

Coping with information gaps in stock productivity for rebuilding and achieving maximum sustainable yield for grouper–snapper fisheries

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Abstract

Maintaining fish stocks at optimal levels is a goal of fisheries management worldwide; yet, this goal remains somewhat elusive, even in countries with well-established fishery data collection, assessment and management systems. Achieving this goal often requires knowledge of stock productivity, which can be challenging to obtain due to both data limitations and the complexities of marine populations. Thus, scientific information can lag behind fishery policy expectations in this regard. Steepness of the stock–recruitment relationship affects delineation of target biomass level reference points, a problem which is often circumvented by using a proxy fishing mortality rate (F) in place of the rate associated with maximum sustainable yield (F_{MSY}). Because MSY is achieved in the long term only if an F proxy is happenstance with F_{MSY} , characterizing productivity information probabilistically can support reference point delineation. For demersal stocks of equatorial and tropical regions, we demonstrate how the use of a prior probability distribution for steepness can help identify suitable F proxies. F proxies that reduce spawning biomass per recruit to a target percentage of the unfished quantity (i.e., SPR) of 40% to 50% SPR had the highest probabilities of achieving long-term MSY. Rebuilding was addressed through closed-loop simulation of broken-stick harvest control rules. Similar biomass recovery times were demonstrated for these rules in comparison with more information-intensive rebuilding plans. Our approach stresses science-led advancement of policy through a lens of information limitations, which can make the assumptions behind rebuilding plans more transparent and align management expectations with biological outcomes.

KEYWORDS

demersal fish, harvest control rule, Lutjanidae, Serranidae, steepness, stock–recruitment

1 | INTRODUCTION

Maintaining fish stocks at biologically sustainable levels is a key tenet of the United Nations' Sustainable Development Goal 14 (United Nations, 2018; Ye et al., 2013), and fisheries legislation has been enacted to ensure that fishery stocks are managed at levels that will maximize social, economic and ecological benefits of exploited species over the long term (Neubauer, Jensen, Hutchings, & Baum, 2013; NOAA, 2007). In theory, maintaining stocks at a level approximating maximum sustainable yield (MSY) is a function of the stock biomass, fishing mortality rate and stock productivity, making it plausible to achieve management targets even in cases where data are limited (Froese et al., 2018). In reality, maintaining biomasses near or rebuilding fisheries to maximally sustainable levels remains a major challenge worldwide, even in industrialized nations with sufficient resources with which to assess and manage fishery stocks. For example, recent estimates suggest that 69% of European stocks are subject to overfishing, and only half of these populations are at sustainable levels (Froese et al., 2018). In the USA, the number of stocks undergoing overfishing has declined since the reauthorization of the Magnuson–Stevens Fishery Conservation and Management Act (MSFCMA) in 2006, which required annual catch limits and accountability measures, but approximately one-fifth of stocks remain below target biomass levels (Patrick & Cope, 2014). The failure to rebuild and maintain stocks near MSY levels is primarily a political issue, as rebuilding plans inherently require managers to confront trade-offs between biological recovery and economic impacts when determining how rapidly to scale back fishing mortality (Hammer et al., 2010). However, uncertainty surrounding stock productivity plays a major role in the stock rebuilding process (Hammer et al., 2010). Gaps in knowledge of stock productivity, in turn, affect the political process; when management actions to reduce fishing pressure do not result in the intended stock recovery trajectory, the credibility of the entire assessment and management process can be undermined (Murawski, 2010). Therefore, the accurate estimation of population productivity, and how the uncertainty regarding this estimation perpetuates into management advice, remains a fundamental information gap for fisheries management.

Fishery legislation has been implemented worldwide to ensure that stocks are managed at levels that will maximize social, economic and ecological benefits of exploited species over the long term (Froese & Proelß, 2010; Smith et al., 2009; Ye et al., 2013). Specifying MSY-based reference points requires knowledge of the productivity of the stock, which is notoriously challenging to measure. Stock–recruitment relationships strongly determine the theoretical stock size (i.e., the spawning stock biomass that is associated with production of MSY, B_{MSY}) at which surplus production is maximized (Brooks, Powers, & Cortés, 2010; Mangel, Brodziak, & DiNardo, 2010; Punt, Smith, Smith, Tuck, & Klaer, 2014). Delineation of reference points like B_{MSY} also depends on natural mortality rates and fishery selectivity (Brodziak, 2002; Mangel et al., 2013). In the USA, the MSFCMA requires that a rebuilding plan be triggered should stock size fall below a pre-defined threshold. In developing stock rebuilding plans,

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estimates of future numbers of recruits are typically required, which contribute to estimation of appropriate fishing mortality rates that will enable rebuilding to occur within expected time frames (Punt & Methot, 2005). In practice, these projections are challenging to reliably produce, as they are affected by multiple unknowns: depensation dynamics, environmental variability and fishing-induced alterations to demographics and resilience (Hammer et al., 2010; Lowerre-Barbieri et al., 2017). As a result, many stocks lack the scientific information that is needed to support delineation of reference points and specification of rebuilding plans, and availability of scientific information lags behind the informational requirements for management.

While it is possible to estimate parameters of stock–recruitment relationships during quantitative stock assessment, data available to stock assessment models often prevent reliable estimation of stock–recruitment steepness (Lee, Maunder, Piner, & Methot, 2012; SEDAR, 2012, 2014a). The steepness parameter defines the shape of the stock–recruitment relationship and has an important influence on determining the stock size where surplus production is maximized (Figure 1). Uncertainty in steepness accordingly creates challenges in selecting optimality-based reference points like MSY, the fishing mortality rate that produces MSY (F_{MSY}), and B_{MSY} . As a consequence of a lack of direct information on steepness, it is often necessary to resort to the use of reference point proxies, such as quantities derived from spawning potential ratio (SPR; Clark, 1991; Goodyear, 1993; Mace & Sissenwine, 1993; Restrepo et al., 1998). For instance, the fishing mortality rate that produces a SPR of $x\%$ of unfished SPR is sometimes implemented as a proxy for F_{MSY} . Such proxy reference points, based on SPR, are utilized globally, and for US fisheries, these proxies are used for $>50\%$ of federally managed stocks in the Alaska and Pacific regions (Cadrin, 2012; Goethel, Smith, Cass-Calay, & Porch, 2018; Punt et al., 2014). In tropical regions of the USA, fisheries are typically managed using regulatory frameworks that are based on MSY reference points or related proxies, despite a variety of challenges in establishing such reference points that largely stems from data limitations (CFMC, 1985; GMFMC, 1984; SAFMC, 1983).

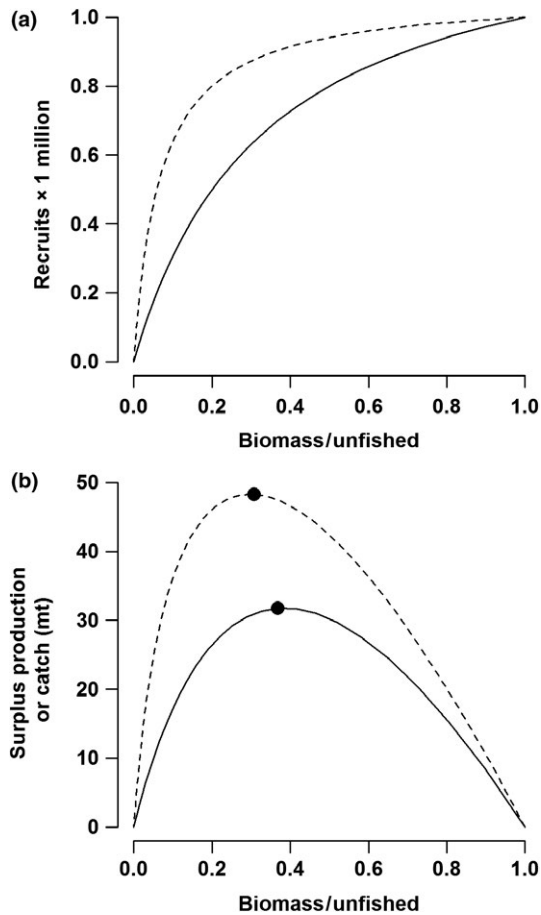


FIGURE 1 (a) Examples of two Beverton–Holt stock–recruitment relationships with different steepness parameter values. (b) Stock–recruitment steepness influences the theoretical stock size (i.e., B_{MSY}) at which surplus production is maximized. Solid dots denote maximum sustainable yield, dashed lines are calculated using steepness of 0.8, and solid lines are calculated using a steepness of 0.5

Problematically, achievement of MSY-based fishery objectives will occur only if the proxy fishing mortality rate is in agreement with F_{MSY} , which would have otherwise been calculated if steepness were known. Sometimes, contradictory statements are made in management arenas that invoke assumptions about steepness as a rationalization for selection of proxy reference points, despite the fact that an absence of information about steepness was the impetus for reliance on proxies in the first place. Furthermore, the assumptions surrounding selection of proxy reference points often remain untested. Here, we build the case that through explicit representation of uncertainty in steepness, selection of proxy reference points can proceed according to derived probabilistic statements about achievement of MSY-based fishery objectives. Through simulation testing, we demonstrate how prior probability distributions representing uncertainty in steepness can be used to improve resolve in selection of proxy reference points. This guidance is particularly aimed at data-limited fish stocks for which quantitative stock assessment is infeasible (otherwise priors for steepness could be incorporated into stock assessment).

We focused simulations on fish stocks of the south-eastern USA and US Caribbean because many of these stocks are faced with data-related challenges in establishing scientifically derived regulatory actions (Berkson & Thorson, 2015; Newman, Berkson, & Suatoni, 2015); however, the framework is applicable to stocks worldwide. Our simulations enabled proxy fishing mortality reference points to be identified that had the highest probabilities of achieving MSY-based fishery objectives, given a specified prior probability distribution for steepness. We then extended our analysis to the design of harvest control rules (HCRs) and examined a family of HCRs known as broken-stick, hockey stick or slope approaches that are designed to implicitly achieve stock rebuilding through the degree to which fishing mortality is reduced in accordance with declining stock size (Dichmont et al., 2016; Ianelli, Hollowed, Haynie, Mueter, & Bond, 2011; Tong, Chen, & Kolody, 2014). Similarities persist between broken-stick HCRs and data-rich implementations of stock rebuilding as set out in US National Standard 1 Guidelines. Both approaches reduce fishing mortality to enable rebuilding, both return fishing mortality to a maximum allowable level upon rebuilding success, and both modify fishing mortality rates during rebuilding as stock size fluctuations may dictate. Accordingly, we examined the performance of broken-stick HCRs in relation to a reference HCR that precisely implements stock rebuilding decisions according to expectations of US National Standard 1 Guidelines. Our focus on broken-stick HCRs is germane to the problem of bridging an existing gap in scientific information about how to ensure that data-limited stocks undergo rebuilding (as necessary), but without the need to specify rebuilding time frames that depend on forecasts of future numbers of recruits (i.e., rebuilding without reliance on stock productivity parameters like steepness).

2 | METHODS

Simulations were carried out in six steps. First, we specified stock dynamics and input values for life history parameters for 17 gonochoristic demersal fishes (families: Balistidae, Carangidae, Lutjanidae and Malacanthidae) and hermaphroditic groupers (family: Serranidae; Table 1). Second, we specified candidate SPR-based fishing mortality proxies (Clark, 1991). Third, we simulated the long-term or end-state performance of these proxies under different scenarios about stock–recruitment steepness. Fourth, we used the simulation outcomes to calculate probability-weighted performance based on prior probability distributions for steepness. Fifth, we specified broken-stick HCRs based on selected proxy fishing mortality reference points and biomass thresholds. Sixth, we subjected overfished stocks to rebuilding under each broken-stick HCR and under the reference US National Standard 1 rebuilding strategy and used closed-loop simulation outcomes to construct steepness probability-weighted performance comparisons of rebuilding success (Walters & Martell, 2004).

TABLE 1 Life histories of demersal fish stocks included in simulation testing

Scientific name	Common name	K , year ⁻¹	L_{∞} mm	Max age	M_{ave} , year ⁻¹	SEDAR number
Gonochoristic assemblage						
<i>Lutjanus analis</i> , Lutjanidae	Mutton snapper (GOM)	0.16	861	40	0.11	15
<i>Lutjanus campechanus</i> , Lutjanidae	Red snapper (GOM)	0.19	856	48	0.09	31
<i>Lutjanus campechanus</i> , Lutjanidae	Red snapper (SATL)	0.24	902	58	0.08	24
<i>Ocyurus chrysurus</i> , Lutjanidae	Yellowtail snapper	0.13	618	23	0.19	27
<i>Rhomboplites au-</i> <i>rorubens</i> , Lutjanidae	Vermilion snapper (SATL)	0.12	506	19	0.22	17
<i>Lopholatilus chamaeleon-</i> <i>ticeps</i> , Malacanthidae	Tilefish (GOM)	0.13	830	30	0.14	22
<i>Lopholatilus chamaeleon-</i> <i>ticeps</i> , Malacanthidae	Golden tilefish (SATL)	0.19	825	40	0.10	25
<i>Seriola dumerili</i> , Carangidae	Greater amberjack (GOM)	0.17	1436	15	0.28	33
<i>Balistes capriscus</i> , Balistidae	Grey triggerfish (GOM)	0.14	590	15	0.27	43
<i>Caulolatilus microps</i> , Malacanthidae	Blueline tilefish (SATL)	0.19	739	43	0.10	50
Hermaphroditic assemblage						
<i>Epinephelus morio</i> , Serranidae	Red grouper (GOM)	0.12	827	29	0.14	42
<i>Epinephelus morio</i> , Serranidae	Red grouper (SATL)	0.21	848	26	0.14	19
<i>Mycteroperca bonaci</i> , Serranidae	Black grouper (GOM)	0.14	1334	33	0.14	19
<i>Mycteroperca microlepis</i> , Serranidae	Gag grouper (GOM)	0.13	1277	31	0.13	33
<i>Hyporthodus niveatus</i> , Serranidae	Snowy grouper (SATL)	0.09	1065	35	0.12	36
<i>Epinephelus guttatus</i> , Serranidae	Red hind (STT)	0.07	601	18	0.25	35
<i>Epinephelus guttatus</i> , Serranidae	Red hind (PR)	0.10	514	17	0.26	35

Notes. K and L_{∞} are von Bertalanffy growth parameters, M_{ave} is average lifetime natural mortality (year⁻¹), Max age is observed maximum age, GOM is Gulf of Mexico, SATL is South Atlantic, STT is Saint Thomas, US Virgin Islands, and PR is Puerto Rico. Southeast Data, Assessment, and Review (SEDAR) stock assessments can be accessed at www.sedarweb.org.

2.1 | Simulated stock dynamics

Seventeen demersal fish stocks were judged to have sufficiently reliable and detailed life history information based on being previously subjected to peer-reviewed quantitative stock assessment (Tables 1 and 2). A few stocks of the same species were included based on life history variation in growth and natural mortality. Population dynamics models were age-structured and functioned on an annual time step (Table 3). Within each annual time step, growth occurred first, followed by reproduction, and lastly by total mortality (i.e., natural mortality plus

fishing mortality). Age-0 or age-1 recruitment (depending on decisions made during stock assessments) was determined according to a re-parameterization of the Beverton–Holt stock–recruitment relationship based on steepness, h (Table 3). Steepness describes the fraction of unfished recruitment when spawning biomass has declined to 20% of its unfished level (Beverton & Holt, 1957; Mace & Doonan, 1988). Inter-annual recruitment variance was specified as 0.6, which is a typical assumption for stochastic recruitment variation (Beddington & Cooke, 1983). Growth in length followed a von Bertalanffy function and length–whole weight conversion followed an

TABLE 2 Summary of age and length at 50% maturity (A50 and L50, respectively) used in simulations and current regulatory minimum harvest size for federal waters

Common name	A50	L50	Federal commercial regulatory size limit
Gonochoristic assemblage			
Mutton snapper (GOM)	3	433 mm TL	406 mm TL
Red snapper (GOM)	2	315 mm TL	330 mm TL
Red snapper (SATL)	2	348 mm FL	—
Yellowtail snapper (SATL & GOM)	2	305 mm TL	305 mm TL (GOM)
Vermilion snapper (SATL)	1	211 mm TL	305 TL
Tilefish (GOM)	2	345 mm TL	—
Golden tilefish (SATL)	3	399 mm TL	—
Greater amberjack (GOM)	4	832 mm FL	914 mm FL
Grey triggerfish (GOM)	1	183 mm FL	356 mm FL
Blueline tilefish (SATL)	3	445 mm TL	—
Hermaphroditic assemblage			
Red grouper (GOM)	3	328 mm TL	457 mm TL
Red grouper (SATL)	3	459 mm TL	508 mm TL
Black grouper (GOM)	7	904 mm TL	610 mm TL
Gag grouper (GOM)	4	605 mm TL	559 mm TL
Snowy grouper (SATL)	5	557 mm TL	—
Red hind (STT)	3	251 mm FL	—
Red hind (PR)	3	232 mm FL	—

Notes. L50 was also used in simulation runs to designate knife-edge selection by the fishery. GOM is Gulf of Mexico, SATL is South Atlantic, STT is Saint Thomas, US Virgin Islands, and PR is Puerto Rico, TL is total length, and FL is fork length. Southeast Data, Assessment and Review (SEDAR) stock assessments can be accessed at www.sedarweb.org.

exponential function (Table 3). For each stock, natural mortality was an inverse function of length, according to the approach of Lorenzen (1996), where natural mortality-at-age was scaled to reflect an average lifetime rate that was obtained from empirical longevity observations (Then, Hoenig, Hall, & Hewitt, 2015). Maturity ogives were available for each stock, and reproductive output was specified as either eggs-per-female at age, where

this information was available from stock assessments, or as spawning weight-at-age.

2.2 | Proxy fishing mortality reference points

Simulated evaluation of fishing mortality proxy reference points was carried out as a factorial combination of stock types (two assemblages: 10 gonochoristic stocks and 7 hermaphroditic stocks), steepness (6 levels) and fishing mortality proxy (5 levels). Stock dynamics were simulated at six discrete steepness levels: $h = 0.4, 0.5, 0.6, 0.7, 0.8$ and 0.9 . Fishing mortality proxies were $F_{\text{SPR}20\%}$, $F_{\text{SPR}30\%}$, $F_{\text{SPR}40\%}$, $F_{\text{SPR}50\%}$ and $F_{\text{SPR}60\%}$. Per-recruit analysis based on age-structured population dynamics (as described above, but setting $h = 1$ and $\sigma^2 = 0$) was used for each stock to identify corresponding fishing mortalities that produced SPRs of $x\%$ of unfished SPR. To enable reasonable comparability of HCR performance across stocks, fishery selectivity was specified as knife-edge at the age coinciding with 50% maturity (Table 2). Given a fishing mortality rate, F , and vulnerable biomass, B_v , calculation of total allowable catch at each annual time step was:

$$\text{TAC} = \frac{F}{F+M} (1 - \exp(-F-M)) B_v \quad (1)$$

Each factorial combination was simulated for a duration of time corresponding to four times the maximum lifespan in years of the specified stock. After ensuring that stable end-state dynamics were produced for all life history types, performance measures were obtained as an average of the terminal 25 years of each simulation run.

2.3 | Harvest control rules

To evaluate rebuilding potential of broken-stick HCRs, simulated stocks were each initialized in a depleted state of 0.1 (or spawning biomass of 10% of unfished biomass). For all of the stocks we considered, depletion of 0.1 was $< 1/2B_{\text{MSY}}$ and thus, stocks were always initialized in overfished states. The stock size of $1/2B_{\text{MSY}}$ is the minimum stock size threshold below which the stock is considered to be overfished. Each broken-stick HCR was used to calculate an annual TAC according to Equation (1). HCRs determined F according to a linear function of depletion (i.e., spawning biomass relative to unfished spawning biomass), until a pre-specified reference depletion threshold, above which F was constant at a maximum rate (Figure 2). The general form of this HCR is known as “broken-stick,” “hockey stick” or “slope,” and this approach is widespread (Dichmont et al., 2016; Ianelli et al., 2011; Punt & Ralston, 2007; Tong et al., 2014). Some broken-stick HCRs use a lower threshold limit, below which the fishery is closed (Punt & Ralston, 2007). Within the existing regulatory frameworks used by the Gulf of Mexico Fishery Management Council, lower limits for fishery closure are not formally specified; however, we did examine some HCRs that included this limit. Thus, each broken-stick HCR is defined according to three reference points: (i) an upper fishing mortality limit; (ii) a depletion threshold below which the

TABLE 3 Equations used in simulating fish stock dynamics

Processes	Equations and parameters
Recruitment (R)	$R_t = \left(\frac{0.8R_0 h B_t}{0.2B_0 (1-h) + (h-0.2) B_t} \right) \exp(\varepsilon_t - \sigma^2/2)$ <p>R_t is the number of recruits; B_t is spawning biomass; R_0 is unfished number of recruits, h is steepness, and ε is normally distributed with mean zero and variance σ^2</p>
Spawning biomass (B)	$B_t = \sum_{age} N_{age,t} \text{Mat}_{age,t} \text{Female}_{age,t} \text{Fecundity}_{age,t}$ <p>N is abundance; Mat is proportion mature; Female is proportion female; Fecundity is eggs-per-female or weight-at-age, depending on the simulated stock</p>
Abundance	$N_{age+1,t+1} = N_{age,t} \exp(-F_t \text{Sel}_{age} - M_{age,t})$ <p>Sel is fishery selectivity, F is fishing mortality, M is natural mortality</p>
von Bertalanffy growth (length in mm)	$L_{age} = L_{\infty} (1 - \exp(-K (age - t_0)))$ <p>L_{∞} is asymptotic length; K is Brody growth coefficient; and intercept parameter t_0.</p>
Whole weight conversion (kg)	$W_{age} = \alpha L_{age}^{\beta}$

Note. In equations, t is annual time step, and age is annual age-class.

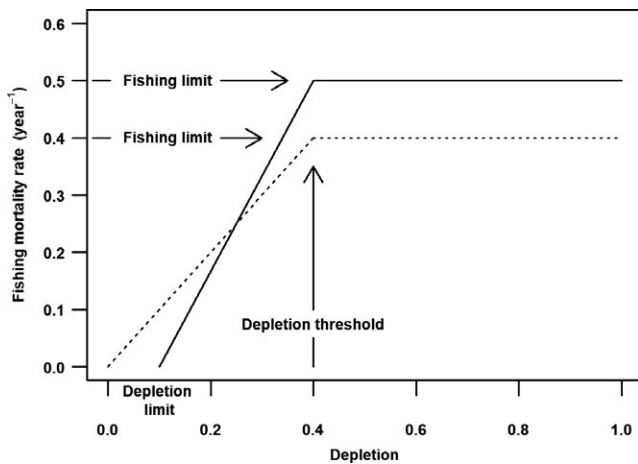


FIGURE 2 Example broken-stick harvest control rules, solid line denotes 0.1 depletion limit below which the fishery is closed, and dotted line denotes zero depletion limit

fishing mortality linearly declines; and (iii) a depletion limit below which the fishery is closed.

In evaluating the use of broken-stick rules for stock rebuilding, we asked whether these simpler HCRs could implicitly lead to achievement of biomass rebuilding within the time expectations outlined in US National Standard 1 Guidelines. Noting that calculated rebuilding times under US National Standard 1 Guidelines will vary based on level of depletion, future recruitment and fish stock biology, we

tested whether broken-stick HCRs could be designed to consistently achieve rebuilding times that were comparable to the NS1 rule. Thus, we specified a reference HCR that approximated several decision-making aspects of the US National Standard 1 Guidelines, as they are currently implemented in the Gulf of Mexico. We refer to this HCR as the NS1 rule, which was applied annually according to the following algorithm:

1. If the stock was considered overfished in the previous year and therefore already has a rebuilding plan, continue to step 2. Note that there is no simulated time delay in implementing a stock rebuilding plan. Otherwise, continue to step 3;
2. If the stock has recovered to at least B_{MSY} in the current year, continue to step 5. Otherwise, continue the rebuilding plan. Identify the current duration of the rebuilding plan. If the current duration has not exceeded T_{max} , calculate $F_{Rebuild}$. If current duration has exceeded T_{max} , $F_{Rebuild}$ is set to the minimum of $0.75F_{MSY}$ and the value of $F_{Rebuild}$ from the previous assessment. Continue to step 4;
3. If the current spawning stock biomass is above the minimum stock size threshold, continue to step 5. Otherwise, develop a rebuilding plan. Calculate the number of years to rebuild to B_{MSY} in the absence of fishing (T_{min}). If T_{min} is less than or equal to 10 years, T_{max} is 10 years. Otherwise, T_{max} is $T_{min} + 1$ generation time. Calculate $F_{Rebuild}$. Continue to step 4;
4. Using $F_{Rebuild}$ (from step 2 or 3), project the stock forward for 1 year using the “known simulated” deterministic

stock–recruitment relationship. The TAC is specified as the projected catch under F_{Rebuild} :

- The stock is not overfished. Using F_{MSY} , project the stock forward for 1 year using the “known simulated” deterministic stock–recruitment relationship. The TAC is specified as the projected catch under F_{MSY} .

Minimum rebuilding time (T_{min}) is the calculated time to rebuild an overfished stock in the absence of fishing, and maximum rebuilding time (T_{max}) is the accepted rebuilding time specified in a rebuilding plan. F_{Rebuild} is the fishing mortality rate that will rebuild the stock to B_{MSY} by T_{max} , and it is calculated through projections using the “known simulated” deterministic stock–recruitment relationship and steepness value. Generation time is the average age of an adult fish obtained from equilibrium unfished age–structure. HCRs were each implemented for a duration of $T_{\text{max}} + 1$ years (this quantity differed by factorial combination of fish life history and steepness level), so that performance measures of the broken-stick HCRs could be contrasted against the reference HCR, which we refer to hereafter as the NS1 rule.

2.4 | Performance measures

Prior to simulation runs, 1,000 time series of recruitment deviations were generated, which were then applied in parallel to each of the factorial combinations; this prevented performance differences from being attributed to chance differences in recruitment (Punt, Butterworth, de Moor, De Oliveira, & Haddon, 2016). Performance measures were calculated by comparing catches and biomass status to “known simulated” MSY and B_{MSY} , which were calculated for each stock and steepness combination.

For analysis of proxy fishing mortality rates, simulated catch and biomass outcomes were reported as ratios of “known simulated” MSY and B_{MSY} , respectively. Their subsequent use in producing probability-weighted performance outcomes required binning of performance measures reported for each simulation run. Each of 1,000 performance outcomes pertaining to a given factorial combination of stock, steepness and fishing mortality proxy was binned into continuous interval categories with relative catches (catches divided by MSY) binned into categories of: 0 to <0.4, 0.4 to <0.8, 0.8 to <1.2, 1.2 to <1.6, 1.6 to <2.0 and 2.0 to <2.4. Likewise, relative biomass (biomass divided by B_{MSY}) was binned into categories between 0 and 4.8 based on an interval size of 0.4.

Performance measures were also specified to evaluate stock rebuilding. First, relative biomass and relative catches were calculated as described above, except that binning used a two-dimensional array (see related approach in Hatton, McCann, Umbanhowar, & Rasmussen, 2006). Second, a binary variable reflected whether recovery to B_{MSY} had been achieved sometime during the time period of year 1 to $T_{\text{max}} + 1$ and the stock was currently in a non-overfished state. Third, a binary variable reflected whether biomass was $>B_{\text{MSY}}$ in the year $T_{\text{max}} + 1$. Finally, we calculated the ratio of total catches between year 1 and $T_{\text{max}} + 1$ between a given broken-stick HCR and the NS1 rule. This calculation was made using paired simulation runs

(i.e., runs subject to identical patterns of stochastic recruitment variation), for example:

$$\text{catch ratio}_i = \frac{\sum \text{catches}_{\text{HCR},i}}{\sum \text{catches}_{\text{NS1},i}} \quad (2)$$

where i is replicate $i = 1, \dots, 1000$.

Catch ratios were then binned according to continuous interval categories between 0 and 10 based on an interval size of 0.2.

2.5 | Probability-weighted performance measures

Given that performance outcomes were conditional on the specified steepness of a simulated stock, it was more desirable to obtain probabilistic performance outcomes that were integrated across plausible states of steepness. Posterior probability-weighted performance outcomes (or unconditional performance) were calculated based on prior probability weightings that were assigned to discrete steepness levels, which were arbitrarily selected (i.e., 0.4, 0.5, 0.6, 0.7, 0.8 and 0.9). Although steepness is a continuous parameter, discrete values were used in our simulations because, in the authors' recent experiences with data-limited fishery management, we have found that highly integrative approaches (those which typically integrate across multiple parameters) are not easily interpretable and can sometimes complicate decision-making (see Butterworth et al., 2010 for further discussion). Thus, we focused on the clarity that constructing analyses based on discrete hypotheses can bring to policy discussions.

Three different priors were specified to represent alternative viewpoints about stock–recruitment steepness: “certain,” where a non-zero weighting was assigned to only one of the steepness levels; “less certain,” where discrete prior probabilities for each steepness level were calculated based on an informative beta prior from a previous meta-analysis (Shertzer & Conn, 2012); and “least certain” using a discrete uniform prior. In the “certain” case, a prior probability of one was assigned to steepness of 0.8, which is close to the mode of 0.84 from the informative beta prior of Shertzer and Conn (2012). In developing any application of Bayesian statistics, specifying prior probabilities can be the most difficult and controversial aspect, particularly because eliciting expert opinion can introduce subjectivity into otherwise rigorous analytical frameworks (Ellison, 2004; Michielsens & McAllister, 2004; Punt & Hilborn, 1997; Wade, 2000). Subjectivity can be avoided by using diffuse priors, which may be prudent for development of public policies, like those for fisheries management (Press, 1989). Thus, we demonstrated both subjective and diffuse priors in our analyses.

Marginalization produced unconditional performance, which was calculated according to probability rules. For example, $P(h, \theta)$ is the joint probability distribution of stock–recruitment steepness, h , and a given performance measure, θ . Because probabilistic outcomes associated with θ are conditional on steepness, the fundamental rule of conditional probability applies:

$$P(h, \theta) = P(h) \times P(\theta|h), \quad (3)$$

where $P(h)$ is prior probability of h , and $P(\theta|h)$ is performance conditional on the specified steepness level. Marginalization across steepness levels, i , for a given bin of θ , is calculated as follows:

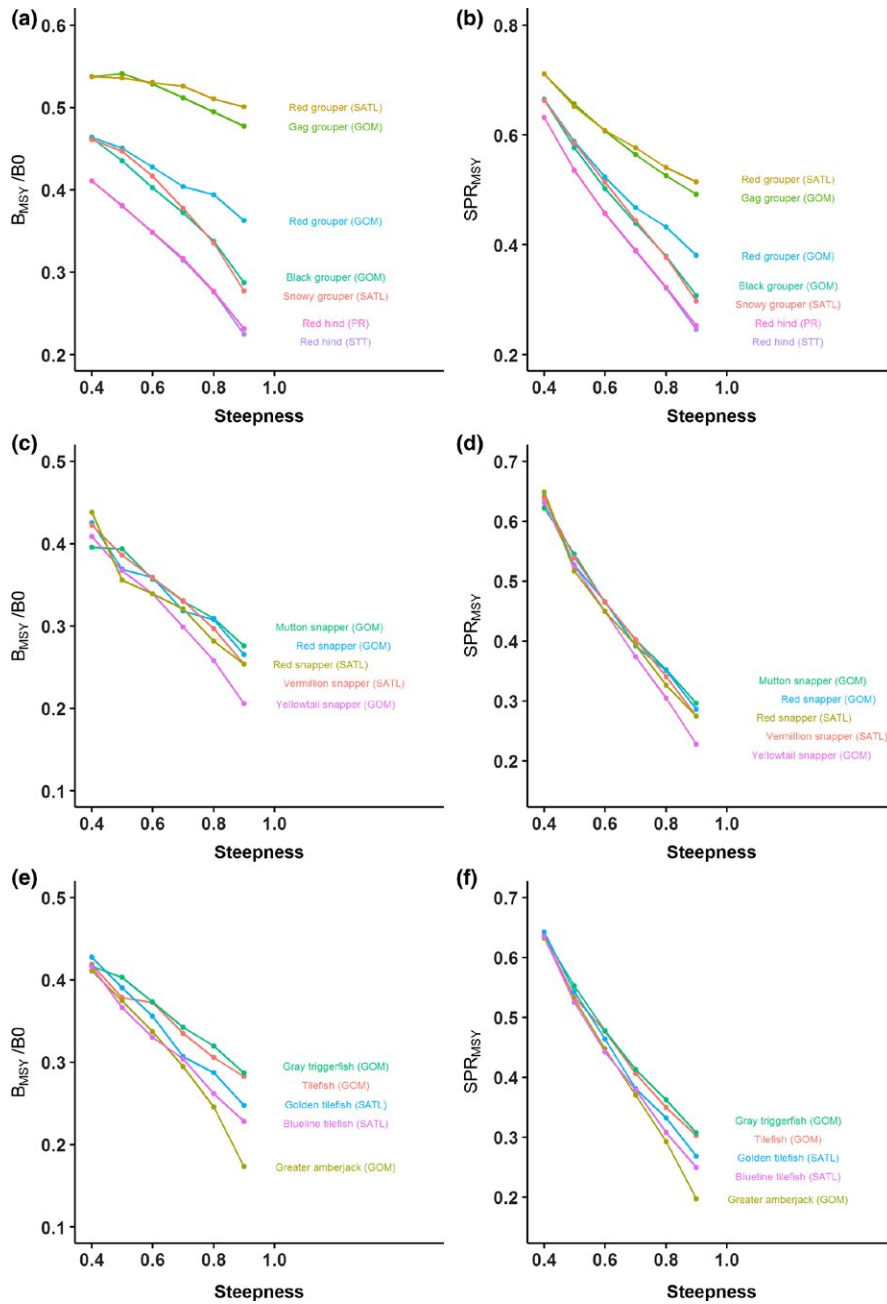


FIGURE 3 Simulated relationships between steepness and B_{MSY}/B_0 (a, c & e) and between steepness and SPR_{at-MSY} (b, d & f) using life history characteristics of gonochoristic and hermaphroditic fish stocks

$$P(\theta_j) = \sum_i P(\theta_j | h_i) \times P(h_i). \quad (4)$$

Calculations were made separately for each combination of performance measure, fishing mortality proxy or HCR, and fish assemblage. Each stock within an assemblage was given equal weighting. Computations were carried out using the software AgenaRisk (Fenton & Neil, 2012).

3 | RESULTS

3.1 | Proxy fishing mortality reference points

For 17 simulated demersal life histories, “known simulated” reference points of B_{MSY}/B_0 and SPR associated with the long-term

achievement of MSY were between 0.2 and 0.5 and between 0.2 and 0.7, respectively, which of course depended on the specified steepness level (Figure 3). For gonochoristic stocks, performance outcomes based on the prior distribution provided by Shertzer and Conn (2012) resulted in $F_{40\%SPR}$ having the greatest probability mass centred around long-term achievement of MSY, while also maintaining biomass in proximity to B_{MSY} (Figures 4b and 5b; Table 4). For the assemblage of hermaphroditic stocks, $F_{50\%SPR}$ had the greatest probability mass centred on long-term achievement of MSY, while also maintaining biomass in proximity to B_{MSY} . In the case of the “least certain” uniform prior for steepness, additional weight is given to lower steepness values, and thus, more conservative fishing mortality proxies were required to achieve MSY-based fishery objectives (Figures 4c and 5c). Conversely, from a viewpoint of certainty

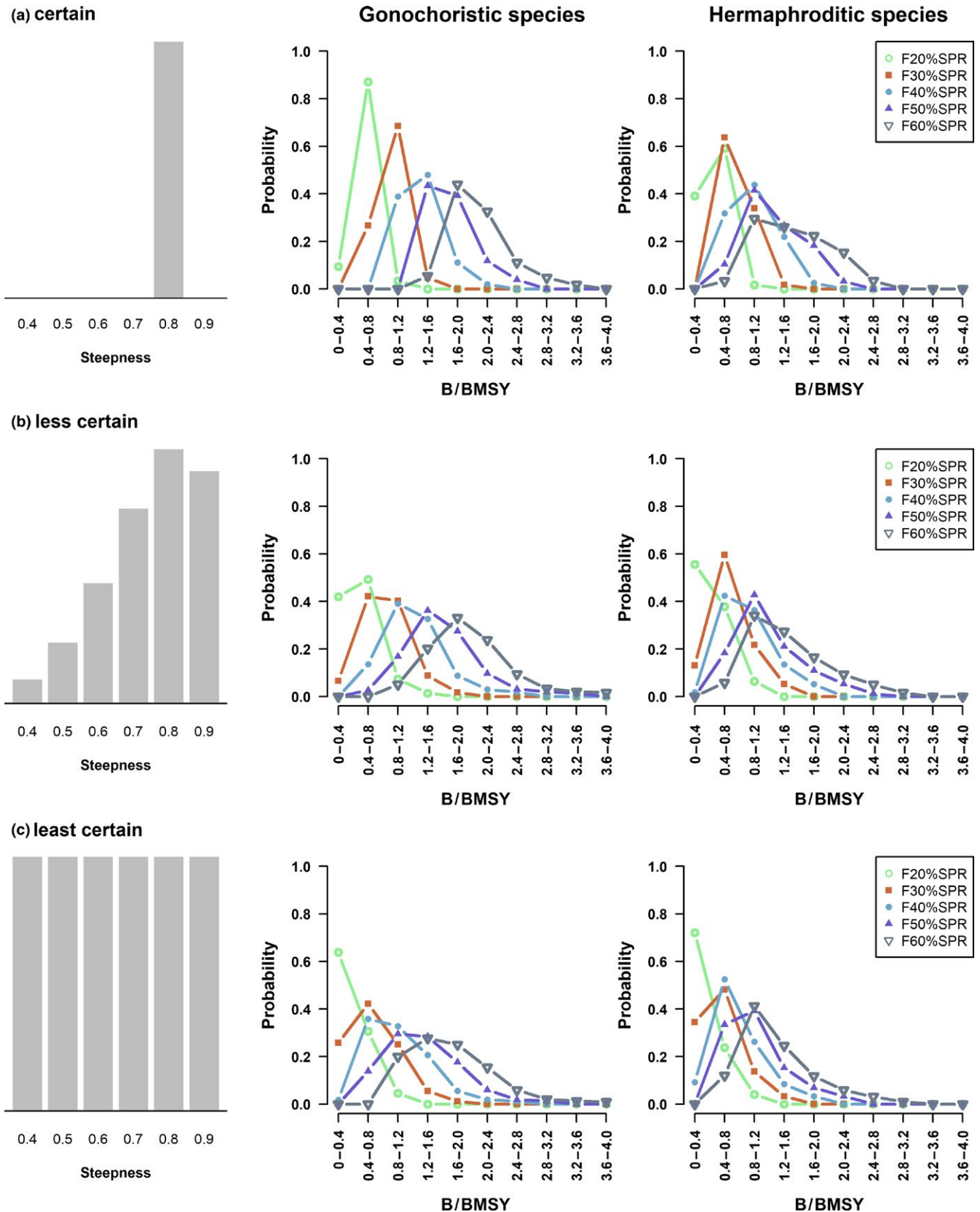


FIGURE 4 Probability-weighted long-term biomass performance (as biomass relative to B_{MSY}) for SPR-based fishing mortality proxies. Histograms shown in each row are steepness prior probability distributions, which are described as: (a) “certain” using a point estimate of 0.8; (b) “less certain” using an informative prior from meta-analysis of demersal fish stocks (Shertzer & Conn, 2012), and (c) “least certain” using a diffuse prior bound between 0.4 and 0.9

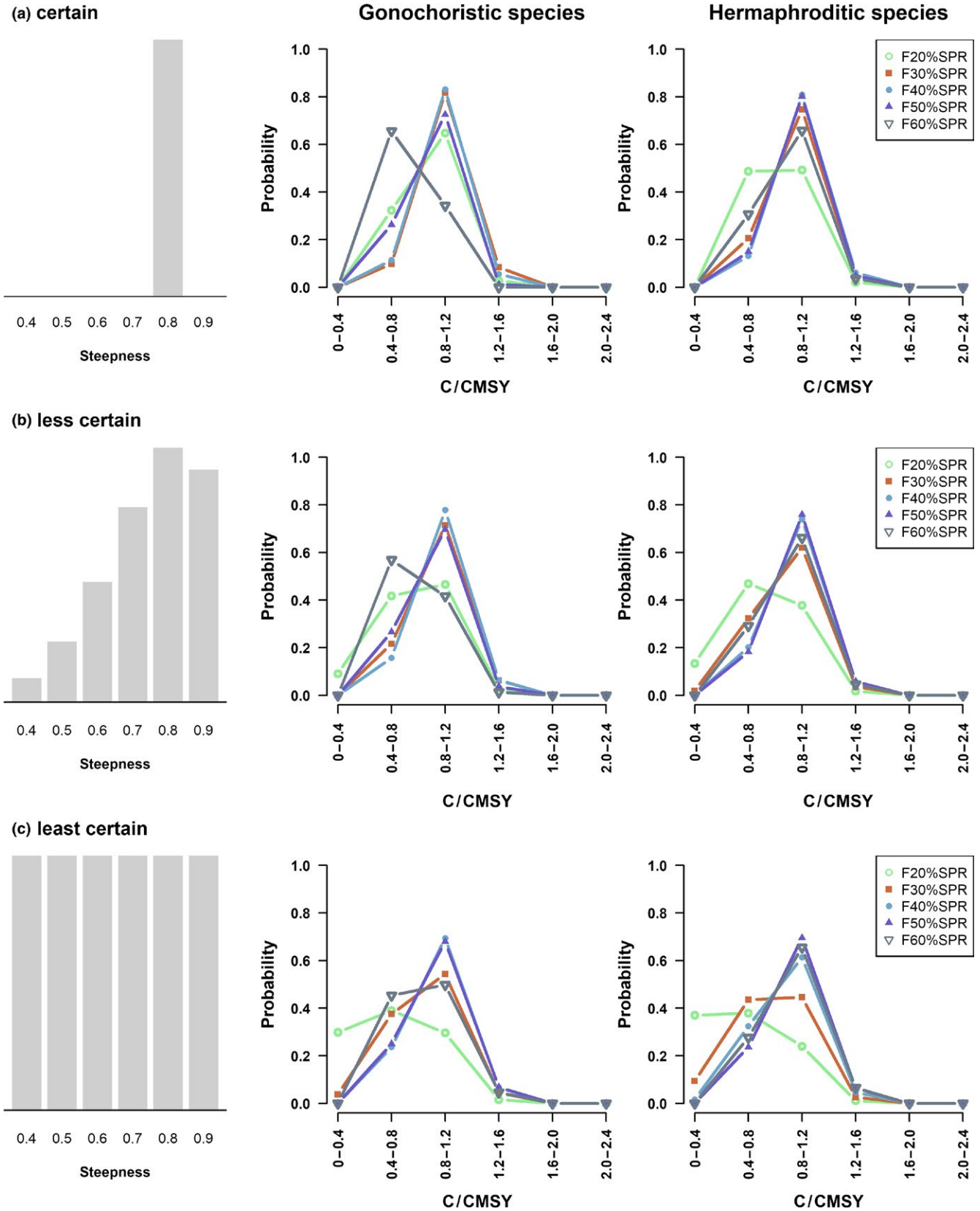


FIGURE 5 Probability-weighted long-term catch performance (as catch relative to MSY) for SPR-based fishing mortality proxies. Histograms shown in each row are steepness prior probability distributions, which are described as: (a) “certain” using a point estimate of 0.8; (b) “less certain” using an informative prior from meta-analysis of demersal fish stocks (Shertzer & Conn, 2012), and (c) “least certain” using a diffuse prior bound between 0.4 and 0.9

TABLE 4 Marginal probabilities of obtaining optimum catch in terms of maximum sustainable yield (MSY) and corresponding biomass, given “less certain” prior for steepness from Shertzer and Conn (2012)

Proxy	Gonochoristic stocks		Hermaphroditic stocks	
	Pr[$0.8 \leq B/B_{MSY} < 1.2$]	Pr[$0.8 \leq C/C_{MSY} < 1.2$]	Pr[$0.8 \leq B/B_{MSY} < 1.2$]	Pr[$0.8 \leq C/C_{MSY} < 1.2$]
$F_{20\%SPR}$	0.07	0.47	0.06	0.38
$F_{30\%SPR}$	0.40	0.71	0.22	0.62
$F_{40\%SPR}$	0.39	0.78	0.36	0.74
$F_{50\%SPR}$	0.17	0.70	0.43	0.76
$F_{60\%SPR}$	0.05	0.42	0.34	0.66

TABLE 5 Stock recovery performance measures for the gonochoristic stock assemblage

Control rule	Fishing limit	Threshold depletion	Closure depletion	Probability recovered	Probability $B > B_{MSY}$	Catch ratio
Certain steepness						
NS1	N/A	N/A	N/A	0.98	0.70	N/A
HCR 1	$F_{40\%SPR}$	0.3	0.0	0.52	0.46	1.04 (0.76–1.51)
HCR 2	$F_{40\%SPR}$	0.3	0.1	0.60	0.54	0.98 (0.88–1.18)
HCR 3	$F_{40\%SPR}$	0.4	0.0	0.65	0.62	0.92 (0.81–1.09)
HCR 4	$F_{40\%SPR}$	0.4	0.1	0.56	0.56	0.92 (0.80–1.11)
HCR 5	$F_{50\%SPR}$	0.4	0.0	0.76	0.76	0.75 (0.53–1.11)
HCR 6	$F_{50\%SPR}$	0.4	0.1	0.84	0.84	0.70 (0.61–0.79)
Less certain steepness prior						
NS1	N/A	N/A	N/A	0.98	0.65	N/A
HCR 1	$F_{40\%SPR}$	0.3	0.0	0.47	0.42	1.12 (0.82–1.48)
HCR 2	$F_{40\%SPR}$	0.3	0.1	0.53	0.48	1.05 (0.87–1.32)
HCR 3	$F_{40\%SPR}$	0.4	0.0	0.59	0.55	0.98 (0.80–1.20)
HCR 4	$F_{40\%SPR}$	0.4	0.1	0.58	0.55	1.01 (0.77–1.18)
HCR 5	$F_{50\%SPR}$	0.4	0.0	0.73	0.70	0.86 (0.59–1.15)
HCR 6	$F_{50\%SPR}$	0.4	0.1	0.79	0.76	0.77 (0.60–0.99)
Least certain steepness prior						
NS1	N/A	N/A	N/A	0.98	0.65	N/A
HCR 1	$F_{40\%SPR}$	0.3	0.0	0.31	0.28	1.25 (0.96–1.69)
HCR 2	$F_{40\%SPR}$	0.3	0.10	0.35	0.31	1.24 (0.97–1.58)
HCR 3	$F_{40\%SPR}$	0.4	0.0	0.41	0.37	1.14 (0.90–1.48)
HCR 4	$F_{40\%SPR}$	0.4	0.1	0.40	0.37	1.13 (0.91–1.37)
HCR 5	$F_{50\%SPR}$	0.4	0.0	0.55	0.52	1.01 (0.71–1.38)
HCR 6	$F_{50\%SPR}$	0.4	0.1	0.62	0.57	0.96 (0.70–1.30)

Notes. NS1 is harvest control rule (HCR) reflecting US National Standard 1 guidelines and HCRs 1 through 6 are broken-stick rules. Probability recovered and Probability $B > B_{MSY}$ measured at expected recovery year of $T_{max} + 1$. Catch ratio reported at median with 50% centred simulation outcomes in parentheses.

in selecting a point estimate for steepness of 0.8, probabilities of achieving MSY-based reference points were centred on $F_{30\%SPR}$ for gonochoristic stocks and $F_{40\%SPR}$ for hermaphroditic stocks (Figures 4a and 5a).

3.2 | Harvest control rules

Based on inferences made about fishing mortality reference points, broken-stick HCRs were specified for gonochoristic stocks to have a

fishing mortality limit of either $F_{40\%SPR}$ or $F_{50\%SPR}$, depletion thresholds (i.e., spawning biomass divided by spawning biomass unfished) of 0.3 or 0.4, and a lower depletion limit for fishery closure of 0.0 or 0.1 (Table 5). For hermaphroditic stocks, broken-stick HCRs were specified to have a fishing mortality limit of either $F_{50\%SPR}$ or $F_{60\%SPR}$, depletion thresholds of 0.4 or 0.5, and a lower depletion limit for fishery closure of 0.0 or 0.1 (Table 6). Both stock assemblages had consistent recovery under the NS1 rule, with 98% of simulations achieving expected recovery time frames. Plots of NS1 outcomes

TABLE 6 Stock recovery performance measures for the hermaphroditic stock assemblage

Control rule	Fishing limit	Threshold depletion	Closure depletion	Probability recovered	Probability $B > B_{MSY}$	Catch ratio
Certain steepness						
NS1	N/A	N/A	N/A	0.98	0.50	N/A
HCR 7	$F_{50\%SPR}$	0.4	0.0	0.66	0.62	0.91 (0.66–1.32)
HCR 8	$F_{50\%SPR}$	0.4	0.1	0.69	0.65	0.88 (0.72–1.12)
HCR 9	$F_{50\%SPR}$	0.5	0.0	0.73	0.69	0.83 (0.70–1.08)
HCR 10	$F_{50\%SPR}$	0.5	0.1	0.77	0.73	0.78 (0.67–1.06)
HCR 11	$F_{60\%SPR}$	0.5	0.0	0.85	0.82	0.66 (0.52–0.89)
HCR 12	$F_{60\%SPR}$	0.5	0.1	0.87	0.84	0.62 (0.50–0.87)
Less certain steepness prior						
NS1	N/A	N/A	N/A	0.98	0.71	N/A
HCR 7	$F_{50\%SPR}$	0.4	0.0	0.53	0.49	1.03 (0.72–1.46)
HCR 8	$F_{50\%SPR}$	0.4	0.1	0.56	0.52	1.02 (0.76–1.30)
HCR 9	$F_{50\%SPR}$	0.5	0.0	0.59	0.55	0.97 (0.72–1.22)
HCR 10	$F_{50\%SPR}$	0.5	0.1	0.64	0.59	0.93 (0.70–1.19)
HCR 11	$F_{60\%SPR}$	0.5	0.0	0.71	0.68	0.80 (0.56–1.05)
HCR 12	$F_{60\%SPR}$	0.5	0.1	0.74	0.71	0.77 (0.53–1.02)
Least certain steepness prior						
NS1	N/A	N/A	N/A	0.98	0.59	N/A
HCR 7	$F_{50\%SPR}$	0.4	0.0	0.37	0.33	1.19 (0.83–1.77)
HCR 8	$F_{50\%SPR}$	0.4	0.1	0.40	0.35	1.20 (0.89–1.60)
HCR 9	$F_{50\%SPR}$	0.5	0.0	0.43	0.38	1.13 (0.83–1.52)
HCR 10	$F_{50\%SPR}$	0.5	0.1	0.48	0.42	1.12 (0.79–1.48)
HCR 11	$F_{60\%SPR}$	0.5	0.0	0.56	0.52	0.97 (0.68–1.33)
HCR 12	$F_{60\%SPR}$	0.5	0.1	0.60	0.55	0.95 (0.63–1.30)

Notes. NS1 is harvest control rule (HCR) reflecting US National Standard 1 guidelines and HCRs 7 through 12 are broken-stick rules. Probability recovered and Probability $B > B_{MSY}$ measured at expected recovery year of $T_{max} + 1$. Catch ratio reported at median with 50% centred simulation outcomes in parentheses.

in year $T_{max} + 1$ indicate non-negligible probabilities of very low catches at stock size slightly below B_{MSY} (Figures 6a and 7a). These low catch simulation runs are those that had initially recovered, but because of stochastic recruitment and life history type, had subsequently fallen just below $1/2B_{MSY}$ (thus becoming overfished again), and are recovering at specified low $F_{Rebuild}$ (and hence low catches).

Each broken-stick HCR differed in recovery probability in a manner that reflected the magnitudes of fishing mortality rates that were dictated by the sloping region of the control rule. The highest probabilities of recovery occurred using fishing mortality limits of $F_{50\%SPR}$, in the case of the gonochoristic assemblage, and $F_{60\%SPR}$, in the case of the hermaphroditic assemblage. Because lowering the fishing mortality limit commensurately lowers fishing mortality at any point during rebuilding (i.e., the sloping region of the HCR; Figure 2), stock recovery is benefited at the expense of long-term achievement of MSY. For example, $F_{40\%SPR}$ provides the highest probability on long-term achievement of MSY for the gonochoristic stocks, while an upper fishing mortality limit of $F_{50\%SPR}$ has the highest probability of ensuring stock recovery during rebuilding. However, some

improvement to recovery probability could also be made by utilizing HCRs that included a non-zero depletion level for fishery closure. Notably, more variable performance outcomes were produced by broken-stick HCRs relative to the data-rich implementation of the NS1 rule (Figures 6 and 7). Broken-stick rules produced more variable recovery patterns than the NS1 rule because the NS1 rule offers more precise control over rebuilding fishing mortality rates (at least under the perfect-information situation that we simulated) and the fishing mortality rebuilding rates imposed by the NS1 rule were also reflective of stock-specific survival and recovery rates.

4 | DISCUSSION

Difficulties in determining MSY-based reference points, whether attributed to unreliable estimates of steepness or attributed to other data limitations, have led to the adoption of proxy reference points for management of many fish stocks within the USA (SEDAR, 2009, 2011). Adoption of such proxies includes a SPR of 26% that is used

in regulating Gulf of Mexico red snapper fisheries (SEDAR, 2014a), which is in contrast to a more conservative SPR of 50% that is used for status determination of the long-lived hermaphroditic goliath grouper (*Epinephelus itajara*, Serranidae), in the south-east USA (SEDAR, 2016b). The most common proxy used for defining fishing mortality rates for south-eastern US demersal reef fish stocks is a SPR of 30%.

Our simulations suggest that achieving MSY-based performance outcomes is most probable when proxies of $F_{40\%SPR}$ and $F_{50\%SPR}$ are used for gonochoristic stocks and hermaphroditic stocks, respectively. Selection of these proxies does depend on (i) the prior probability distribution selected for steepness, (ii) the life histories included in our demersal fish assemblages, (iii) the assumed Beverton–Holt form of the stock–recruitment relationship and (iv) the assumption that fishery selectivity was coincident with the age at 50% maturity. Brooks et al. (2010) suggested that a SPR of 30% would only be appropriate for very resilient stocks and reinforced the importance of selecting a level of SPR based on life history characteristics. Our results support this conclusion on the basis that a SPR of 30% was most strongly supported only in simulations relying on the higher steepness point estimate (i.e., the “certain” steepness scenario of 0.8 shown in Figures 4 and 5), where the possibility of stocks having low steepness was not acknowledged.

Our analysis contributes to evidence across a variety of fish stocks that are both long-lived and have non-negligible probabilities of low steepness (i.e., low resiliency *sensu* Clark, 2002) that $F_{40\%SPR}$ should be close to optimum F , particularly when recruitment to the fishery coincides with maturity (Clark, 2002). Proxies for F_{MSY} have similarly been proposed between $F_{35\%SPR}$ and $F_{40\%SPR}$ for some species of Pacific rockfishes (*Sebastes* spp., Sebastidae), Dover sole (*Microstomus pacificus*, Pleuronectidae), Pacific hake (*Merluccius productus*, Merlucciidae) and some groundfish stocks of the north-west Atlantic (Brodziak, 2002; Clark, 1991, 1993; NEFSC, 2008). Mace (1994) similarly suggests that $F_{40\%SPR}$ be adopted as a target fishing mortality rate when the stock–recruitment relationship is unknown. However, several studies caution that $F_{40\%SPR}$ may be too low for a variety of life histories (e.g., protogynous hermaphroditism; this study), under prevailing environmental conditions, and where there is considerable uncertainty in growth parameters and the rate of natural mortality. Thus, failure to identify fishing mortality proxies that coincide with F_{MSY} can lead to either unsustainable fishing or loss of potential yield (Brodziak, 2002; Cadrin, 2012; Dorn, 2002; Restrepo et al., 1998).

Like Babcock, McAllister, and Pikitch (2007), our comparison of broken-stick HCRs highlighted a trade-off where higher catches during rebuilding could be maintained, but at the expense of lower probability of achieving biomass rebuilding targets within T_{max} years. Across all simulation scenarios that we considered, HCRs that included a non-zero lower biomass limit for fishery closure did improve rebuilding to levels at or above B_{MSY} because these HCRs more dramatically reduced fishing mortality as stock size was depleted. This conclusion is also supported elsewhere (Benson, Cooper, & Carruthers, 2016). Given that less-than-optimal fishing

mortality limits (i.e., $F_{50\%SPR}$ in the case of the gonochoristic assemblage) can also improve stock recovery, but clearly at a cost to long-term catches, there persists a limitation to the use of broken-stick HCRs in achieving both MSY-based fishery objectives and recovery expectations, when performance is made in comparison with the NS1 rule. We also note that stock-specific differences in performance outcomes were not presented in detail, but are evidenced by the result that more variable recovery outcomes (i.e., spread of performance outcomes) occurred under broken-stick HCRs than under the NS1 rule that directly uses MSY-based quantities derived from the stock-specific life history parameters, rather than approximations (proxies) of those quantities used in the broken-stick HCRs.

A few caveats should be considered when interpreting the results of our closed-loop simulations. First, like Benson et al. (2016), our perfect-information simulations suggest that higher complexity rules, like the NS1 rule, will outperform lower complexity broken-stick HCRs; however, in reality, the reliability of stock assessments and of projections about future recruitment could affect this expectation. Second, previous examinations of stock rebuilding strategies have cautioned that life history differences across diverse taxa can sometimes lead to disparate performance outcomes for broken-stick HCRs (Babcock et al., 2007; Benson et al., 2016; Carruthers & Agnew, 2016). We offer the same caution and suggest that careful consideration is needed to avoid potential pitfalls. However, relative to previous studies, our analysis has a more nuanced focus on two fish assemblages having similar life histories, rather than contrasting outcomes across a few diverse taxa. Arguably, we have identified reference points and HCRs that performed reasonably well for these assemblages of the south-east USA and of the US Caribbean region. Third, we maintained knife-edge selectivity at the age coinciding with 50% maturity during the closed-loop simulations. It is plausible that more precautionary protection of spawning stock biomass through larger length restrictions on minimum capture size could reduce stock recovery times (but would also change proxy fishing mortality reference points). Finally, we did not consider potential compensatory dynamics in the stock–recruitment relationship, which could complicate rebuilding from low stock sizes; this effect is thought to be relatively uncommon (Hilborn, Hively, Jensen, & Branch, 2014).

Similar to previous studies, our analysis of rebuilding performance addressed the policy question of whether simpler HCRs perform consistently with other rebuilding plans requiring more detailed information (Babcock et al., 2007; Benson et al., 2016; Carruthers & Agnew, 2016; NRC 2013; Patrick & Cope, 2014). Our analysis purposefully evaluates HCRs that are designed to cope with policy-led mandates that can sometimes outpace information availability. It is worthwhile to note that some regions under US MSFCMA jurisdiction already use broken-stick HCRs as an established means of setting catch limits under certain circumstances (Punt & Ralston, 2007). But where development of HCRs remains an unresolved issue, such as for data-limited stocks in the south-east USA and the US Caribbean, the approach we present enables decision-making to proceed unimpeded by uncertainty in stock–recruitment steepness

and rebuilding can be achieved without reliance on information about future numbers of recruits. Our analysis provides a way forward for meeting rebuilding guidelines, specifically those under US fishery policy, when future recruitment levels cannot be reliably predicted. Improved alignment of management expectations with biological outcomes should increase confidence in the fishery management process (Murawski, 2010) and subsequently help to sustain the benefits of well-managed fisheries to society.

Our analysis also stresses science-led advancement of fishery policy through a lens of information limitations. Importantly, we were able to present broken-stick performance in the context of whether the information-intensive rebuilding expectations of the NS1 rule can be met through these simpler HCRs, which is relevant for design of data-limited HCRs. We cannot overstate the importance of constructing viable decision-making criteria for data-limited demersal fish stocks. In the USA, most fish stocks are subject to the 2006 amendment to the US MSFCA that requires specification of annual catch limits to prevent overfishing (NOAA, 2007). Currently, >70% of all stocks (across a variety of life history types including pelagic and demersal stocks) in the US South Atlantic and Gulf of Mexico are considered data-limited, as are all 179 stocks in the US Caribbean (Anon. 2013; Berkson & Thorson, 2015; Newman et al., 2015; SEDAR, 2016a,c). While the broken-stick HCRs, as we have formulated them, require information about stock depletion that is typically considered a data-rich quantity, this information can be obtained from spatial distribution of fishing effort, relative abundance indices, stock reconstruction or expert opinion (Carruthers et al., 2014; Froese, Demirel, Coro, Kleisner, & Winker, 2017). In addition, length frequency data can be used to calculate SPR as a measure of the relative reproductive status of the stock (Hordyk, Loneragan, & Prince, 2015; Hordyk, Ono, Prince, & Walters, 2016; Rudd & Thorson, 2017).

The approach presented here, while specific to particular species aggregates within two tropical US regions, could be applied elsewhere. Our analysis addresses a common circumstance where selection of a "best" management option is scenario-dependent (Butterworth, Punt, & Smith, 1996; IWC, 2004; Punt et al., 2016; Rademeyer, Plagányi, & Butterworth, 2007; Sainsbury, Punt, & Smith, 2000). By scenario-dependent, we mean that expected performance outcomes of policy choices will be dramatically influenced by alternative competing states of nature, making selection of a policy option difficult without considering the weight of evidence for each scenario. As a further example, consider the case of the western Atlantic stock of bluefin tuna (*Thunnus thynnus*) where highly fluctuating recruitment levels have led to the development of both "low" and "high" future recruitment scenarios and have resulted in competing views and management deadlock for decades (Porch & Laretta, 2016). In this case, as well as other instances where multiple potential future recruitment levels are projected (e.g., South Atlantic king mackerel *Scomberomorus cavalla*; SEDAR, 2014b), the provisioning of management advice could benefit from an understanding of how degree of belief surrounding these competing assumptions would influence perceptions about selecting

among policy options. Our approach is also relevant to the situation where multiple uncertain parameters persist, in which the effects of uncertainty in steepness are considered along with other uncertainties in, for instance, natural mortality (Forrest, McAllister, Dorn, Martell, & Stanley, 2010) or selectivity and discard patterns (Goethel et al., 2018). Similarities can also be drawn between our approach and those that more broadly confront uncertainty in defining biological reference points (Jiao, Reid, & Nudds, 2010). Each of these approaches, as well as our analysis, shares the implication that uncertainty in fisheries systems can be propagated through numerical approaches to provide management guidance in the form of probabilistic statements about expected management outcomes.

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