	3.179	3
Maturity	ma_{50}	29 cm	17.7 cm	60 cm
	ma_{95}	35 cm	21 cm	85 cm
Steepness	h	0.58	0.65	0.8
Recruitment variation	σ_r	0.5	0.5	0.8
Movement range	$2\sigma_x$	1	3	5
Fishing gear selectivity	v_{50}	26 cm	22 cm	60 cm
	v_{95}	32 cm	26 cm	75 cm
Survey gear selectivity	vb_{50}	10 cm	10 cm	18 cm
	vb_{95}	12 cm	12 cm	20 cm

Table 4. Economic information for three model species along the central coast of California.

Species	Total Average landings (kg)	Percent Commercial landings	Price per Kilogram
Lingcod	60,272	19.6%	\$3.26
Gopher rockfish	48,825	37.9%	\$3.95
Blue rockfish	27,406	3.5%	\$15.18

Table 5. Description of simulation scenarios.

Scenario	Recruitment	Fishing Pressure	Movement
(1) Base scenario	Deterministic	Low	No
(2) High fishing pressure	Deterministic	High	No
(3) Stochastic recruitment	Stochastic	Low	No
(4) Stochastic + high fishing	Stochastic	High	No
(5) Movement	Stochastic	Low	Yes
(6) Movement + high fishing	Stochastic	High	Yes

Table 6. Probability of being overfished under each harvest strategy in each uncertainty scenario. Green indicates $P < 0.25$, yellow indicates $0.25 \leq P \leq 0.75$, and red indicates $P > 0.75$ of being overfished.

Historical	Harvest	No Movement			Movement		
		Blue	Gopher		Blue	Gopher	
Fishing	Strategy	rockfish	rockfish	Lingcod	rockfish	rockfish	Lingcod
F=M	Restrepo	0.01	0.00	0.01	0.01	0.00	0.01
	MPA-LBSPR	0.05	0.00	0.03	0.05	0.00	0.08
	Bounded	0.06	0.00	0.02	0.06	0.00	0.03
	Density Ratio	0.08	0.00	0.03	0.08	0.00	0.10
	Dtree	0.08	0.00	0.04	0.08	0.00	0.10
F=3M	Restrepo	0.75	0.40	0.26	0.74	0.40	0.27
	MPA-LBSPR	1.00	0.86	0.69	1.00	0.95	0.92
	Bounded	0.99	0.95	0.71	1.00	1.00	0.94
	Density Ratio	1.00	0.76	0.57	1.00	0.85	0.83
	Dtree	0.98	0.76	0.55	0.98	0.86	0.72

Table 7. Probability of being collapsed ($SSB_{curr} < 10\%SSB_0$) under each harvest strategy in each uncertainty scenario. Green indicates $P \leq 0.25$, yellow indicates $0.25 < P \leq 0.75$, and red indicates $P > 0.75$ of being collapsed.

Historical	Harvest	No Movement			Movement		
		Blue	Gopher		Blue	Gopher	
Fishing	Strategy	rockfish	rockfish	Lingcod	rockfish	rockfish	Lingcod
F=M	Restrepo	0.00	0.00	0.00	0.00	0.00	0.00
	MPA-LBSPR	0.00	0.00	0.00	0.00	0.00	0.00
	Bounded	0.00	0.00	0.00	0.00	0.00	0.00
	Density Ratio	0.00	0.00	0.00	0.00	0.00	0.00
	Dtree	0.00	0.00	0.00	0.00	0.00	0.00
F=3M	Restrepo	0.25	0.20	0.11	0.25	0.21	0.12
	MPA-LBSPR	0.68	0.39	0.19	0.70	0.53	0.40
	Bounded	0.70	0.43	0.19	0.71	0.70	0.43
	Density Ratio	0.68	0.35	0.16	0.70	0.41	0.28
	Dtree	0.51	0.35	0.15	0.52	0.42	0.23

Table 8. Average (across simulations) coefficient of variation in catches over 20 year time horizon.

Historical	Harvest	No Movement			Movement		
		Blue	Gopher	Lingcod	Blue	Gopher	Lingcod
Fishing	Strategy	rockfish	rockfish	Lingcod	rockfish	rockfish	Lingcod
F=M	Restrepo	0	0	0	0	0	0
	MPA-LBSPR	0.14	0.15	0.24	0.13	0.14	0.23
	Bounded	0.14	0.15	0.21	0.15	0.17	0.2
	Density Ratio	0.17	0.12	0.22	0.17	0.12	0.23
	Dtree	0.17	0.19	0.25	0.17	0.18	0.24
F=3M	Restrepo	0	0	0	0	0	0
	MPA-LBSPR	0.2	0.31	0.34	0.19	0.36	0.31
	Bounded	0.22	0.27	0.32	0.21	0.22	0.3
	Density Ratio	0.18	0.39	0.4	0.17	0.47	0.36
	Dtree	0.22	0.39	0.41	0.24	0.46	0.43

Figures

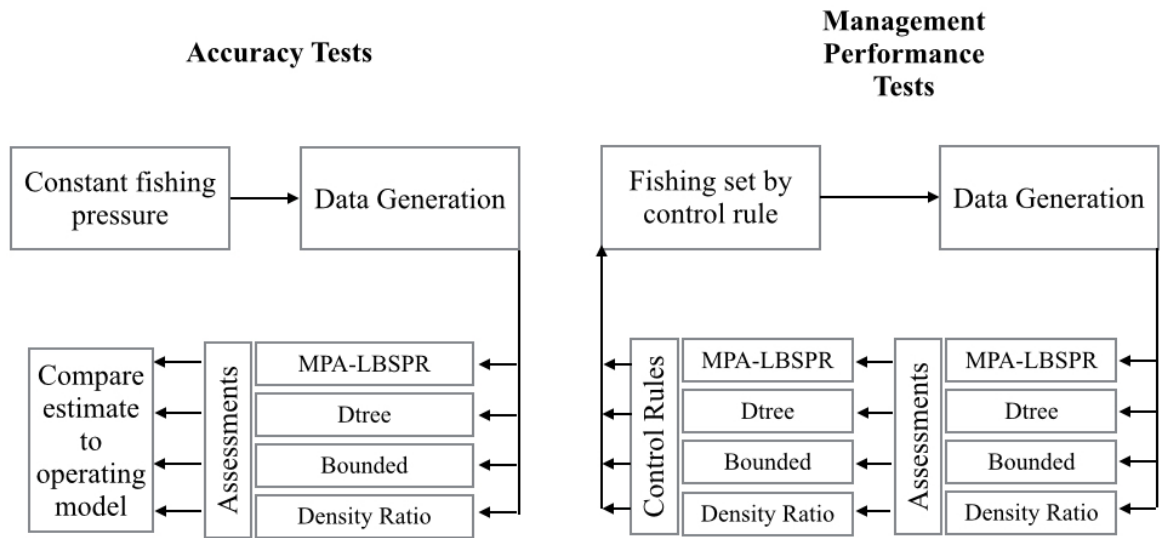


Figure 1. Flow chart describing sequence of events in accuracy and management performance tests.

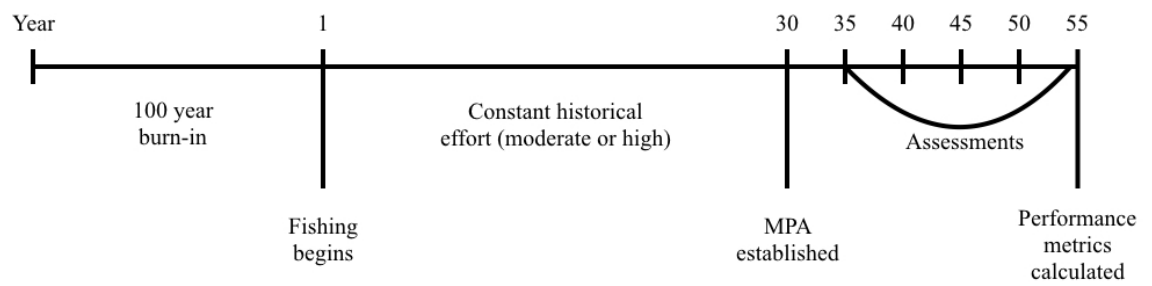


Figure 2. Timeline describing the sequence of events in each Monte Carlo simulation run.

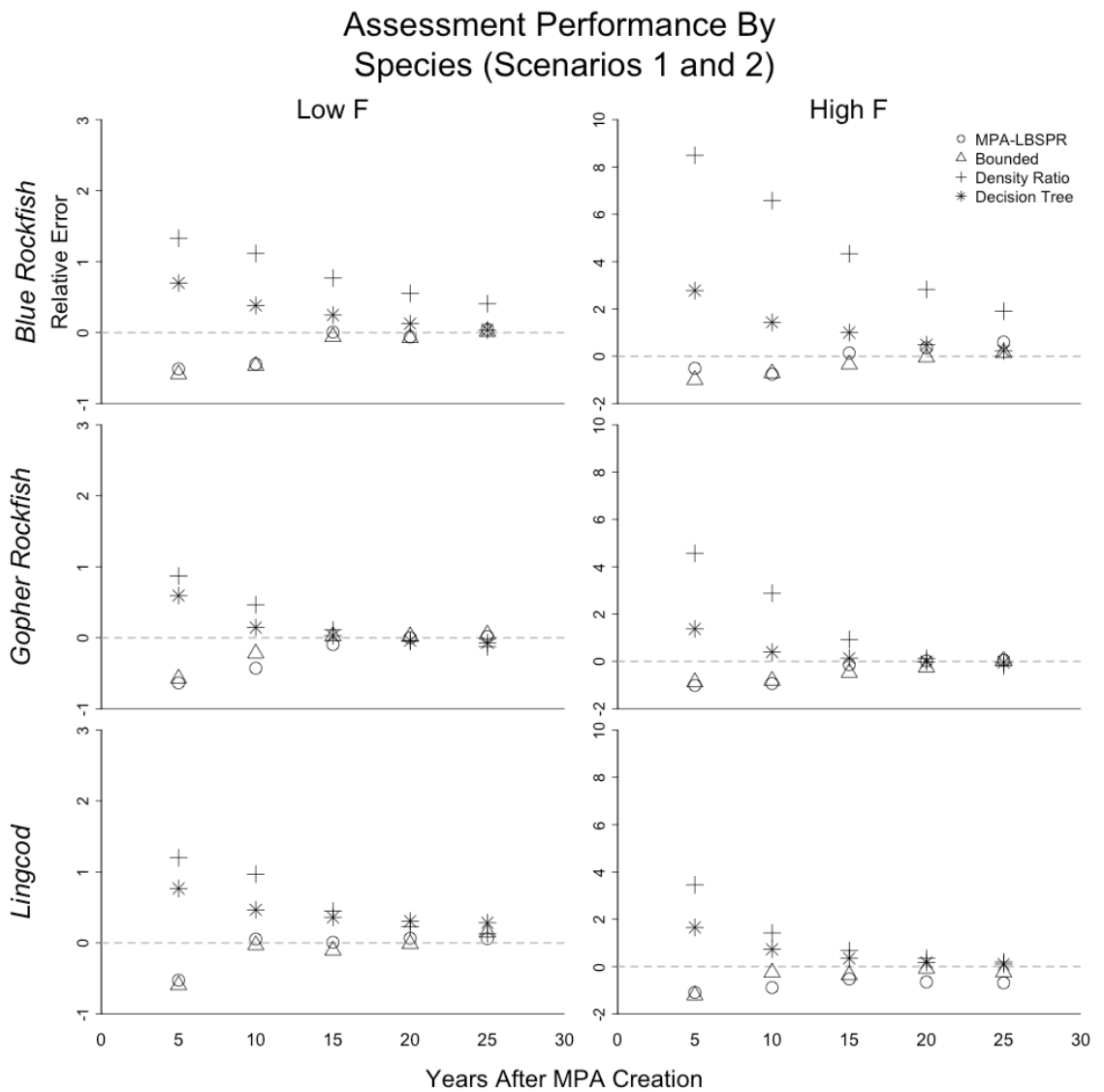


Figure 3. Relative error in the estimation of F (MPA-LBSPR and Bounded) and depletion (DR and Dtree) over time in deterministic scenarios. The accuracy under low fishing effort is shown in the left panels, and accuracy under high fishing effort is shown on the right.

Assessment Performance (Scenarios 3 and 4)

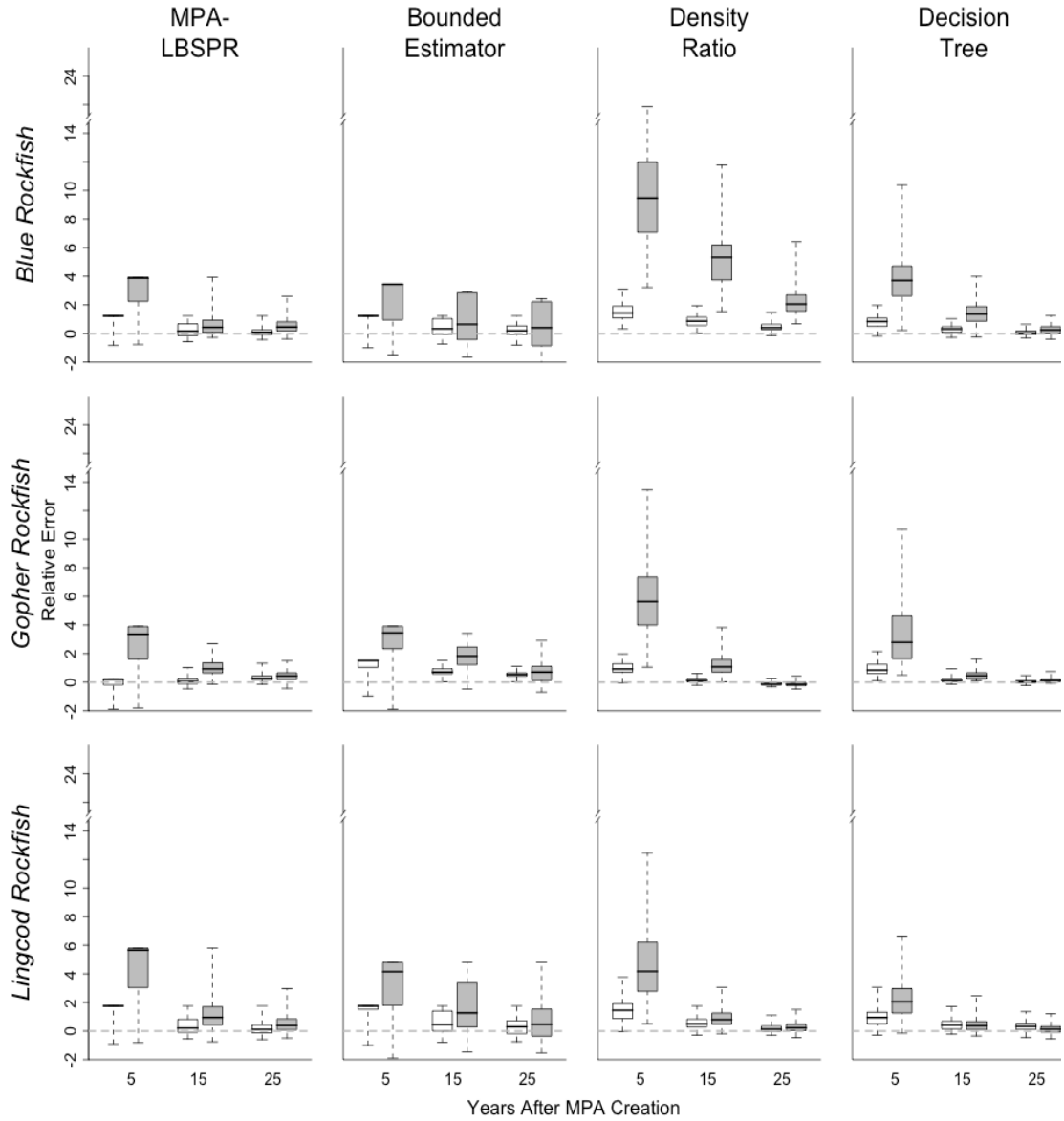


Figure 4. Relative error in estimates of SPR (MPA-LBSPR and Bounded) and depletion (DR and Dtree) for each species when no movement is present. The white boxes show the distribution at relative error under low historical fishing effort ($F=M$), and the grey boxes show the distribution at relative error under high historical fishing effort ($F=3M$).

Assessment Performance (Scenarios 5 and 6)

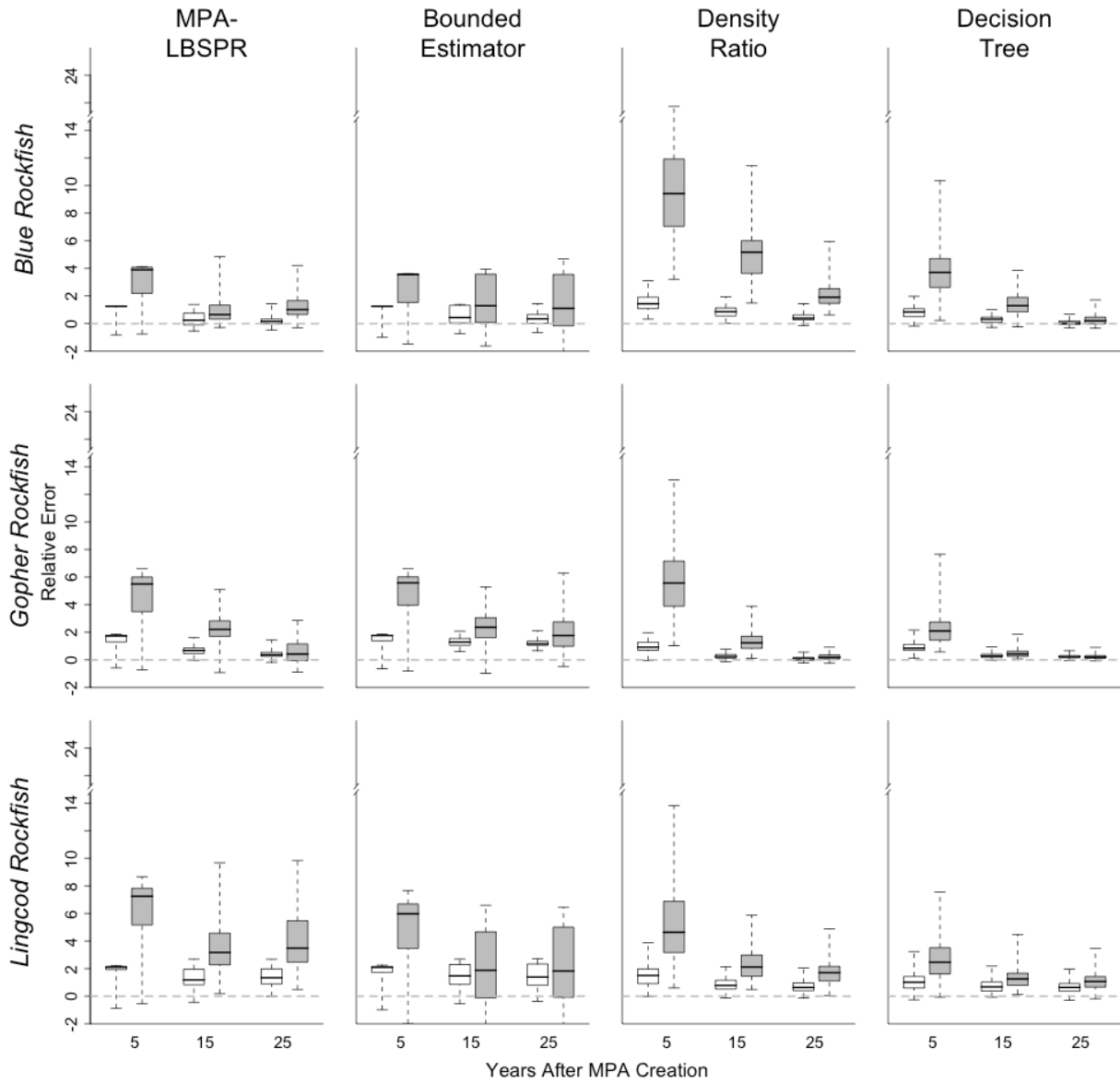


Figure 5. Relative error of assessment methods for each species when movement is present. The white boxes show the distribution at relative error under low historical fishing effort ($F=M$), and the grey boxes show the distribution at relative error under high historical fishing effort ($F=3M$).

Long-term Performance of Management Strategies: Blue Rockfish

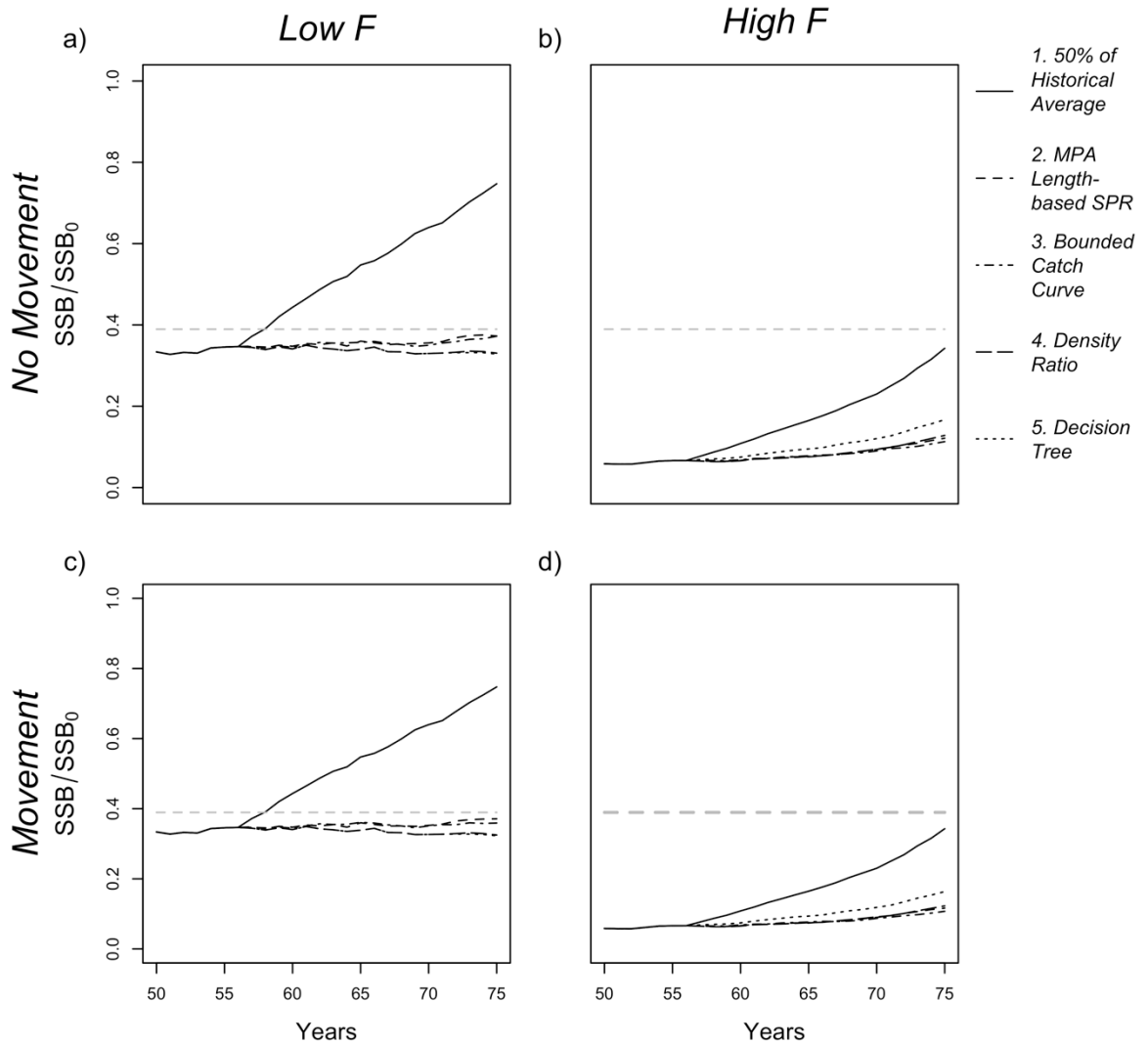
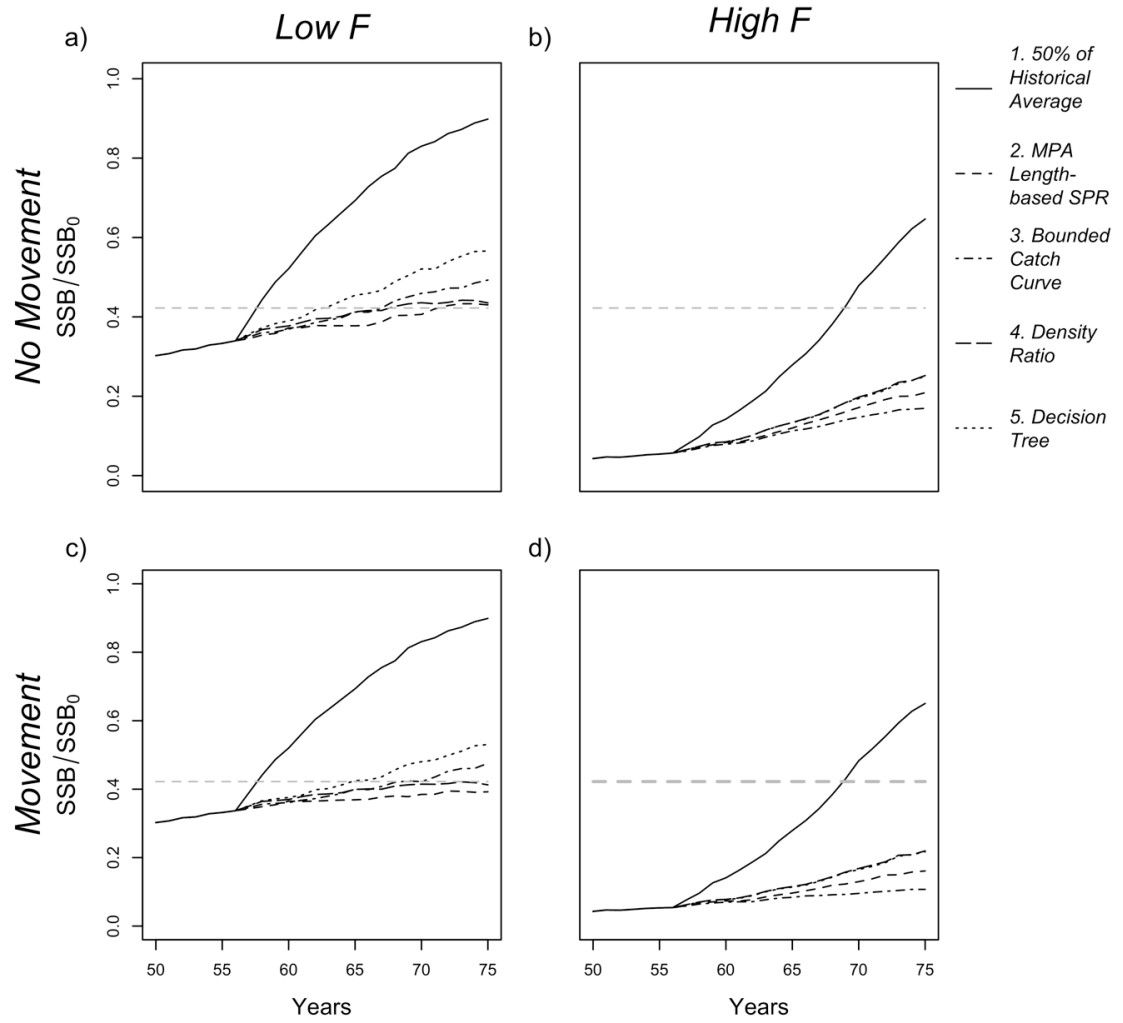


Figure 6. Long-term performance of each management strategy for blue rockfish under a) $F=M$ and no movement, b) $F=3M$ and no movement, c) $F=M$ and movement, d) $F=3M$ and movement. The dashed horizontal line shows the target depletion level for blue rockfish.

Long-term Performance of Management Strategies: Gopher Rockfish



Long-term Performance of Management Strategies: Gopher Rockfish

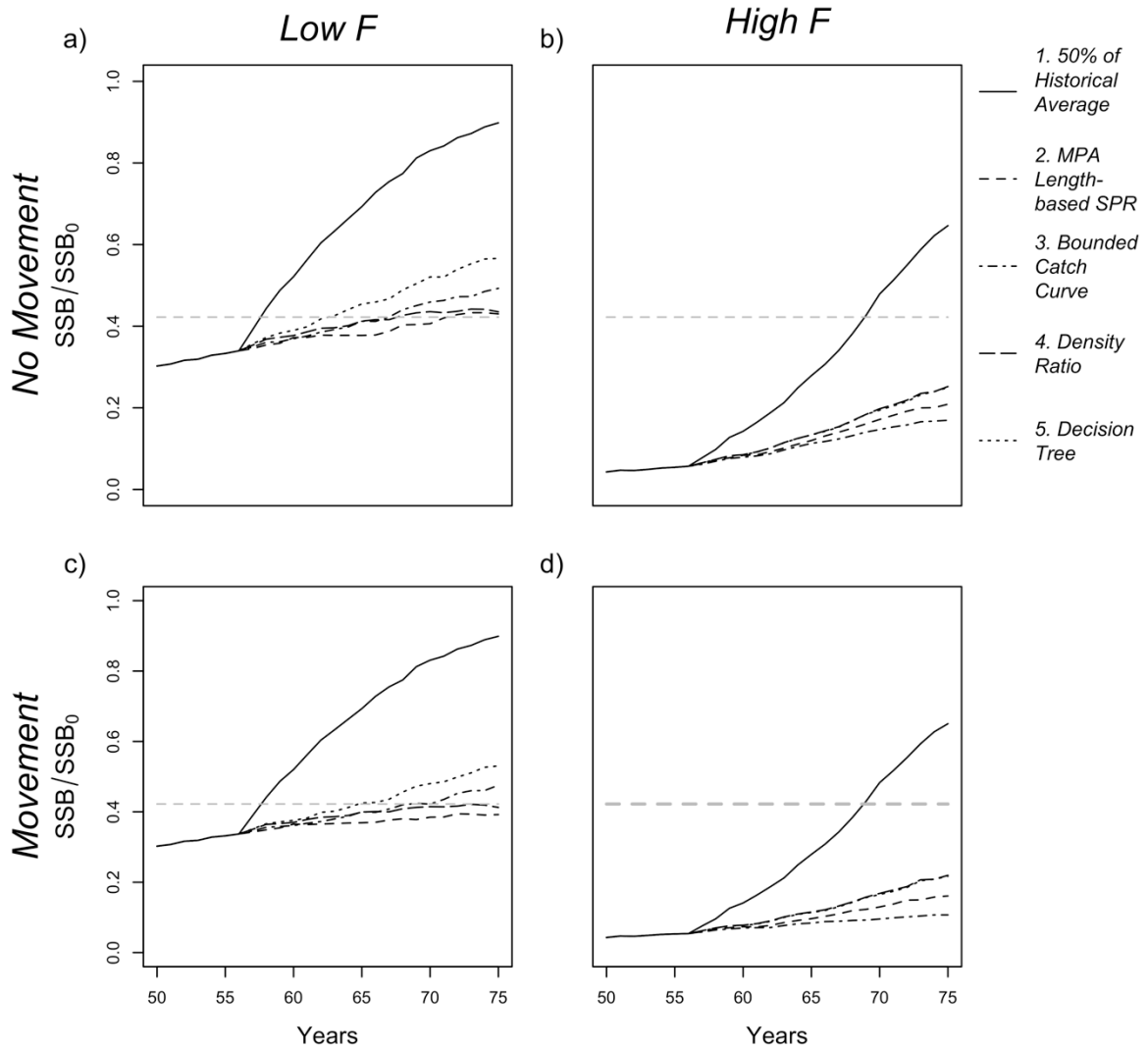


Figure 7. Long-term performance of each management strategy for Gopher rockfish under a) $F=M$ and no movement, b) $F=3M$ and no movement, c) $F=M$ and movement, d) $F=3M$ and movement. The dashed horizontal line shows the target depletion level for gopher rockfish.

Long-term Performance of Management Strategies: Lingcod

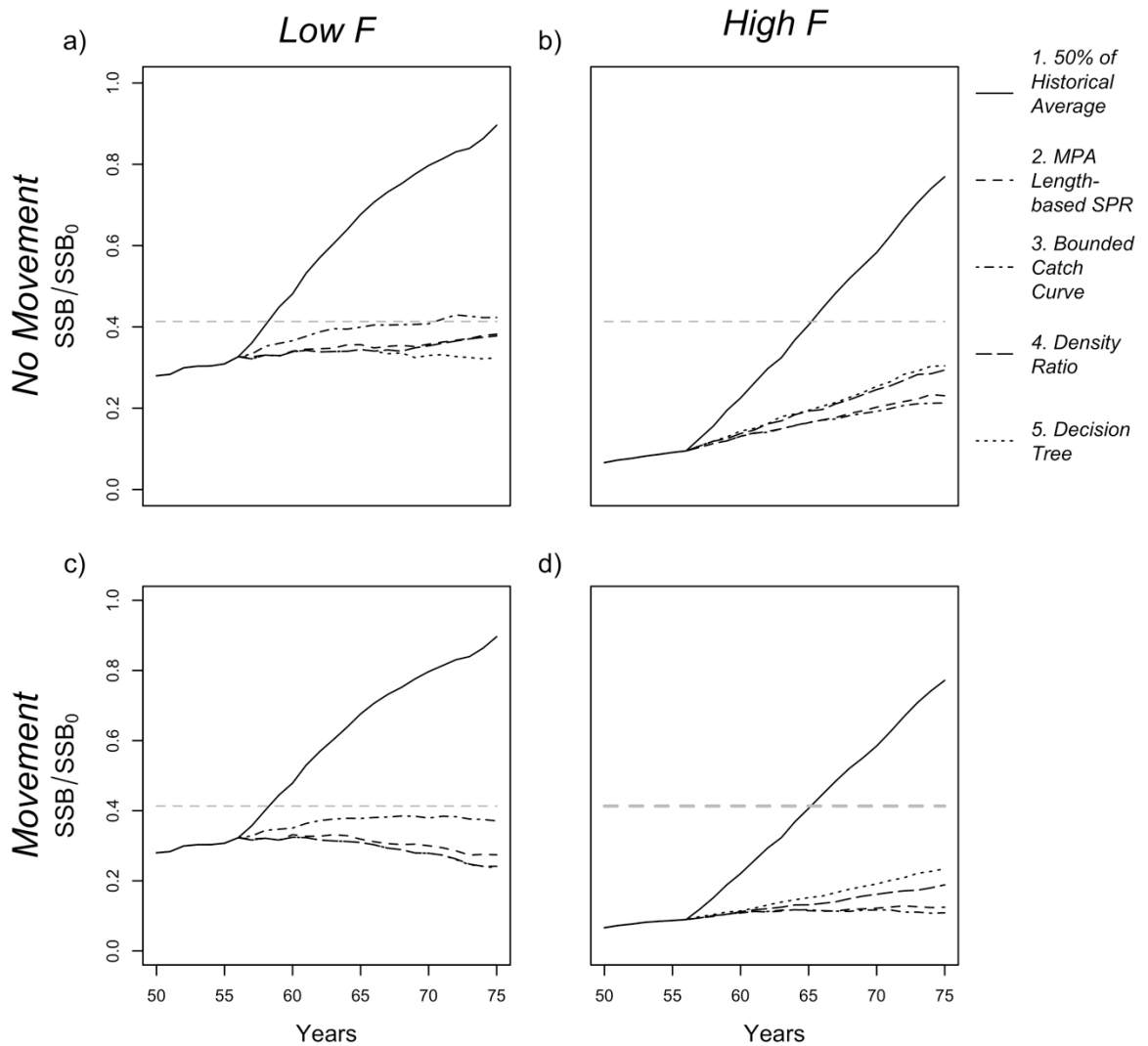


Figure 8. Long-term performance of each management strategy for Lingcod under a) $F=M$ and no movement, b) $F=3M$ and no movement, c) $F=M$ and movement, d) $F=3M$ and movement. The dashed horizontal line shows the target depletion level for lingcod.

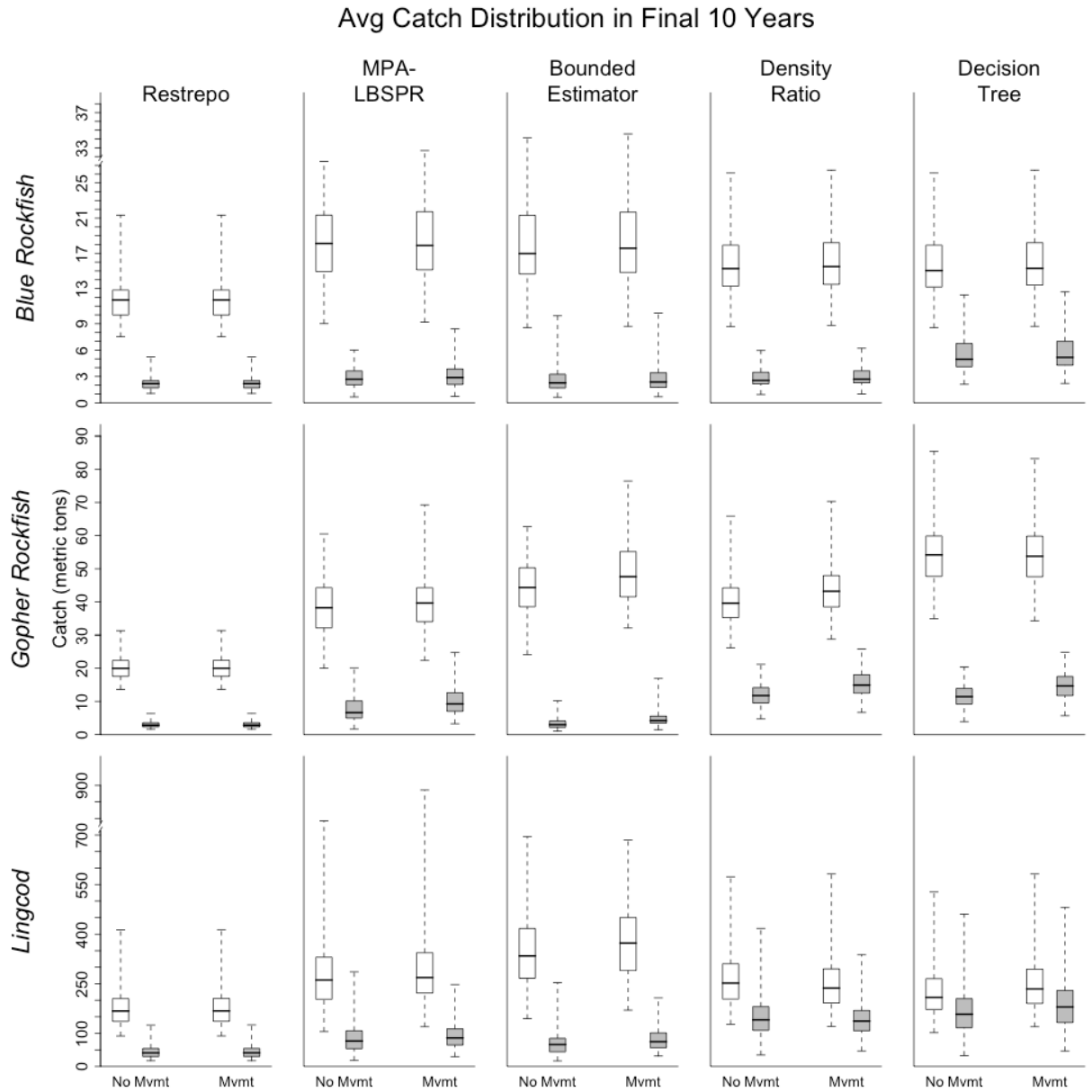


Figure 9. Distribution of average catch in final 10 years of simulation under low ($F=M$; white) and high ($F=3M$; grey) historical fishing. The results of the no movement scenarios are on the left, and the scenarios with movement on the right.

Appendix

An age-structured, spatially-structured operating model with 25 uniform patches was used to test each of the assessment/management procedures described in the main text. A burn-in period of 100 years was used to determine equilibrium unfished conditions. After that time, the population was fished by a single fleet at a constant historical fishing mortality for 30 years. A no take marine protected area (MPA) was created in the center five patches (representing 20% of the available habitat) in year 31. The total fishing effort remained unchanged, but was concentrated into the open patches. The section below describes the structure of the operating model in detail.

Operating Model

1. Fish Biology

The length of individual fish at a given age (L_a) was given by

$$L_a \sim N(\bar{L}_a, \sigma_{L_a}^2) \quad [1]$$

where $\sigma_{L_a}^2$ was the variance and L_a was the mean length-at-age as described by the von Bertalanffy growth equation:

$$\bar{L}_a = L_\infty(1 - e^{-k(a-t_0)}) \quad [2]$$

L_∞ was the average maximum length, k was the growth rate, and t_0 was the theoretical time at length zero (set to 0). The variance in length-at-age was proportional to \bar{L}_a (Sainsbury 1980):

$$\sigma_{L_\infty} = CV_{L_\infty} L_\infty \quad [3]$$

$$\sigma_{L_a}^2 = \sigma_{L_\infty}^2 (1 - e^{-k(a)})^2 \quad [4]$$

where $\sigma_{L_\infty}^2$ was the variance around the asymptotic length, and CV_{L_∞} was the coefficient of variation for L_∞ . The weight (W_a) at age a was given by

$$W_a = w_1 \bar{L}_a^{w_2} \quad [5]$$

where w_1 and w_2 were allometric growth parameters. Fecundity (f_a) was based on the mean length at age:

$$f_a = f_1 \bar{L}_a^{f_2} \quad [6]$$

where f_1 and f_2 were fecundity parameters. The probability that an individual was mature (m_a) was also length-based, and was given by the logistic equation

$$m_a = \frac{1}{1 + \exp(-\ln(19)[(\bar{L}_a - \mu_{50})/(\mu_{95} - \mu_{50})])} \quad [7]$$

where μ_{50} and μ_{95} were the lengths at which 50% and 95% of fish attained

reproductive maturity, respectively.

2. Abundance

The number of fish, N , at age a in patch i at time $t+1$ was given by

$$N_{a,i,t+1} = \begin{cases} R_{i,t+1} & \text{if } a = 1 \\ (N_{a-1,i,t}e^{-M/2} - C_{a-1,i,t})e^{-M/2} & \text{if } 1 < a \leq A \end{cases} \quad [8]$$

where $R_{i,t+1}$ was the number of recruits to patch i at time $t + 1$ (see Equations 9-14), M was the instantaneous rate of natural mortality, $N_{a,i,t}$ was the number of fish at age a at time t in patch i , $C_{a,i,t}$ was the catch at age a in patch i at time t (see Equation 18), and A was the maximum age. The maximum age was defined as the first age class with $\leq 0.1\%$ of R_0 , the initial level of recruitment, under unfished conditions.

3. Egg Dispersal and Recruitment

Assuming that half the population is female, the number of eggs ($E_{i,t}$) produced in patch i at time t was given by

$$E_{i,t} = \sum_{a=1}^A 0.5N_{a,i,t}f_a m_a \quad [9]$$

The eggs produced in each patch joined a common pool, and the total number of eggs (E_t) at time t was given by

$$E_t = \sum_i E_{i,t} \quad [10]$$

The eggs then underwent density-dependent mortality following a Beverton-Holt stock-recruitment relationship, which allowed for autocorrelation in recruitment residuals from year to year:

$$R_t = \frac{E_t}{\alpha + \beta E_t} \exp\left(\epsilon_t - \frac{\sigma_R^2}{2}\right) \quad [11]$$

$$\epsilon_t = \rho_R \epsilon_{t-1} + \sqrt{1 - \rho_R^2} \tau_t; \tau_t \sim N(0, \sigma_R^2) \quad [12]$$

where R_t was the total number of recruits in time t , ρ_R was the extent of temporal autocorrelation in recruitment, τ_t was the normally distributed error around the mean stock–recruitment relationship for year t , and σ_R was the standard deviation of τ_t . α and β were parameterized as follows:

$$\alpha = \frac{(1 - h)E_0}{4hR_0} \quad [13]$$

$$\beta = \frac{5h - 1}{4hR_0} \quad [14]$$

where E_0 was total number of eggs produced under unfished conditions, R_0 was the total number of recruits under unfished conditions, and h was the steepness of the population. The steepness is defined as the fraction of unfished recruits that are produced when the population produces 20% of E_0 . Recruits were distributed equally across all patches.

4. Movement

Movement of fish in Chapter 4 is described by non-directional diffusion. There is no movement beyond the spatial patches of the modeled shoreline, and end cells wrap to prevent edge effects. The proportion of fish, $X_{i,\hat{i}}$, that move from patch \hat{i} to i is given by

$$X_{i,\hat{i}} = \frac{\hat{X}_{i,\hat{i}}}{\sum_i \hat{X}_{i,\hat{i}}} \quad [15]$$

where

$$\hat{X}_{i,\hat{i}} = \exp\left(-\frac{(\hat{i} - i)^2}{2\sigma_x^2}\right) \quad [16]$$

$\hat{X}_{i,\hat{i}}$ is the probability that a fish in cell \hat{i} will move to cell i .

5. Fishery Dynamics

The midyear exploitable biomass in patch i , $X_{i,t}$, was given by

$$X_{i,t} = \sum_a N_{a,i,t} e^{-M/2} V_a \bar{W}_a \quad [17]$$

where age-specific selectivity (V_a) followed a logistic curve (Equations 22-23). The total effort (E_t) was allocated in proportion to the exploitable biomass available in each patch open to fishing:

$$E_{i,t} = \begin{cases} E_t \frac{X_{i,t}}{\sum_i X_{i,t}} & \text{for patches open to fishing} \\ 0 & \text{for patches closed to fishing} \end{cases} \quad [18]$$

The instantaneous fishing mortality rate ($F_{i,t}$) in each patch at time t was a product of the effort in each patch and a catchability parameter, q , which was constant across patches and from year to year:

$$F_{i,t} = E_{i,t} q \quad [19]$$

Catch in each year was assumed to be known without error. Catch data were generated yearly. The catch was taken midyear, and the catch at age ($C_{a,i,t}$) in patch i in time t was given by

$$C_{a,i,t} = N_{a,i,t} e^{-M/2} (1 - e^{-F_{i,t} V_a}) \quad [20]$$

The total catch in weight in year t was given by

$$C_t = \sum_i C_{i,t} = \sum_a C_{a,i,t} \bar{W}_a \quad [21]$$

6. Selectivity

The selectivity of the fishing gear on length L fish followed a two-parameter logistic equation:

$$s_L = \frac{1}{1 + \exp(-\ln(19)[(L - l_{50})/(l_{95} - l_{50})])} \quad [22]$$

where l_{50} was the length at 50% selectivity and l_{95} was the length-at-95%-selectivity.

Selectivity at length was then converted to selectivity-at-age (V_a) for use in the age-based operating model using the following equation:

$$V_a = \int_{L=0}^{L=\infty} s_L \left(\frac{1}{\sqrt{2\pi}\sigma_{L_a}} e^{\frac{-(L-\bar{L}_a)}{2\sigma_{L_a}^2}} \right) dL \quad [23]$$

Sampling Model

Catch (in weight), fishery and survey catch-per-unit effort (CPUE) data, and size-

and age-composition data from both surveys and catches were generated for use in the various assessment methods tested. Catch data were generated yearly and assumed to be known without error. The data collection model assumed that the lengths of η individuals were randomly sampled from both the fishery catch and the survey catch at the end of each year. Age-composition data were assumed to be multinomially distributed about the true age composition. Lengths were generated based on equation [24], where the probability of an individual at age a being in length class g is given by:

$$P_{g,a} = \begin{cases} \phi\left(\frac{l_{g+1}^e - L_a}{\sigma_{L_a}}\right) & \text{if } g = 1 \\ \phi\left(\frac{l_{g+1}^e - L_a}{\sigma_{L_a}}\right) - \phi\left(\frac{l_g^e - L_a}{\sigma_{L_a}}\right) & \text{if } 1 < g \leq G \\ 1 - \left(\frac{l_g^e - L_a}{\sigma_{L_a}}\right) & \text{if } g = I \end{cases} \quad [24]$$

where ϕ is the standard normal cumulative distribution, l_g^e is the lower bound of length class g , and G the total number of length classes. The width of the size classes was 10 mm, with the upper bound of the maximum size class set to $1.5L_\infty$ (rounded to the upper 10 mm).

The age-length probability matrix was modified for the expected age-length

distribution of the catch ($\dot{P}_{g,a}$) to account for the selectivity-at-length by multiplying the age – length transition matrix by the selectivity at length class g (S_g):

$$p_{g,a} = P_{g,a}S_g \quad [25]$$

The age-length transition matrix for the catch was standardized, so that the probability of an individual in the catch-at-age a being in one of the G length classes was 1:

$$\dot{P}_{g,a} = \frac{p_{g,a}}{\sum_a p_{g,a}} \quad [26]$$

Data from the MPA was generated via a simulated survey. An instantaneous mortality rate (J_i) was applied in each of the five closed patches with gear that had the same selectivity as the fishery. The survey catch- at-age ($I_{a,i,t}$) was given by

$$\begin{cases} 0 & \text{for patches open to fishing} \\ I_{a,i,t} = (N_{a,i,t}e^{-M/2})(1 - e^{-JV_a}) & \text{for patches closed to fishing} \end{cases} \quad [27]$$

The fishery-independent size- and age-compositions were generated from the survey catch-at-age following the same procedure outlined above.