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ARTICLE

Surplus Production Model Accuracy in Populations Affected by a No-Take Marine Protected Area

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Abstract
Marine protected areas (MPAs) are increasingly used as a tool in fisheries management. However, implementation of an MPA violates common assumptions for fishery stock assessments that provide estimates of abundance and fishing mortality for management. Thus, it is important to understand the effects of MPAs on estimates from stock assessments. We conducted a simulation study to determine the effects of MPAs on accuracy of surplus production model (SPM) stock assessments. We simulated the dynamics of a population that had part of its range in an MPA, and we assessed the population with spatially aggregated and spatially explicit SPMs under a range of conditions, including different MPA sizes (percentage of the total stock area), different rates of migration between MPA and non-MPA regions, and scenarios with high and low observation error in the indices of abundance. We also considered a scenario in which there was no available index of abundance within the MPA. We used the median of the absolute value of relative error and the median relative error from 200 replicates/scenario to test SPM accuracy. In most cases, spatially explicit SPMs performed better in both accuracy and bias than spatially aggregated SPMs. The accuracy of the assessments also increased as MPA size increased except under the scenario of no index of abundance within the MPA; for that scenario, accuracy increased as MPA size decreased. Monitoring of the stock within the MPA is essential for conducting accurate stock assessments in areas with MPAs.

Marine protected areas (MPAs) have been increasingly used and suggested as a fisheries management tool, often replacing or used in combination with traditional management measures, such as regulating the amount of harvest or fishing effort. Although the term MPA can refer to a wide range of protection, the most conservative type is a no-take MPA in which no harvest is allowed (Wenzel and D'Iorio 2011). One of the benefits of using MPAs in fisheries management is that the underlying theory is intuitive: when an area within a population's range is protected from fishing, that area should develop a greater biomass of fish than the fished areas. Increased biomass within the MPA should result in a "spillover effect" wherein biomass shifts from the MPA to the fished area (Crowder et al. 2000; Halpern and Warner 2002), thereby sustaining a fishery while conserving adult biomass. The spillover effect has been largely thought of as a subsidy of larvae from the MPA to the fished regions (e.g., Punt and Methot 2004). Adult movement could create the same source–sink dynamics between the MPA and fished areas, but many species that are managed by MPAs have low movement rates as adults (e.g., Kaplan et al. 2009; for reasoning, see Hilborn et al. 2004). Other benefits of MPAs include protection of habitat, refuge for populations that are at very low abundances, and protection for species that are not targeted by surrounding fisheries (Kelleher 1999).

Most of the research on MPAs has focused on population dynamics, whereas much less work has considered the effects of MPAs on the methods used to inform fisheries management. Marine protected areas can have substantial negative effects on

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the accuracy of stock assessment models that are used to provide estimates of abundance and fishing mortality rate (F; Punt and Methot 2004; Field et al. 2006). Stock assessments typically assume that each individual within a given size-class or age-class in a population is equally vulnerable, on average, to the fishery. By design, MPAs change the vulnerability of a portion of the population to fishing by protecting it from fishing pressure. Thus, stock assessment techniques may not accurately portray a population that has an MPA within its range and may result in biased estimates of F and available biomass (B; Field et al. 2006).

Some techniques have been developed to account for the spatial changes an MPA makes in the distribution of fish. For example, Punt and Methot (2004) investigated the ability of spatially explicit and spatially aggregated statistical catch-at-age (SCAA) stock assessments to estimate B and F of stocks with spatial dynamics that included an MPA. Punt and Methot (2004) found that spatially explicit SCAA assessments substantially improved the accuracy of total B and F estimates relative to spatially aggregated SCAA assessments. The characteristics of the MPA and population also affect assessment model performance, as larger MPAs, lower migration rates, and surveys with lower observation error lead to more accurate estimates of B (Punt and Methot 2004). Application of SCAA assessments is often impractical or impossible for stocks with incomplete or unavailable age data, but the performance of non-age-structured assessments has not been tested in scenarios that include the use of MPAs in management. Density ratios have also been proposed as a method for managing data-poor fisheries in areas with MPAs (Babcock and MacCall 2011; McGilliard et al. 2011). Surplus production models (SPMs) constitute a common method of assessing stocks for which age-structured data are either incomplete or impractical to obtain (Prager 1994). Surplus production models require less data and have fewer estimated parameters than age-structured models (Laloë 1995). Surplus production models include many aspects of population dynamics in a simple model, and they produce estimates that are easily translated into reference points commonly used to inform management, such as maximum sustainable yield (MSY) or the equilibrium B that would produce MSY (B_{MSY}; Hilborn and Walters 1992; Quinn and Deriso 1999; Jacobson et al. 2002). Although age-structured methods are often preferred, SPMs are still commonly used in assessing fish stocks, especially those in tropical regions, where age-structured methods are impractical due to difficulties with accurate fish age estimation (Pauly 1987).

The goal of our study was to compare the accuracy of spatially aggregated and spatially explicit SPMs for assessing stocks that are managed with MPAs. Specifically, the objective of this paper was to examine the accuracy of SPM estimates when (1) part of the stock's range includes an MPA and (2) the spatial resolution of the available data is confined to one region inside the MPA and one region outside of the MPA. We used simulations to examine the effects of MPA size, migration rate (z), level of observation error in the index of abundance, and spatial aggregation of the data on estimates from spatially explicit and spatially aggregated SPMs.

METHODS

We conducted numerical experiments in which we simulated population dynamics and fishery data sets by using a data-generating model, estimated abundance and F by using several SPMs, and compared SPM estimates with true values to determine SPM accuracy. The population dynamics were based on stylized fish stocks and followed a deterministic logistic growth model. The data-generating model described the population dynamics for a range of MPA sizes and z-values and produced a 50-year time series of catch and indices of abundance. The assessment models were spatially explicit or spatially aggregated versions of SPMs and were fitted to the indices of abundance by using a maximum likelihood approach. Each SPM was fitted to 200 replicate data sets for each scenario that differed in their random observation errors. All of the models were written in AD Model Builder (Fournier et al. 2012).

Data-generating model.—Population dynamics were generated by use of a spatially explicit, discrete-time, logistic growth model with two regions. One region became a no-take MPA in year 20, and the other region remained open to fishing throughout the simulation. The population was simulated for 50 years, and the first year of the simulation was also the first year of the targeted fishery. The population began at 90% of carrying capacity (K) in year 1 to represent a population that was lightly affected by a nontarget fishery prior to development of the targeted fishery. Fishing mortality rapidly increased until the population was largely depleted and an MPA was established in year 20, at which point F either remained high or gradually decreased to the F that would achieve MSY (F_{MSY}). These patterns of F were used to avoid the well-known problem of uninformative, "one-way-trip" data sets (Hilborn and Walters 1992).

The data-generating model calculated the true total B for each year, the observed index of abundance (observation error included), and the fishery catch in each region (C_{Area}, where $Area$ = the MPA or the fished area). The data-generating model followed a discrete-time Schaefer (1954) production model with logistic growth, migration between two regions, and fishing (Hannesson 1998; see Table 1 for definitions of the variables):

$$\begin{aligned} B_F(t+1) = {} & B_F(t) + rB_F(t)\left[1 - \frac{B_F(t)}{K(1-m)}\right] \\ & + zm\left[\left(\frac{1-m}{m}\right)B_{MPA}(t) - B_F(t)\right] \\ & - F_F(t)B_F(t) \end{aligned}$$

and

$$\begin{aligned} B_{MPA}(t+1) = {} & B_{MPA}(t) + rB_{MPA}(t)\left[1 - \frac{B_{MPA}(t)}{Km}\right] \\ & + z(1-m)\left[\left(\frac{m}{1-m}\right)B_F(t) - B_{MPA}(t)\right] \\ & - F_{MPA}(t)B_{MPA}(t). \end{aligned}$$

TABLE 1. Definitions of the symbols used in data-generating and assessment models (MPA = marine protected area).

Symbol	Definition
I_{Region}	Index of biomass in one of the regions; subscript F denotes the fished region, and subscript *MPA* denotes the MPA region
$\hat{I}_{Region}$	Predicted index of biomass in one of the regions; subscript F denotes the fished region, and subscript *MPA* denotes the MPA region
r	Intrinsic rate of increase (= 0.2 or 0.4)
K	Carrying capacity of the entire population (= 1,000 units)
m	MPA size expressed as a proportion of the total stock area
z	Migration rate
σ	SD of observation error
δ	Normally distributed observation error
F_{Area}	Annual fishing mortality rate
q_s	Catchability of the survey (= 0.005)
t_{max}	Number of years in the simulation (= 50)
C	Total annual catch
B	Biomass

Population parameters (K, z, MPA size expressed as a proportion of the total stock area [m], and the intrinsic rate of increase [r]) were constant across simulations within a scenario. The value for K was a generic maximum total B (Table 1). Migration rate, z, was defined as the probability that an individual will move from one region to the other within a year (Hannesson 1998). The z parameter represents a combination of a fish's propensity for movement and the size or arrangement of an MPA or a complex of MPAs. For example, a low z may represent a stock with moderate amounts of movement and a single large MPA within its range, whereas a high z may represent a stock with a low rate of movement and a network of small MPAs within its range. The equation is scaled so that if the populations in both areas are equal in proportion to K, there will be no net movement.

The index of biomass produced within the data-generating model was the product of biomass (B_{Area}), survey catchability (q_s), and a random lognormal observation error with a median of zero and an SD determined by the scenario:

$$S_{Area}(t) = B_{Area}(t) q_s e^{\sigma \delta(t)}.$$

The random observation errors changed in each replicate of each scenario. Fishery catch in each region (C_F or C_{MPA}) was calculated as the product of B and F for that area,

$$C_{Area}(t) = B_{Area}(t) F_{Area}(t).$$

Our simulation experiment followed an incomplete factorial design with four levels of MPA size, four levels of z, two patterns of changing F over time, two levels of r, and two levels of observation error for the index of biomass. The experiments only considered one pattern of F for $r = 0.4$, but both patterns of F for $r = 0.2$. The value of 0.4 for r is similar to estimated maximum population growth rates for the barndoor skate *Dipturus laevis* (Gedamke et al. 2009), South Atlantic albacore *Thunnus alalunga* (Polacheck et al. 1993), and Namibian hakes (cape hake *Merluccius capensis* and deepwater hake *M. paradoxus*; Polacheck et al. 1993), but this level may be considered relatively high (Shepherd and Litvak 2004). Therefore, we also included the lower level of r, which is similar to estimates for species such as the Atlantic cod *Gadus morhua* (Hutchings 1999). The MPA sizes considered were 5, 10, 20, and 40% of the total stock area. The two largest MPA sizes were used for comparison with results from Punt and Methot (2004). Marine protected areas in this range of sizes have also been recommended or evaluated by several authors (Boersma and Parrish 1999; Crowder et al. 2000; Jones 2001). The two smaller MPA sizes were included to represent the more common MPA sizes implemented in current fisheries (NOAA 2010). To simulate different types of populations and MPA configurations, we considered four levels of z: 0.2, 0.3, 0.4, and 0.5 per year.

The two F patterns were the same before implementation of the MPA (i.e., year 20; Figure 1). In the first F scenario, the F decreased to F_{MSY} in the non-MPA region after implementation of the MPA. In the alternative F scenario, effort that had taken place within the MPA prior to simulation year 20 was displaced to the region that was open to fishing. Redistribution of fishing effort when an MPA is implemented may more accurately describe actual fishing behavior in relation to MPAs (Rijnsdorp et al. 2001; Dinmore et al. 2003). Fishing mortality in the $r = 0.4$ scenario followed the same pattern as that in the $r = 0.2$ scenario but was doubled in magnitude to create approximately the same decline in B and to reflect the different level of F_{MSY} for a faster-growing population. We included two levels of observation error, low (log-scale SD = 0.2) and high (log-scale SD = 1.0), to represent good and poor indices of biomass, respectively. The assumed log-scale SD was the same for the indices of abundance used in the spatially aggregated estimation models and those used in the spatially explicit models. For each level of r and each pattern of fishing effort, we also simulated a set of scenarios in which there was no available index of biomass within the MPA; this was used to model a situation in which (1) only fishery-dependent data were available or (2) monitoring was not conducted within the MPA.

Estimation models.—Data sets were fitted with spatially explicit and spatially aggregated SPMs. Spatially explicit SPMs had the same form as the data-generating model except that observed C was subtracted in each year. The dynamics of the spatially aggregated model followed a simple Schaefer SPM

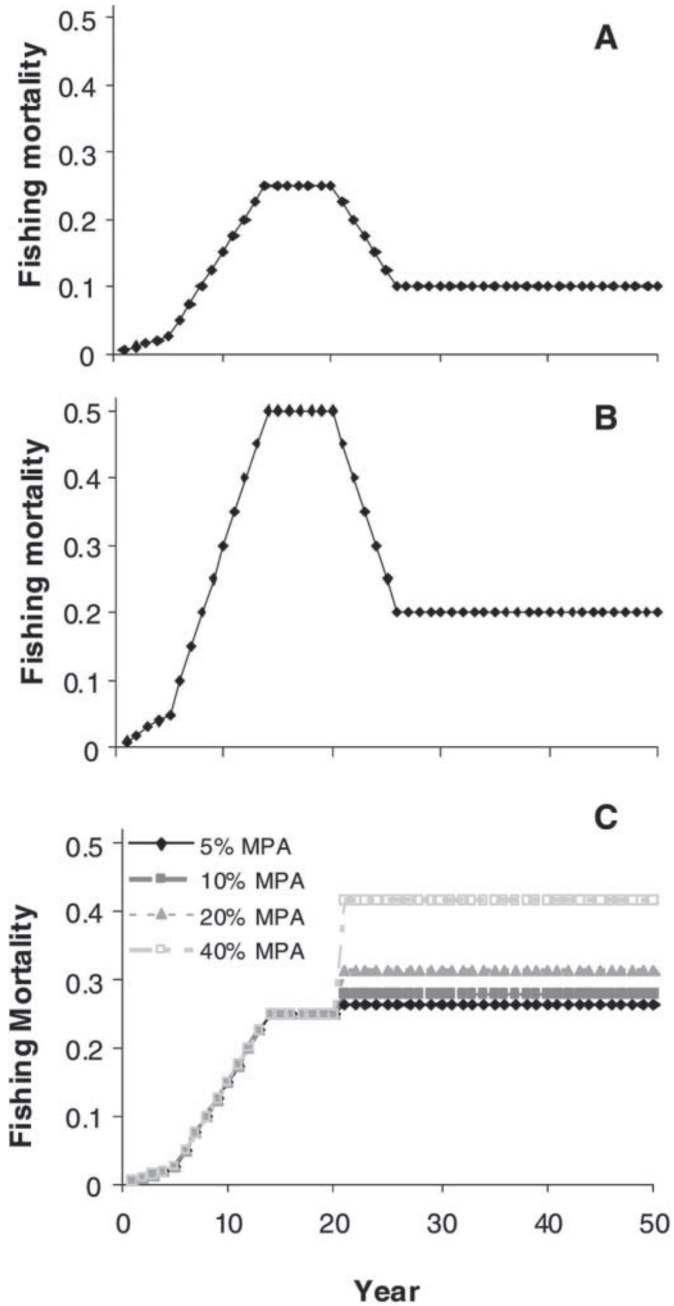

FIGURE 1. Pattern of annual fishing mortality (F) in the fished region over time for scenarios in which **(A)** the intrinsic rate of increase (r) equals 0.2 and F was reduced to the level that supports maximum sustainable yield (F_{MSY}) after implementation of the marine protected area (MPA), **(B)** r equals 0.4 and F was reduced to F_{MSY} after MPA implementation, and **(C)** r equals 0.2 and fishing effort originally occurring in the MPA region was redistributed to the non-MPA region after MPA implementation. In the F_{MSY} scenarios, the fishing effort applies to all MPA sizes (MPA = 5–40% of the total stock area). After the first 20 years, F in the MPA was zero.

(Hilborn and Walters 1992),

$$B(t+1) = B(t) + rB(t)\left[1 - \frac{B(t)}{K}\right] - C(t).$$

The estimated parameters of the model were z (in the spatially explicit models), K, r, the initial B as a proportion of K, and q_s. Estimation models were given the correct parameter values as starting values for the estimation to avoid potential problems caused by poor starting values. Although analysts in the field would not have the correct values, the models were relatively insensitive to starting values; we ran a subset of the estimation models for which the starting values were changed by 10%, but the results were not different. The parameters were estimated by minimizing the concentrated negative log-likelihood ($-LL$) functions. For the spatially explicit scenarios, the concentrated $-LL$ function assumed lognormal observation errors for the indices of biomass within the MPA (I_{MPA}) and outside of the MPA (I_F),

$$-LL = t_{max}\log_{10}\left\{\sum[\log_{10}(\hat{I}_F) - \log_{10}(I_F)]^2 + \sum[\log_{10}(\hat{I}_{MPA}) - \log_{10}(I_{MPA})]^2\right\}.$$

For the spatially aggregated SPMs, the concentrated $-LL$ function assumed lognormal observation errors about a spatially aggregated I or only an I from outside of the MPA,

$$-LL = 0.5t_{max}\log_{10}\left\{\sum[\log_{10}(\hat{I}) - \log_{10}(I)]^2\right\}.$$

The effect of time (years) since the MPA was implemented on the accuracy of the results was considered by conducting a subset of simulations with 25-, 30-, and 40-year time series. Effects of the shorter time series were only evaluated in the scenarios with low r.

Assessment evaluation.—We evaluated the accuracy of SPMs by calculating the percent relative error of estimated B (B_{error}) in the last simulation year from the 200 simulated data sets for each estimation model,

$$B_{error} = \left(\frac{B_{pred} - B_{true}}{B_{true}}\right) \times 100,$$

where B_{true} is the actual B of the population and B_{pred} is the predicted B from the SPM.

We summarized the bias and accuracy of the models by using the median of the relative error (MRE) or the median of the absolute value of relative error (MARE) for each assessment model under each MPA size, z, fishing effort scenario, level of survey error SD, pattern of fishing effort, and level of r. We used the median instead of the mean because medians are not as susceptible to the influence of large outliers, which were present in the results. We compared true and estimated values of B in the last year of the simulation (30 years after the establishment of the MPA) to indicate overall accuracy of the model for most of the evaluations. We also used the accuracy of parameter estimates—specifically r, K, q_s, and initial B—as indicators of overall model performance because they are used to calculate biological reference points (e.g., MSY) and to inform management decisions.

RESULTS

Population Trends

The populations in all of the scenarios began at 90% of K and then declined rapidly for 20 years until they reached approximately 10–20% of K (Figure 2). In the scenarios with low r and decreased fishing effort, after the MPA was established in year 20 the populations slowly increased for 25–27 years until reaching equilibrium B. Equilibrium B varied among MPA sizes. When only 5% of the total stock area was included in the MPA ($m = 0.05$), the populations recovered to about 46.5% of K. When the MPA included 40% of the total stock area ($m = 0.4$), the populations recovered to around 68.6% of K. Differences in z affected the final equilibrium B by less than 1% of K. In the scenarios with a high r and decreased fishing effort, the population increased until it reached equilibrium after the MPA was implemented, but equilibrium B levels were slightly higher than those in the lower-r scenarios. When only 5% of the total area was included in the MPA, the populations recovered to about 51.7% of K (Figure 2). When the MPA included 40% of the total area, the populations recovered to around 71.9% of K. Differences in z affected the final equilibrium B by approximately 0.5%.

The dynamics were very different in the scenarios with a low r and redistributed fishing effort (Figure 2). In most cases, the population continued to decline after implementation of the

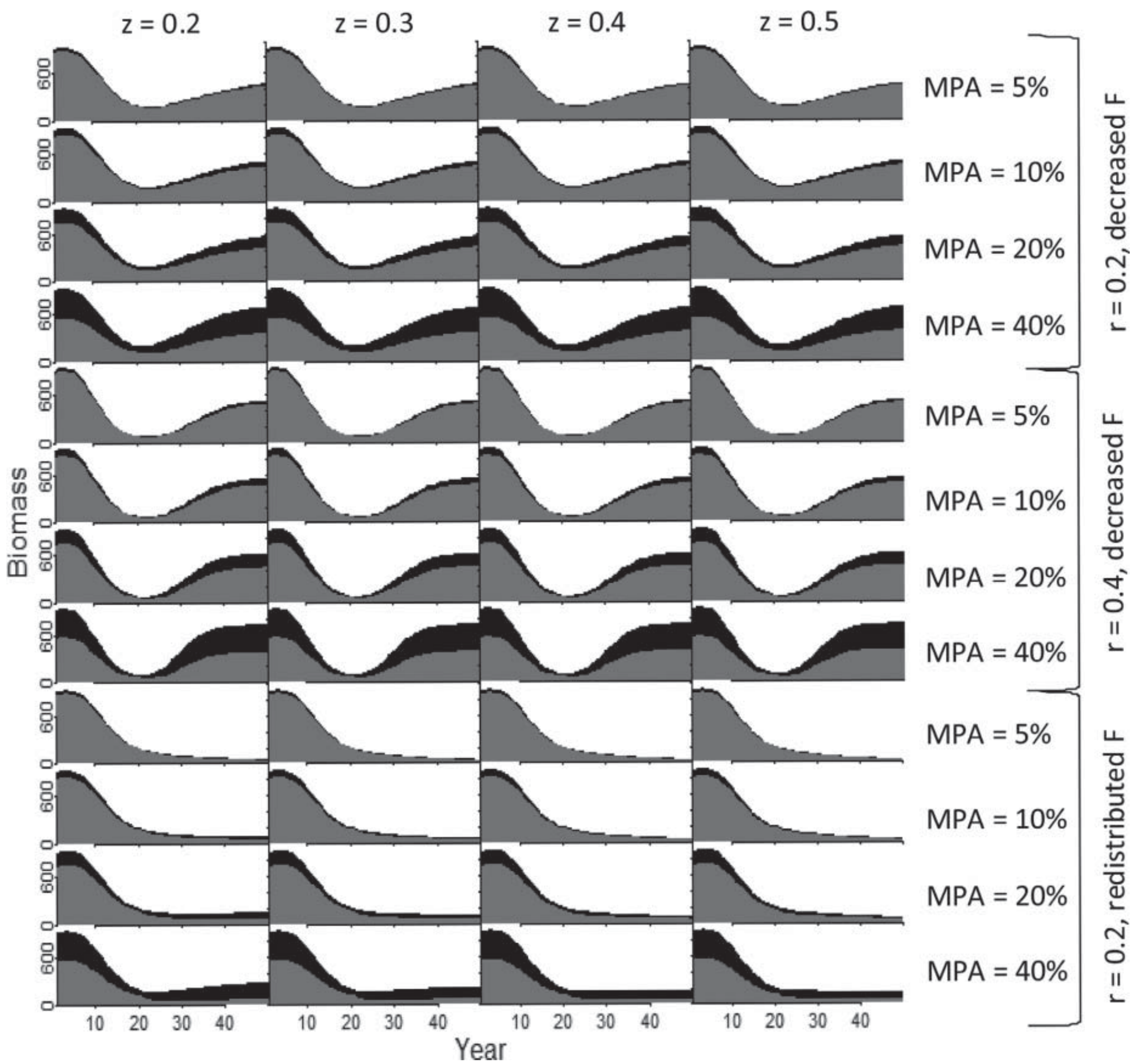

FIGURE 2. Biomass (units) in the marine protected area (MPA) region (black shading) and non-MPA region (gray shading) for each scenario defined by MPA size (MPA = 5–40% of the total stock area), migration rate (z), intrinsic rate of increase (r), and fishing mortality (F) pattern (F patterns are defined in Figure 1).

MPA, although at a slower pace than before MPA implementation, and the population reached 3.4–14.2% of K by the final year of the simulation. Only when the MPA was 40% of the total area and z was lower than 0.5 did the population increase after MPA implementation, reaching 17.5% of K when z was 0.4 and 28.2% of K when z was 0.2. Migration rates affected the final B to a greater degree in the redistributed fishing effort scenario because of the greater disparity in mortality between the two regions.

Accuracy of Surplus Production Models

The accuracy of estimates of B in the last year of the simulations differed substantially between SPMs and among scenarios. The spatially explicit models were the most accurate in most of the scenarios, but occasionally the spatially aggregated models were more accurate or less biased. The MAREs of the spatially aggregated models ranged from 82.2% to 717% of the corresponding spatially explicit models (Table 2), but on average the MAREs of the spatially aggregated models were 45% higher than those of the spatially explicit models. The MREs of the spatially aggregated models showed more bias than the spatially explicit models in 54% of the scenarios, and the majority of these were scenarios involving low observation error. The spatially explicit models tended to be negatively biased, whereas the spatially aggregated models were usually positively biased. For models in which no survey data were available from within the MPA, the MARE was 1.0–35.5 times higher than those of other models and the differences increased as MPA size increased (Figure 3). In addition, estimates of B from the models with no MPA survey data showed substantial negative bias.

For scenarios with a low value of r and decreased fishing effort, the spatially explicit and spatially aggregated SPMs did not differ substantially in the MARE of B for the last year of the simulation, as MARE ranged from 1.4% to 5.2%; however, the spatially explicit SPMs did have 15% lower MAREs on average (Figure 3). The models had substantially higher errors (MARE = 10.3–25.1%) in the high-observation-error scenarios than in the low-observation-error scenarios, as may be expected. In the high-observation-error scenarios, the MAREs of the spatially explicit models were 10% lower than those of the spatially aggregated models on average. The scenarios with a high value of r and a low observation error showed that the spatially aggregated SPMs had MAREs that were 1.4–7.2 times larger than those of the spatially explicit assessments (spatially aggregated SPMs: MARE range = 2.5–8.8%; spatially explicit SPMs: MARE range = 1.1–3.3%). In the scenarios with the higher level of observation error, the spatially explicit and spatially aggregated SPMs had similar performance, with the most accurate model differing among scenarios.

The SPMs were less accurate in the scenarios with a low value of r and redistributed fishing effort than in the scenarios with decreased fishing effort. The MARE range of the spatially explicit models with low observation error was 4.5–12.7%, while the spatially aggregated SPMs had a MARE of 9.6–19.7% (Table 2). There was a greater disparity between the MAREs of the spatially explicit and spatially aggregated SPMs in the redistributed fishing effort scenarios; MAREs of the spatially aggregated SPMs were on average 1.5 times the MAREs of spatially explicit SPMs. The SPMs with no MPA survey data were also less accurate in the redistributed fishing effort scenarios, with MAREs that were 1.6–5.0 times larger than those for the decreased fishing effort SPMs.

The accuracy and bias of estimated B depended on MPA size and, to a lesser extent, z (Figure 3). In most of the spatially explicit SPMs, the accuracy increased with increasing MPA size regardless of r, observation error, or pattern of fishing effort. Bias did not change with MPA size or z in the spatially explicit SPMs. The same trend was seen in most scenarios for the spatially aggregated SPMs. For the spatially aggregated models with no information from the MPA, however, error increased with increasing MPA size in all scenarios and the estimates of B were highly negatively biased. For the spatially aggregated SPMs, accuracy and bias improved with increasing z. Migration rate did not affect accuracy in the spatially explicit SPMs with decreased fishing effort; however, in the redistributed fishing effort scenarios, error increased with increasing z. Migration rate was an important factor in accuracy of the spatially aggregated SPMs, for which higher levels of z usually produced lower errors in models with survey data from the MPA and in models without MPA data. However, in all of these cases, MPA size had a more pronounced effect on accuracy than did z.

Patterns in the accuracy of parameter estimates were different than those for B in the last simulation year (Figure 4). In general, the spatially explicit SPMs produced more accurate estimates of r, K, q_s, and initial B than the spatially aggregated SPMs. The MARE for the initial B parameter estimate was up to 40% lower in the spatially explicit SPMs than in the spatially aggregated SPMs. The other parameters were estimated with approximately the same degree of accuracy in both types of SPM. However, trends in parameter estimates across MPA sizes did not coincide with those seen in the B estimates. The spatially explicit SPMs tended to produce somewhat less-accurate estimates with increasing MPA sizes (0–10% higher MARE for $m = 0.4$ than for $m = 0.05$), while the spatially aggregated assessments often produced more accurate estimates with increasing MPA sizes (10–50% lower MARE for $m = 0.4$ than for $m = 0.05$). The errors of estimates for r, K, q_s, and initial B from the models with no MPA survey data were consistently higher than the errors in parameter estimates from other models.

The general pattern of relative error in B in the assessment models changed depending on how many years of data were available after the MPA was established (Figures 5, 6). In all cases, the range of relative errors was narrower with 20 or 30 years of data as opposed to 5 years of data after MPA implementation. In the scenarios with an r-value of 0.2 and decreased fishing effort, this reflected an increase in the range of relative error by 300–650% in models with 5 years of post-MPA data (Figure 5). The same pattern was observed in the scenarios with

TABLE 2. Median of the absolute value of relative error (MARE) and median of the relative error (MRE) for each assessment model (i.e., spatially explicit surplus production model [SPM], spatially aggregated SPM, and assessments without survey data from the marine protected area [MPA]) under each scenario defined by migration rate (z), MPA size (percentage of the total stock area), observation error, intrinsic rate of increase (r), and fishing effort scenario (decreased or redistributed effort). For each scenario, the MARE and MRE closest to zero are italicized; the MARE and MRE with the largest absolute values are in bold.

Log-scale observation error SD	z	MPA size (%)	Spatially explicit SPM MRE	Spatially explicit SPM MARE	Spatially aggregated SPM MRE	Spatially aggregated SPM MARE	No information from MPA MRE	No information from MPA MARE
			Decreased fishing effort, $r = 0.2$					
0.2	0.2	5	*0.3*	*4.7*	−0.4	5.1	**−9.6**	**9.9**
0.2	0.2	10	*0.2*	*4.2*	0.8	4.7	**−18.0**	**18.0**
0.2	0.2	20	*0.3*	*3.0*	2.4	3.6	**−30.7**	**30.6**
0.2	0.2	40	*0.3*	*1.4*	3.7	3.8	**−51.2**	**51.2**
0.2	0.3	5	*0.1*	*4.8*	−0.9	5.1	**−8.9**	**9.5**
0.2	0.3	10	0.1	*4.3*	*0.0*	4.4	**−16.9**	**16.9**
0.2	0.3	20	*0.3*	*3.1*	1.2	3.3	**−29.1**	**29.1**
0.2	0.3	40	*0.4*	*1.6*	2.4	2.7	**−49.3**	**49.3**
0.2	0.4	5	*0.04*	*4.8*	−1.1	5.2	**−8.5**	**9.1**
0.2	0.4	10	*0.1*	*4.2*	−0.3	4.3	**−16.2**	**16.2**
0.2	0.4	20	*0.3*	*3.2*	0.6	3.5	**−28.1**	**28.1**
0.2	0.4	40	*0.5*	*1.7*	1.7	2.2	**−48.2**	**48.2**
0.2	0.5	5	*−0.03*	*4.9*	−1.1	5.2	**−8.2**	**8.8**
0.2	0.5	10	*−0.1*	*4.2*	−0.5	4.5	**−15.7**	**15.7**
0.2	0.5	20	*0.3*	*3.2*	0.4	3.7	**−27.4**	**27.4**
0.2	0.5	40	*0.5*	*1.8*	1.4	1.9	**−47.5**	**47.5**
1	0.2	5	*−4.0*	*22.5*	−6.8	25.0	**−21.8**	**33.6**
1	0.2	10	−3.4	*19.0*	*−2.9*	21.7	**−31.4**	**34.7**
1	0.2	20	−5.5	*13.1*	*0.7*	17.1	**−46.5**	**46.5**
1	0.2	40	−6.2	11.5	*−1.0*	*10.3*	**−63.8**	**63.8**
1	0.3	5	*−4.8*	*23.4*	−9.4	25.0	**−21.4**	**34.0**
1	0.3	10	−5.3	*19.4*	*−4.6*	22.4	**−30.8**	**34.0**
1	0.3	20	−5.3	*14.1*	*−0.7*	17.9	**−45.4**	**45.4**
1	0.3	40	−5.7	*10.6*	*−2.2*	11.1	**−62.5**	**62.5**
1	0.4	5	*−6.7*	*23.8*	−10.2	25.1	**−21.1**	**34.1**
1	0.4	10	*−6.3*	*19.7*	−6.8	22.3	**−30.4**	**33.2**
1	0.4	20	−5.1	*14.9*	*−1.9*	18.2	**−44.7**	**45.3**
1	0.4	40	−5.3	*10.4*	*−2.5*	10.7	**−63.2**	**63.2**
1	0.5	5	*−7.3*	*23.5*	−10.4	25.0	**−20.9**	**33.9**
1	0.5	10	*−7.2*	*20.6*	−7.7	22.6	**−30.1**	**33.5**
1	0.5	20	−5.1	*15.3*	*−2.6*	18.4	**−43.4**	**44.2**
1	0.5	40	−5.6	*10.7*	*−2.7*	11.1	**−61.2**	**61.2**
			Decreased fishing effort, $r = 0.4$					
0.2	0.2	5	*−0.7*	*3.2*	1.5	4.6	**−6.8**	**7.7**
0.2	0.2	10	*−0.4*	*2.6*	4.2	4.6	**−11.8**	**11.8**
0.2	0.2	20	*−0.3*	*1.7*	7.9	7.9	**−19.4**	**19.4**
0.2	0.2	40	*−0.2*	*1.2*	8.8	8.8	**−36.8**	**36.8**
0.2	0.3	5	−0.7	*2.5*	*0.4*	4.1	**−6.7**	**7.6**
0.2	0.3	10	*−0.4*	*3.1*	2.3	3.6	**−11.6**	**11.6**
0.2	0.3	20	*−0.4*	*2.1*	5.0	5.0	**−19.2**	**19.2**
0.2	0.3	40	*−0.2*	*1.3*	5.8	5.8	**−35.9**	**35.9**
0.2	0.4	5	*−0.7*	*1.9*	1.3	4.27	**−6.6**	**7.5**
0.2	0.4	10	*−0.3*	*3.3*	3.4	3.37	**−11.5**	**11.5**
0.2	0.4	20	*−0.3*	*2.0*	4.2	3.40	**−19.1**	**19.1**

TABLE 2. Continued.

Log-scale observation error SD	z	MPA size (%)	Spatially explicit SPM		Spatially aggregated SPM		No information from MPA	
			MRE	MARE	MRE	MARE	MRE	MARE
0.2	0.4	40	−0.2	*1.2*	*−0.2*	4.20	**−32.3**	**32.3**
0.2	0.5	5	−0.7	*1.6*	*−0.5*	4.22	**−6.5**	**7.5**
0.2	0.5	10	*−0.6*	3.3	0.7	*3.21*	**−11.4**	**11.4**
0.2	0.5	20	*−0.2*	*2.0*	2.4	2.49	**−18.9**	**18.9**
0.2	0.5	40	*−0.1*	*1.2*	3.2	3.19	**−30.1**	**30.1**
1	0.2	5	−8.2	*16.6*	*3.8*	17.30	**−21.7**	**25.0**
1	0.2	10	−7.5	*12.6*	*5.6*	14.53	**−29.8**	**29.8**
1	0.2	20	−7.8	10.3	*6.1*	*9.94*	**−34.2**	**34.2**
1	0.2	40	*−5.4*	*8.3*	6.8	9.62	**−25.7**	**25.7**
1	0.3	5	−8.8	*16.7*	*1.1*	17.46	**−21.2**	**24.6**
1	0.3	10	−8.0	*13.0*	*2.5*	13.50	**−29.3**	**29.3**
1	0.3	20	−7.4	10.4	*2.7*	*8.64*	**−38.7**	**38.7**
1	0.3	40	−5.5	*7.3*	*3.6*	7.34	**−34.2**	**34.2**
1	0.4	5	−8.6	*16.3*	*0.2*	16.95	**−20.8**	**24.2**
1	0.4	10	−7.7	*12.6*	*1.5*	12.76	**−30.1**	**30.1**
1	0.4	20	−7.4	9.7	*1.1*	*8.09*	**−42.1**	**42.1**
1	0.4	40	−5.2	7.2	*2.0*	*6.32*	**−35.9**	**35.9**
1	0.5	5	−9.6	*16.7*	*−0.4*	16.86	**−20.7**	**24.6**
1	0.5	10	−8.0	12.7	*0.2*	*12.64*	**−28.5**	**28.5**
1	0.5	20	−7.1	9.5	*0.2*	*7.77*	**−40.6**	**40.6**
1	0.5	40	−5.2	7.1	*0.8*	*5.93*	**−37.5**	**37.5**
			Redistributed fishing effort, $r = 0.2$					
0.2	0.2	5	*−2.1*	*9.0*	4.2	12.1	**−48.9**	**48.9**
0.2	0.2	10	*−0.8*	*7.7*	8.6	12.3	**−61.5**	**61.5**
0.2	0.2	20	*−0.9*	*7.0*	13.6	14.1	**−71.2**	**71.2**
0.2	0.2	40	*−0.3*	*4.5*	19.7	19.7	**−82.9**	**82.9**
0.2	0.3	5	−3.8	*9.8*	*−0.8*	13.7	**−41.3**	**41.3**
0.2	0.3	10	−2.4	*9.2*	*1.3*	12.0	**−54.9**	**54.9**
0.2	0.3	20	*−1.9*	*8.4*	4.2	10.4	**−65.4**	**65.4**
0.2	0.3	40	*−0.7*	*6.1*	8.4	10.5	**−78.9**	**78.9**
0.2	0.4	5	−4.6	*11.8*	*−3.6*	15.3	**−36.4**	**36.4**
0.2	0.4	10	−3.5	*10.8*	*−1.3*	13.8	**−50.3**	**50.3**
0.2	0.4	20	−3.2	*9.4*	*0.9*	11.4	**−61.0**	**61.0**
0.2	0.4	40	*−1.1*	*7.3*	3.6	9.8	**−75.8**	**75.8**
0.2	0.5	5	−4.7	*12.7*	*−4.3*	16.2	**−33.7**	**34.2**
0.2	0.5	10	−3.8	*11.7*	*−3.0*	14.5	**−47.1**	**47.1**
0.2	0.5	20	−3.2	*10.7*	*−0.6*	11.9	**−58.2**	**58.2**
0.2	0.5	40	−1.8	*8.6*	*1.0*	9.6	**−72.7**	**72.7**
1	0.2	5	*−3.1*	*41.4*	28.7	55.9	**−47.8**	**57.7**
1	0.2	10	*−3.3*	*37.8*	25.7	57.4	**−62.5**	**64.7**
1	0.2	20	*−3.1*	*33.3*	21.4	46.0	**−72.9**	**72.9**
1	0.2	40	*−5.5*	*22.1*	8.9	42.0	**−82.3**	**82.3**
1	0.3	5	*−0.7*	*45.8*	10.3	**55.9**	**−40.7**	55.6
1	0.3	10	*−5.9*	*42.3*	14.3	54.9	**−54.3**	**58.6**
1	0.3	20	*−4.1*	*39.8*	10.3	49.3	**−68.8**	**69.1**
1	0.3	40	−4.0	*30.1*	*0.2*	46.2	**−80.5**	**80.5**
1	0.4	5	−5.1	*48.9*	*−0.1*	54.6	**−37.8**	**55.7**
1	0.4	10	*−5.2*	*46.7*	8.2	53.0	**−50.1**	**56.9**

TABLE 2. Continued.

Log-scale observation error SD	z	MPA size (%)	Spatially explicit SPM		Spatially aggregated SPM		No information from MPA	
			MRE	MARE	MRE	MARE	MRE	MARE
1	0.4	20	−7.7	*45.8*	*5.8*	51.6	**−63.7**	**64.3**
1	0.4	40	−3.5	*35.5*	*−3.1*	48.2	**−77.4**	**77.4**
1	0.5	5	−4.8	53.8	*−2.4*	*51.2*	**−37.4**	**56.2**
1	0.5	10	−7.0	*49.0*	*5.7*	51.6	**−47.2**	**57.2**
1	0.5	20	−6.9	*48.0*	*5.4*	53.8	**−61.1**	**61.8**
1	0.5	40	*−2.8*	*41.3*	−5.4	51.3	**−76.4**	**76.4**

redistributed fishing effort (Figure 6), but the ranges of relative error were only widened by 140–260%. The ranges of relative error under the redistributed fishing effort scenarios were almost always wider (i.e., less precise) than the ranges under the scenarios with decreased fishing effort. In addition, the ranges of relative error were 150–300% narrower from the smallest MPA size to the largest MPA size in all cases, regardless of fishing effort pattern. The spatially explicit and spatially aggregated SPMs showed the same pattern of error, but the spatially aggregated estimation models were usually more biased than the spatially explicit models. The spatially explicit SPMs also resulted in improved accuracy for all scenarios, with the greatest differences observed in the early years and at lower MPA sizes. In most cases, the bias decreased as more years of data were included in the analysis.

DISCUSSION

Marine protected areas can significantly affect the accuracy of stock assessment results, and information collected from within the MPA is essential for accurate assessment of a population. While spatially explicit SPMs provided the most accurate estimates of B across all of the scenarios we considered, they may not be feasible for application to many stocks because they require an index of abundance within the MPA. In the absence of abundance index data for the MPA, the SPMs tended to underestimate B and K and to overestimate r, q_s, and initial B. The largest bias occurred with the largest MPA sizes, although this was expected because the assumptions of the assessment are violated to a lesser degree with a small MPA than with a larger MPA. Unfortunately, most MPAs do not appear to have the necessary data collection programs to provide indices of abundance. Only 29% of MPAs have sufficient information available to evaluate progress against their management objectives (Jones 2001), and the inability to collect data from MPAs has been identified as a problem with the management strategy (Field et al. 2006). Our study supports suggestions that the monitoring of populations within an MPA is crucial in addition to regulating the fishery outside of the MPA (e.g., Pomeroy et al. 2005).

Larger MPAs almost always produced a more accurate stock assessment when information was available for the full range of the stock. Punt and Methot (2004) reported similar results for SCAA assessments. Some authors have suggested that for an MPA to be an effective conservation measure, it must occupy at least 20% and up to 40% of a population's habitat (Boersma and Parrish 1999; Jones 2001). However, most actual MPAs occupy a much lower percentage of the total habitat, and less than 1% of marine resources are considered to be fully protected from fishing (Boersma and Parrish 1999). Most modeling studies have focused on large MPAs that occupy 20–70% of the population's range (e.g., Sumaila 2002; Punt and Methot 2004), although some have explored the effects of smaller reserves (10–15% of the range; e.g., Watson et al. 2000). Specifically, these studies have focused on the recommendations that emphasize large, "no-take" reserves (e.g., Pauly et al. 1998), which differ from other forms of MPA that vary widely in the level of protection afforded to them. Our results suggest that if these large MPAs are implemented in the future, spatially explicit assessments will be important tools for evaluating their effectiveness.

Migration rates can also affect the accuracy of stock assessments when an MPA is part of the management for a fishery. Punt and Methot (2004) found a decrease in accuracy of stock assessments with increasing migration rates. In our study, accuracy was less affected by z than by MPA size, and the effect of z depended on MPA size, pattern of fishing effort, and the presence of a survey within the MPA. In the scenarios with low r and decreased fishing effort, z had a negligible effect on accuracy of B estimates. In the scenarios with higher r, increased z resulted in increased accuracy of the assessment—a pattern opposite that reported for age-structured methods (Punt and Methot 2004). However, the redistributed fishing effort scenarios caused higher errors with increasing z in the spatially explicit SPMs, coinciding with the results of Punt and Methot (2004). The difference between fishing effort scenarios probably occurred because increased movement violates the assumption that the population is distributed homogeneously in the assessed area (Punt and Methot 2004), and the disparity in population density between the two areas was greater in the redistributed fishing effort scenarios than in the decreased fishing effort scenarios.

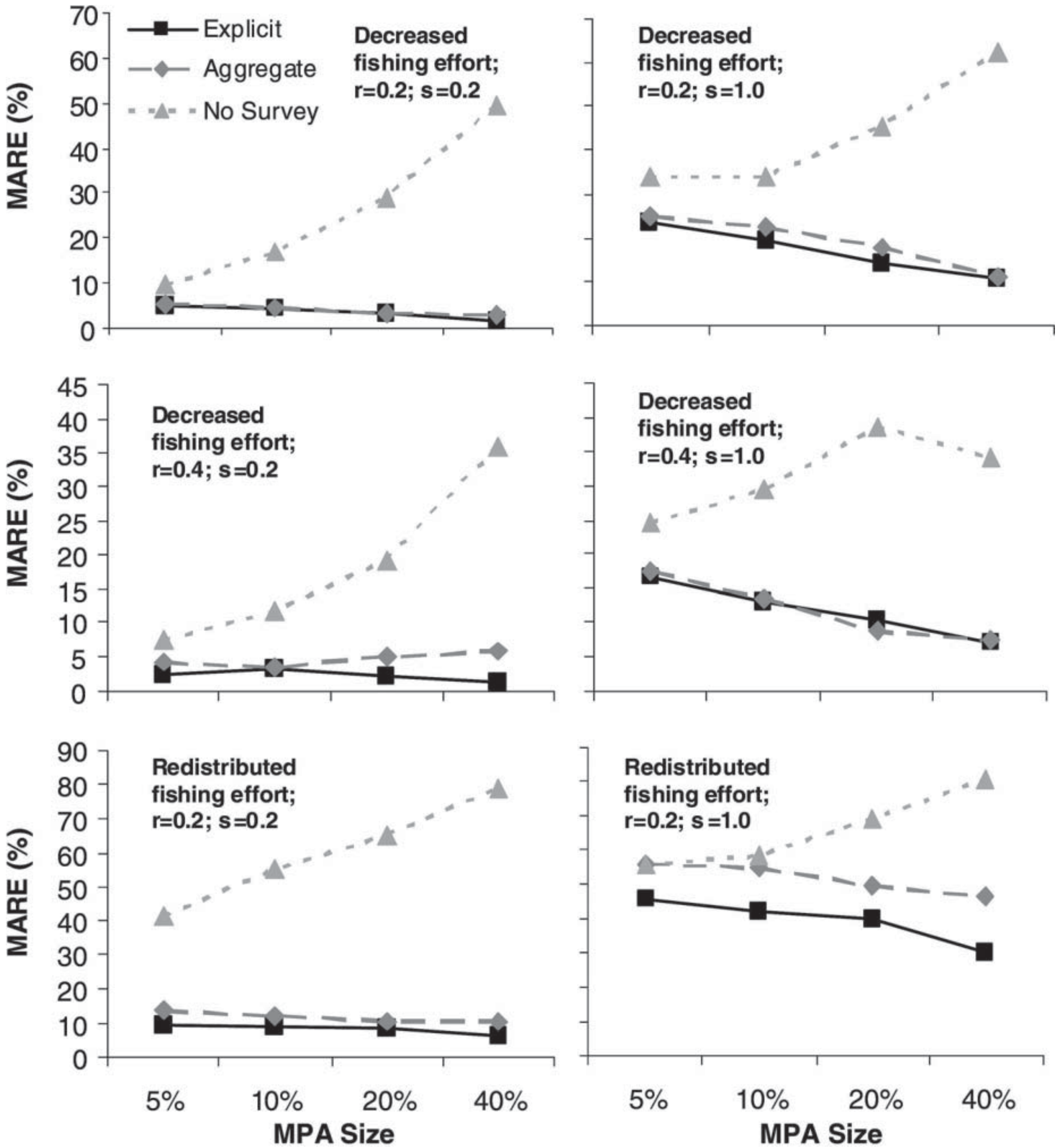

FIGURE 3. Median absolute value of relative error (MARE) of estimated biomass in simulation year 50 for the spatially explicit surplus production model (Explicit), the spatially aggregated model (Aggregate), and the model in which no survey data were available from the marine protected area (MPA; No Survey) under scenarios with a low or high observation error ($s = 0.2$ or 1.0), a low or high intrinsic rate of increase ($r = 0.2$ or 0.4), and a pattern of decreased or redistributed fishing effort. Migration rate is 0.3 for all scenarios shown; MPA size is 5–40% of the total stock area.

Spatially aggregated models did not perform much worse than the spatially explicit models in most of the scenarios tested. Logistic SPMs tend to be fairly robust to violations of assumptions (Prager 2002); therefore, especially at the smaller MPA sizes for which the spatial assumptions of SPMs are violated to a lesser degree, spatially explicit SPMs are not necessarily an improvement over traditional spatially aggregated models. In addition, Ludwig and Walters (1985) emphasized the necessity of not overtaxing the available data to fit into a more complex model; this observation suggests that especially in cases where the z or the proportion of K protected by the MPA is unknown, spatially aggregated SPMs may be a rational assessment approach because spatially explicit methods would require additional assumptions to be made. However, the spatially explicit

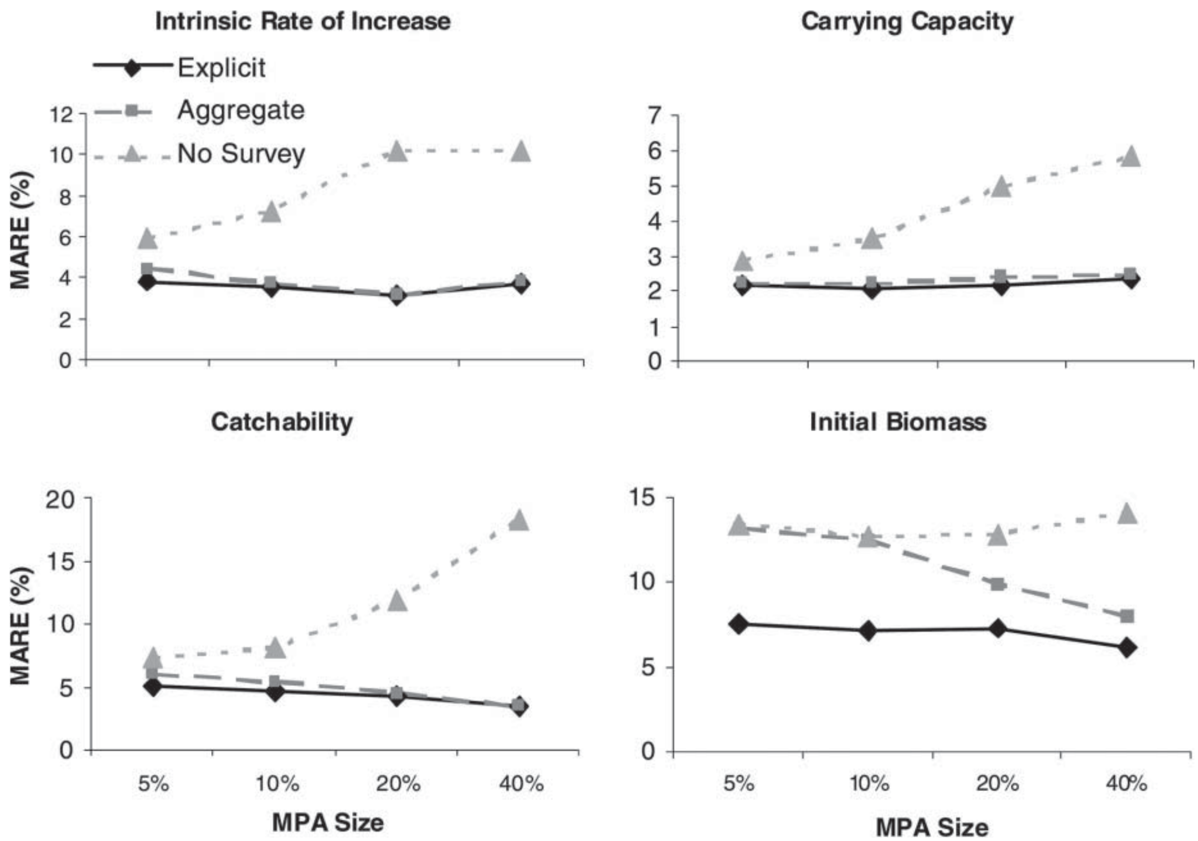

FIGURE 4. Median absolute value of relative error (MARE) of the parameter estimates from the spatially explicit surplus production model (Explicit), the spatially aggregated model (Aggregate), and the model in which no survey data were available from the marine protected area (MPA; No Survey) under scenarios with low observation error ($s = 0.2$), an intrinsic rate of increase (r) equal to 0.2, decreased fishing effort, and a migration rate equal to 0.3. The MPA size is 5–40% of the total stock area.

SPMs did perform better than the spatially aggregated SPMs in most of the scenarios we considered, so the spatially explicit models should be the first choice for any assessment. The spatially explicit SPMs did not have greatly increased complexity relative to the traditional spatially aggregated SPMs, but the accuracy of estimated B was better, especially for the scenarios in which the overall fishing effort remained high.

The precision of B estimates was highly dependent on the number of years of data that were available from both regions. When more years of data were available, the ranges of the relative error of estimated B were smaller, and in most cases the bias improved as well. The greatest precision was achieved when data were available for the 20 or 30 years after the MPA was instituted, suggesting that some time is necessary for SPMs to produce accurate estimates of B. Consistent, accurate surveys from both the fished region and the MPA were key factors in producing the accurate estimates observed at the end of the time series. Our results and those from Punt and Methot (2004) describe a single large MPA, but extrapolation to a network of smaller MPAs is possible (Field et al. 2006). This is important because of the "single large or several small" debate among ecologists (McNeill and Fairweather 1993; Roberts and Hawkins 1997; Walters 2000). Because MPA size in the data-generating and estimation models in our study was defined as the proportion of total stock area that was protected by the MPA, the results may be interpreted as the effects of several different kinds of MPA on the accuracy of an SPM. For example, a scenario that involves a large MPA could have the same proportion of K protected as a series of smaller MPAs, but the z would be higher for a network of smaller MPAs. However, our study assumed a closed population, so the results are not applicable to a subpopulation with extensive migration from outside the modeled area.

The pattern of F after MPA implementation had a substantial effect on the relative performance of SPMs. Spatially explicit and spatially aggregated SPMs produced similar estimates under the decreased fishing effort scenario when an index of abundance within the MPA was available. However, the presence of an MPA had a negative effect on the accuracy of spatially aggregated SPM stock assessments in scenarios with redistributed fishing effort. The redistributed effort scenario may be more realistic because total fishing effort remains approximately the

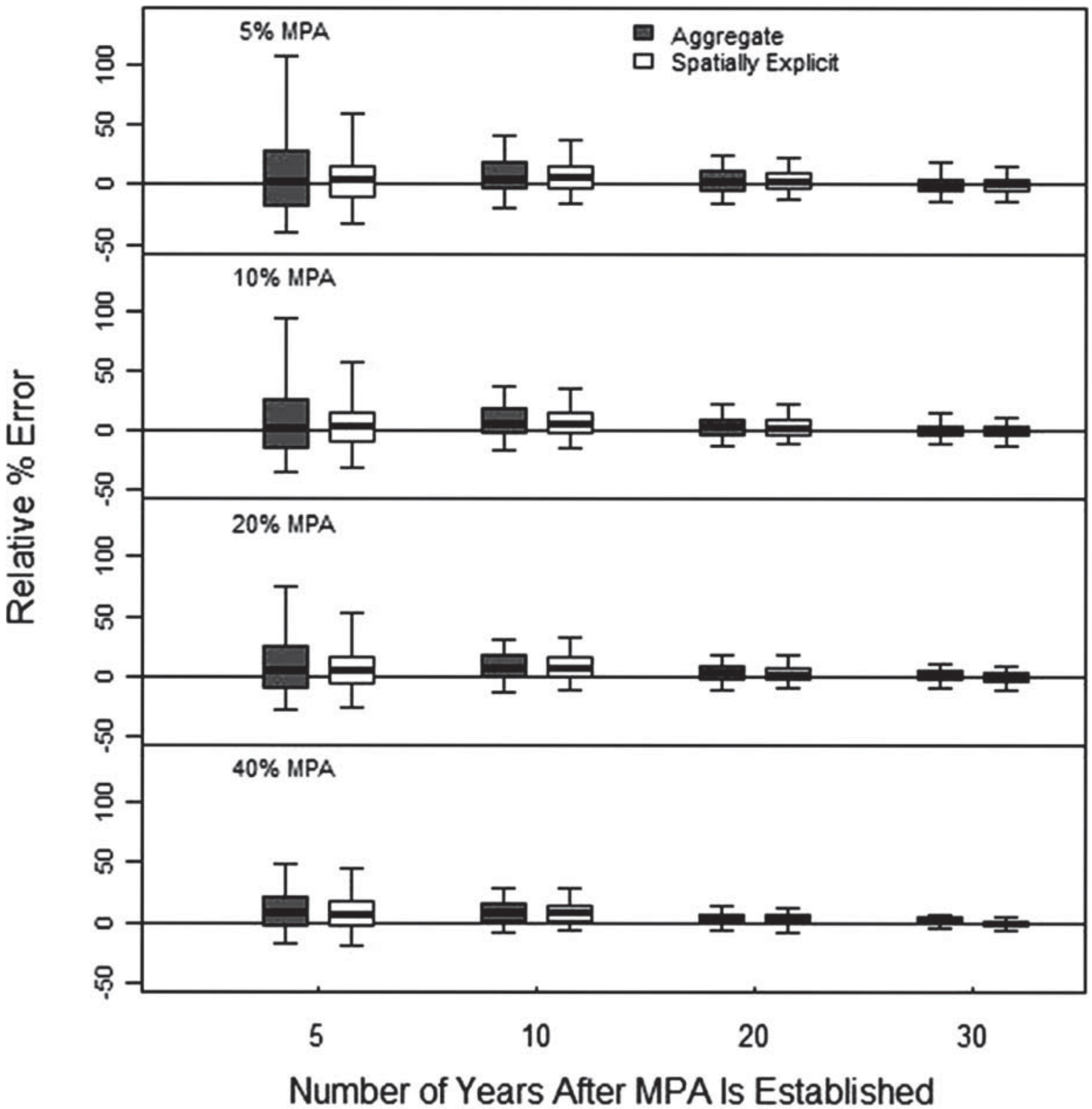

FIGURE 5. Box plots of the relative percent error in total biomass from scenarios of decreased fishing effort, an intrinsic rate of increase equal to 0.2, a migration rate of 0.3, and low observation error ($s = 0.2$) for both spatially explicit and spatially aggregated assessment models through time (MPA = marine protected area; MPA size = 5–40% of the total stock area). The dark line within each box is the median, ends of the box represent the interquartile range, and ends of whiskers indicate the 2.5th and 97.5th percentiles.

same when an MPA is implemented unless the MPA coincides with effort controls (Rijnsdorp et al. 2001; Dinmore et al. 2003). Thus, the spatially explicit SPM may produce more accurate estimates in practice even though the spatially aggregated and spatially explicit SPMs performed similarly in many of the scenarios.

The accuracy of the estimates depends largely on the accuracy of abundance indices. Scenarios with more observation error in the indices of abundance had greater ranges of overall error but were not more biased than scenarios with less observation error. Our comparisons assumed that the SDs of errors were the same both inside and outside of the MPA and for the spatially aggregated indices. In some situations, this may be unrealistic if sampling effort is proportional to the area of each region. We conducted an additional set of simulations for the scenario of an MPA size equal to 5%; in these simulations, the log-scale SD was 0.2 for the fished area and 1.0 for the MPA. The results of these simulations still did not affect bias but did affect accuracy, as the range of error was greater than when the log-scale SD was 0.2 for both areas. As we would expect, the

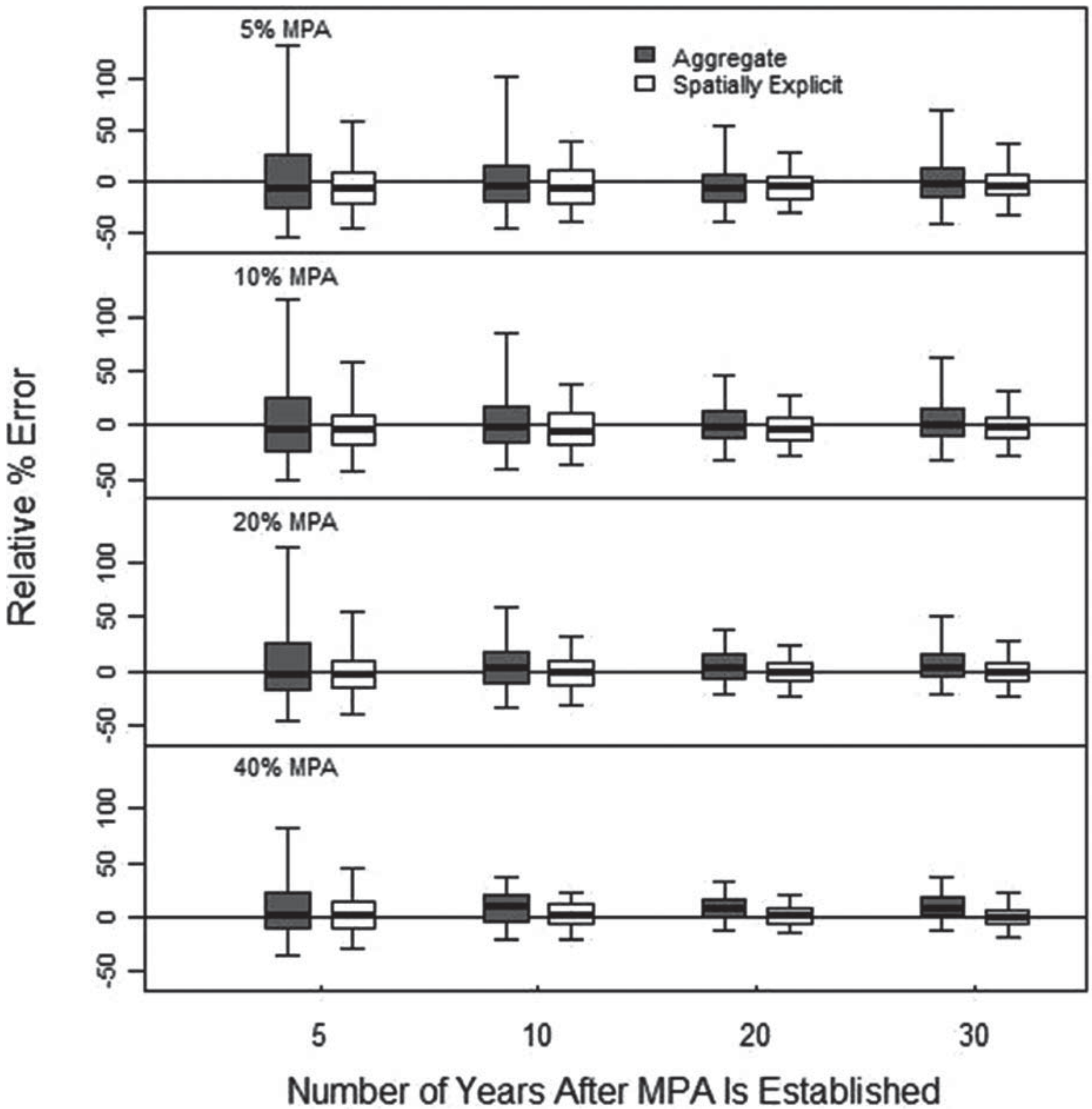

FIGURE 6. Box plots showing the relative percent error in total biomass from scenarios of redistributed fishing effort, an intrinsic rate of increase equal to 0.2, a migration rate of 0.3, and low observation error (s = 0.2) for both spatially explicit and spatially aggregated surplus production models through time (MPA = marine protected area; MPA size = 5–40% of the total stock area). Box plot elements are defined in Figure 5.

difference in results decreased as MPA size increased because the difference in region size was smaller.

Use of MPA management could improve stock assessment accuracy if many of the recommendations of past studies were implemented. Positive effects of MPAs on fish stocks are highly dependent on variables other than MPA size, such as the characteristics of the area, the behavior and life history traits of the fish (Holland 2002), and the success of management in actually protecting the area. Larger MPAs have a greater positive effect on fish populations than smaller MPAs provided that the protected regions are of similar quality (Pelletier and Magal 1996; Nowlis and Roberts 1999). However, an MPA with higher-quality habitat can lead to better results than a larger but low-quality MPA (Lundberg and Jonzén 1999; Rodwell et al. 2003) because higher-quality areas can support greater densities of fish. Despite the potential benefits of MPAs, few MPAs with sufficiently good management have been demonstrated as generating substantial improvement in the biomass of fish they were established to protect (Kelleher 1996; Hilborn et al. 2004).

Alternative approaches to management of data-poor species with MPAs within their ranges have been developed. The ratio of density within an MPA to density outside of the MPA has been suggested as a metric that can be used directly in a control rule to manage fishing effort (Babcock and MacCall 2011; McGilliard et al. 2011). This approach uses density within the MPA as a proxy for unfished density, and it performs comparably to control rules that rely on more-data-rich assessment approaches (Babcock and MacCall 2011; McGilliard et al. 2011). Our study is not directly comparable with those of McGilliard et al. (2011) and Babcock and MacCall (2011) because we did not perform a management strategy evaluation; however, the density ratio does appear to be an important source of information for spatially explicit SPMs. In particular, SPMs were more accurate in scenarios with large MPAs and low z than in scenarios with small MPAs and high z when fishing effort was redistributed.

Our study likely represents a best-case scenario for the performance of SPMs, especially between spatially explicit and spatially aggregated models. However, we believe that it provides a useful comparison of the relative performance of SPMs for stocks that have MPAs within their ranges. In most cases, the assessment model was exactly the same as the data-generating model. If we had used a stochastic age-structured model as the data-generating model, performance of the SPMs probably would have been substantially poorer, as has been observed in other studies (NRC 1998; Punt et al. 2002). Our simulations also assumed no error in the catch, and the spatially explicit SPMs assumed that MPA size was known. The area of an MPA is likely to be known, but the spatially explicit SPM requires an assumption about the proportion of K within the MPA, which may differ from the spatial extent of the MPA because limiting resources for the population might not be evenly distributed. Other requirements for accurate SPM estimates in this study were an informative F scenario and indices that were actually proportional to population size. The results may be less accurate if the F time series is not as informative as the ones we tested or if q_s changes over time.

In conclusion, the accuracy of estimates from SPM stock assessments, like those from age-structured assessments, can be substantially affected by inclusion of an MPA within the stock's range. However, substantial improvements in accuracy can be made by collecting data for indices of abundance within the MPA and by using a spatially explicit assessment model. A substantial period of time was necessary for estimates of B to become unbiased after MPA implementation. However, the SPMs evaluated here performed well under a broad range of circumstances and could be useful in assessing stocks with ranges that include MPAs.

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REFERENCES

Babcock, E. A., and A. D. MacCall. 2011. How useful is the ratio of fish density outside versus inside no-take marine reserves as a metric for fishery management control rules? Canadian Journal of Fisheries and Aquatic Sciences 68:343–359.

Boersma, P. D., and J. K. Parrish. 1999. Limiting abuse: marine protected areas, a limited solution. Ecological Economics 31:287–304.

Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science 66:799–820.

Dinmore, T. A., D. E. Duplisea, B. D. Rackham, D. L. Maxwell, and S. Jennings. 2003. Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. ICES Journal of Marine Science 60:371–380.

Field, J. C., A. E. Punt, R. D. Methot, and C. J. Thomson. 2006. Does MPA mean 'major problem for assessments'? considering the consequences of place-based management systems. Fish and Fisheries 7: 284–302.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233–249. Available: admb-project.org. (January 2012).

Gedamke, T., J. M. Hoenig, W. D. DuPaul, and J. A. Musick. 2009. Stock–recruitment dynamics and the maximum population growth rate of the barndoor skate on Georges Bank. North American Journal of Fisheries Management 29:512–526.

Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5:361–366.

Hannesson, R. 1998. Marine reserves: what would they accomplish? Marine Resource Economics 13:159–170.

Hilborn, R., K. Stokes, J. J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, K. L. Cochrane, S. Garcia, S. J. Hall, G. P. Kirkwood, K. Sainsbury, G. Stefansson, and C. Walters. 2004. When can marine reserves improve fisheries management? Ocean and Coastal Management 47:197–205.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Holland, D. S. 2002. Integrating marine protected areas into models for fishery assessment and management. Natural Resource Modeling 15: 369–386.

Hutchings, J. A. 1999. Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. Canadian Journal of Fisheries and Aquatic Sciences 56:1612–1623.

Jacobson, L. D., S. X. Cadrin, and J. R. Weinberg. 2002. Tools for estimating surplus production and F_{MSY} in any stock assessment model. North American Journal of Fisheries Management 22:326–338.

Jones, P. J. S. 2001. Marine protected area strategies: issues, divergences and the search for middle ground. Reviews in Fish Biology and Fisheries 11: 197–216.

Kaplan, D. M., L. W. Botsford, M. R. O'Farrell, S. D. Gaines, and S. Jorgensen. 2009. Model-based assessment of persistence in proposed marine protected area designs. Ecological Applications 19:433–448.

Kelleher, G. 1996. A global representative system of marine protected areas. Ocean and Coastal Management 32:123–126.

Kelleher, G., editor. 1999. Guidelines for marine protected areas. International Union for the Conservation of Nature and Natural Resources (IUCN), Gland, Switzerland.

Laloë, F. 1995. Should surplus production models be fishery description tools rather than biological models? Aquatic Living Resources 8: 1–16.

Ludwig, D., and C. J. Walters. 1985. Are age-structured models appropriate for catch-effort data? Canadian Journal of Fisheries and Aquatic Sciences 42:1066–1072.

Lundberg, P., and N. Jonzén. 1999. Spatial population dynamics and the design of marine reserves. Ecology Letters 2:129–134.

McGilliard, C. R., R. Hilborn, A. MacCall, A. E. Punt, and J. C. Field. 2011. Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks? ICES Journal of Marine Science 68:201–211.

McNeill, S. E., and P. G. Fairweather. 1993. Single large or several small marine reserves? an experimental approach with seagrass fauna. Journal of Biogeography 20:429–440.

NOAA (National Oceanic and Atmospheric Administration). 2010. A functional classification system for marine protected areas in the United States. National Marine Protected Areas Center, Silver Spring, Maryland. Available: http://www.mpa.gov/pdf/helpful-resources/factsheets/class_system_0806.pdf. (August 2012).

Nowlis, J. S., and C. M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. U.S. National Marine Fisheries Service Fishery Bulletin 97:604–616.

NRC (National Research Council). 1998. Improving fish stock assessments. National Academy Press, Washington, D.C.

Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. Pages 7–34 *in* D. Pauly and G. R. Morgan, editors. Length-based methods in fisheries research: ICLARM conference proceedings 13. ICLARM (International Center for Living Aquatic Resources Management), Manila.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. Fishing down marine food webs. Science 279:860–863.

Pelletier, D., and P. Magal. 1996. Dynamics of a migratory population under different fishing effort allocation schemes in time and space. Canadian Journal of Fisheries and Aquatic Sciences 53:1186–1199.

Polacheck, T., R. Hilborn, and A. E. Punt. 1993. Fitting surplus production models: comparing methods and measuring uncertainty. Canadian Journal of Fisheries and Aquatic Sciences 50:2597–2607.

Pomeroy, R. S., L. M. Watson, J. E. Parks, and G. A. Cid. 2005. How is your MPA doing? a methodology for evaluating the management effectiveness of marine protected areas. Ocean and Coastal Management 48: 485–502.

Prager, M. H. 1994. A suite of extensions to a non-equilibrium surplus-production model. U.S. National Marine Fisheries Service Fishery Bulletin 92:374–389.

Prager, M. H. 2002. Comparison of logistic and generalized surplus-production models applied to swordfish, *Xiphias gladius,* in the North Atlantic Ocean. Fisheries Research 58:41–57.

Punt, A. E., and R. D. Methot. 2004. Effects of marine protected areas on the assessment of marine fisheries. Pages 133–154 *in* J. B. Shipley, editor. Aquatic protected areas as fisheries management tools. American Fisheries Society, Symposium 42, Bethesda, Maryland.

Punt, A. E., A. D. M. Smith, and G. Cui. 2002. Evaluation of management tools for Australia's south east fishery: 2. how well can management quantities be estimated? Marine and Freshwater Research 53:631–644.

Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Rijnsdorp, A. D., G. J. Piet, and J. J. Poos. 2001. Effort allocation of the Dutch beam trawl fleet in response to a temporarily closed area in the North Sea. International Council for the Exploration of the Sea, C.M. 2001/N:01, Copenhagen.

Roberts, C. M., and J. P. Hawkins. 1997. How small can a marine reserve be and still be effective? Coral Reefs 16:150.

Rodwell, L. D., E. B. Barbier, C. M. Roberts, and T. R. McClanahan. 2003. The importance of habitat quality for marine reserve: fishery linkages. Canadian Journal of Fisheries and Aquatic Sciences 60:171–181.

Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bulletin of the Inter-American Tropical Tuna Commission 1:27–56.

Shepherd, T. D., and M. K. Litvak. 2004. Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. Fish and Fisheries 5:141–152.

Sumaila, U. R. 2002. Marine protected area performance in a model of the fishery. Natural Resource Modeling 15:439–451.

Walters, C. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected area: how large should protected areas be? Bulletin of Marine Science 66:745–757.

Watson, R., J. Alder, and C. Walters. 2000. A dynamic mass-balance model for marine protected areas. Fish and Fisheries 1:94–98.

Wenzel, L., and M. D'Iorio. 2011. Definition and classification system for U.S. marine protected areas. Office of Ocean and Coastal Resource Management, National Oceanic and Atmospheric Administration Ocean Service, Silver Spring, Maryland. Available: www.mpa.gov/pdf/helpful-resources/factsheets/mpa_classification_may2011.pdf#level_of_protection. (July 2011).