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Stock status and reference points for sharks using data-limited methods and life history

or

(2 Alternative titles)

(1) Can overfished and overfishing reference points be predicted with data-limited stock assessment methods and life history? Application to shark stocks

(2) Evaluating data-limited methods for determining stock status and reference points for sharks

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Running title: data-limited reference points for sharks

Abstract

Worldwide, many shark populations are classified as data poor, making it difficult to assess their status. However, for many sharks, their longevity, late maturation, and low production of pups make them highly vulnerable to exploitation and highlight the need to assess their status. We compared reference points and stock status estimated from full stock assessments for 33 shark populations with those derived analytically, empirically, or through simulation. There was excellent agreement between overfished status estimated from an assessment and determined from analytical methods using life history and an index of abundance; in 70% of cases the analytical estimate of status was robust to assumptions of initial index depletion. We reviewed the ratio between fishing mortality at MSY (F_{MSY}) and natural mortality (M) for chondrichthyans, from published studies and shark stock assessments. We then compared conclusions on overfishing status from the stock assessments to those derived with F_{MSY} proxies and found very good agreement. Finally, we conducted a simulation study across representative life history parameters and different fishery selectivity patterns to explore the resulting range of F_{MSY} to M ratios. As a rule of thumb, F_{MSY} should not exceed 0.20M for low productivity stocks, 0.50M for stocks of intermediate productivity, and 0.80M for the most productive shark stocks when immature individuals are harvested, which is the norm in the vast majority of cases examined. A triage method is proposed that provides a roadmap for using these data-limited methods as an initial step towards assessment of stock status and sustainability of chondrichtyans.

Keywords Biological reference points, data-limited methods, depletion, sharks, stock assessment, stock status

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Acknowledgements

References

Supporting Information

Introduction

Multiple indicators are used by different management bodies worldwide to characterize the status of fish stocks (e.g., Regional Fishery Management Organizations, Food and Agriculture Organization, International Union for the Conservation of Nature, and Convention on International Trade in Endangered Species). Although the indicators differ, the objectives are broadly similar in that some measure of vulnerability of the stock is derived and is then matched to recommendations for appropriate management response. Sustainability and responsible resource use are common goals across these different management fora.

A key element of determining stock status is the estimation, or specification, of reference points that serve as a basis for comparing with current stock size estimates. Two types of reference points are traditionally used to assess and manage fish stocks: a stock size reference point, which determines whether the stock is in an overfished condition, and an exploitation reference point, which identifies whether overfishing is taking place. In the ecological literature, these indicators are also referred to as state and pressure indicators, respectively (Jennings 2005). To determine overfished status, the current biomass estimate (B_{CUR}) or abundance estimate is compared to a reference point, typically the biomass or abundance at maximum sustainable yield (B_{MSY}), and it is concluded that the stock is overfished if $B_{\mathrm{CUR}}<B_{\mathrm{MSY}}$ or if B_{CUR} is less than some proportion of B_{MSY}. Similarly, overfishing status is determined by comparing the current fishing mortality estimate (F_{CUR}) to the fishing mortality at MSY

(F_{MSY}) or some proxy of F_{MSY}, with a conclusion that overfishing is occurring if $F_{\mathrm{CUR}}>F_{\mathrm{MSY}}$. These status determinations are ultimately used to manage the stock and the fisheries that exploit them (Clarke and Hoyle 2014).

Stock status and reference points are most often obtained from stock assessments of varying degree of complexity, but which require, at a minimum, some information on the biology, catch or effort, and measures of relative abundance of the stock. This endeavor requires financial commitment, supporting infrastructure, and scientific training to collect, analyze, and interpret fishery data (Geromont and Butterworth 2015). In many developing countries, resources are insufficient to meet these requirements (Evans 2000). And in both developing and developed countries, data for non-target species are especially poor with respect to discarded amounts (Musick *et al*. 2000; FAO 2012; Oliver *et al*. 2015) and basic biological studies are typically lacking (FAO 2009; Costello *et al*. 2012). Illegal, unreported, and unregulated (IUU) fishing is another factor limiting the ability to perform assessments (Bray 2000; Agnew *et al*. 2009).

Chondrichthyan fishes (sharks, skates, rays, and chimaeras) suffer substantial mortality as bycatch, particularly in longline fisheries (Watson and Kerstetter 2006; Gilman *et al*. 2007; Mandelman *et al*. 2008; Oliver *et al*. 2015). In addition, IUU fishing activities are often cited as a major issue for sharks (FAO 2014). Even when landings are reported, more than 75% of catches for sharks and rays are aggregated at the level of Order or Family (FAO 2014). Chondrichthyan landings reported to FAO reached a peak in 2003 and declined in the following decade by almost 20%, apparently owing to increased fishing pressure and ecosystem attributes that led to population declines rather than to improved fisheries management (Davidson *et al.* 2016).

On the whole, chondrichthyan fishes are a particularly data-limited group, which explains why most stocks worldwide have not been assessed with formal fisheries stock assessment methods (Cortés *et al*. 2012). According to IUCN Red List criteria, one-quarter of chondrichthyan species worldwide are classified as threatened due to overfishing whereas only one-third of species are considered safe from extinction (Dulvy *et al*. 2014).

The past decade has seen the emergence of numerous data-limited methods (e.g., Carruthers *et al.* 2012, 2014; Newman *et al*. 2014). Some of these methods are focused on providing catch advice (MacCall 2009; Berkson *et al*. 2011), while others look to reconstruct stock dynamics (Stock

Reduction Analysis, Dick and MacCall 2011), or characterize stock status by 'borrowing' information from more data rich stocks (Punt *et al*. 2011; Jiao *et al*. 2009, 2011). Brooks *et al.* (2010) derived analytical overfished reference points based only on knowledge of the life history, and demonstrated how overfished status could be evaluated with an index of abundance. They found that predictions of the overfished condition obtained with their method matched those of more complex stock assessment methods applied to nine shark species. Mangel *et al*. (2013) also noted the close agreement between reference points estimated from stock assessment data and the analytical reference points of Brooks et al. (2010).

Data-limited approaches for specifying fishing mortality reference points have existed for decades. A common rule of thumb relates natural mortality (M) and F_{MSY}. For example, Francis (1974), suggested $F_{MSY}=M$. However, Zhou *et al.* (2012) showed that this "rule" is not supported by empirical data. For chondrichthyans, Au *et al.* (2008) concluded that $F_{\mathrm{MSY}}=0.5M$ based on stock-recruit and abundance-per-recruit relationships, whereas Zhou *et al.* (2012) found that $F_{\mathrm{MSY}}=0.41M$ using Bayesian hierarchical errors-in-variables models. However, these studies did not consider the effect of selectivity on the estimates of biological reference points (F_{BRP}).

Our study aimed to test the ability of data-limited approaches to replicate results obtained in shark stock assessments worldwide. The first objective was to evaluate the accuracy and robustness of overfished status determined by a data-limited method relative to results from a suite of full stock assessments. We did this by comparing analytically derived reference points using the Brooks *et al.* (2010) method and hypotheses about initial depletion for an index of abundance to assessment results. The second objective was to compare predictions of overfishing status based on empirical F_{MSY} proxies with those from the stock assessments. In addition to the F_{MSY} proxies from Au *et al*. (2008) and Zhou *et al*. (2012), we developed another one by calculating the ratio of F_{MSY} and M from all of the stock assessments in our analysis. The estimate of F in the last assessment year was compared to each of the F_{MSY} proxies to determine overfishing. In a few cases, we were also able to use externally derived estimates of F obtained from tagging experiments or a catch curve to predict overfishing status using the F_{MSY} proxies; these predictions were also compared with overfishing status from stock assessments. The third objective was to explore through simulation how the ratios of F_{MSY} and M vary across a range of life histories, given different relationships between fishery selectivity and maturity (median age and slope of the ogives) and shape of fishery selectivity (flat-topped or dome-shaped).

Based on our findings, we conclude by proposing a triage approach that provides a roadmap on how these data-limited methods can be applied to chondrichthyan stocks to provide an initial assessment of stock status and sustainability.

Materials and methods

Derivation of overfished reference points

Overfished reference points are typically expressed in terms of absolute abundance or biomass, the scale of which is strongly influenced by catch. For example, B_{MSY} is defined here as the spawning stock biomass of mature ("spawning") individuals that results from fishing at F_{MSY}. In data-poor situations, catches may be unknown or poorly known, inhibiting determination of scale. An alternative in such cases is to express the reference point relative to unfished conditions so that it refers to an optimal depletion, B_{MSY} / B_0, and the scale is then relative rather than absolute.

In Brooks *et al*. (2010), analytical reference points were derived for optimal depletion in terms of $\hat{\alpha}$, the maximum lifetime reproductive rate (number of spawners produced by each spawner over its entire lifetime) at low stock density (Myers *et al*. 1997). It has been shown that $\hat{\alpha}$ can be simply calculated as the product of unexploited spawners per recruit ($SPR_{F=0}$) and the slope at the origin of a stock-recruit curve (Myers *et al*. 1997; Brooks and Powers 2007). One convenient feature of shark life history is that the slope at the origin of a stock-recruit curve is effectively a measure of the survival of age-0 individuals (pup survival), S_0, (Brooks *et al*. 2010). Therefore, given life history information on maturity at age (m_a), fecundity at age (p_a, the number of offspring produced per breeding female per year), and natural mortality at age (M_j), it is possible to directly calculate $\hat{\alpha}$ as:

$$\hat{\alpha} = S_0 SPR_{F=0} = S_0 \sum_{a=r}^{A} m_a p_a \prod_{j=r}^{a-1} e^{-M_j} \qquad (1)$$

where r is the age of recruitment and A is maximum age. We will use $\hat{\alpha}$ as a measure of productivity henceforth. For a Beverton-Holt stock-recruit function, an overfished reference point for optimal stock depletion that corresponds to maximizing yield in terms of number rather than biomass (Maximum Excess Recruitment, MER; Goodyear 1980) is derived in Brooks *et al*. (2010):

$$\frac{B_{MER}}{B_0} = \frac{\sqrt{\hat{\alpha}} - 1}{\hat{\alpha} - 1}. \qquad (2)$$

Optimal depletion was also derived for the Ricker stock-recruit function (Brooks *et al*. 2010), although it is thought to be less appropriate in general than the Beverton-Holt relationship for sharks (Cortés *et al.* 2012). As discussed in Brooks *et al.* (2010), the analytical derivation assumes that all fish are fully mature and fully selected by the fishery. When that is not the case, one can numerically solve for the optimal depletion to maximize yield in terms of number (MER) or biomass (MSY). Differences between B_{MER} / B_0 and B_{MSY} / B_0 were found to be minor for values of $\hat{\alpha}$<4, which is the case for many shark stocks (Brooks *et al*. 2010).

We calculated optimal depletion using Equation (2) for 33 shark stocks, primarily from the Atlantic Ocean, but also including stocks from the Pacific and Indian Oceans (Table 1, Table S1). The stock assessments included surplus production (n = 12), age-structured production (n = 9), age-structured (n = 8), stock-reduction (n = 3) models, and a model based on an index of abundance (Table 1; Table S1). We obtained first-year survivorship (S_0) and life history values to calculate $SPR_{F=0}$, including M, directly from the stock assessments. If the life history values used in the stock assessment were not reported, we used published values that approximated the implied biology (e.g., the intrinsic rate of increase, r_{max}, used in a Bayesian production model). For the age-structured assessments, we compared the predicted optimum depletion (B_{MER} / B_0) to assessment-estimated B_{MSY} / B_0 values. We did not make this comparison for surplus production models because the estimate of depletion in a production model refers to total population biomass. The analytical optimum depletion refers to mature biomass and ranges from 0 to 0.5, whereas for a surplus production model it ranges from 0 to 1 (Brooks *et al*. 2010).

Evaluating overfished status

We used Equation (2) to predict optimum depletion (B_{MER} / B_0) using the life history values from the assessments. The optimal depletion reference point (B_{MSY} or B_{MER}) is considered a target, i.e. the point where removals are maximized within sustainability constraints. Rather than determining overfished status based on being strictly above or below this target, where random fluctuations may push the stock to vary from overfished to not overfished even in the absence of changes in fishing pressure, many management bodies aim to keep a stock from declining below some threshold less than this target. The threshold is intended to serve as a trigger, such that more stringent management controls may be implemented if a stock declines below the threshold (threshold here is similar to 'limit' in the FAO Precautionary Approach (1995)).

Having calculated the target for optimal depletion, the next step is to calculate an overfished threshold, which can be defined as some proportion, *p*, of that target. We used the formula to determine the appropriate proportion, *p*, that was adopted for shark management in the USA, $p = (1\text{-}M)$ (Restrepo *et al*. 1998). The motivation for defining $p = (1\text{-}M)$ relates to the magnitude of expected fluctuations around B_{MSY}, i.e. "small fluctuations for low M and large fluctuations for high M" (Restrepo *et al*. 1998). With this definition, a stock would be considered overfished if:

$$\frac{B_{CUR}}{B_0} < p\frac{B_{MER}}{B_0}. \qquad (3)$$

To compare predicted overfished status from the analytical method to the assessment estimate of overfished status, we need a measure of current stock depletion to compare with the optimal depletion threshold. Current stock depletion (B_{CUR} / B_0) can be inferred from an index of abundance that is scaled by unexploited stock size B_0. In data-poor situations it is very unlikely that an index spanning the entire period of exploitation exists; however, if an index of abundance I_t that does not extend back in time to unexploited conditions is available, that index can be scaled as:

$$D_t = I'_t\, d = \frac{I_t}{I_{t=1}}\frac{I_{t=1}}{I_{unfished}}. \qquad (4)$$

In (4), $D_t = B_{CUR} / B_0$, is an index of depletion, I'_t is the current depletion of the index (I_t) relative to its initial value ($I_{t=1}$), and *d* is a hypothesis about the depletion level at the beginning of the index from its unexploited level ($I_{unfished}$) (Goodyear 2003). Overfished status can be evaluated by looking at the most recent depletion index value (D_{CUR}), such that the stock is considered overfished if:

$$\frac{D_{CUR}}{\frac{B_{MER}}{B_0}} < p. \quad (5)$$

We compared the overfished status determination from the 33 stock assessments with that derived from the index of hypothesized depletion and the analytical reference points. To derive hypothesized depletion for a given stock, we endeavored to use the most representative index of abundance available from each stock assessment. Ideally this was the longest survey time series, but in other cases we used a hierarchical index of abundance that combines multiple indices into a single series (Conn 2010) or a fishery-dependent index from the main fishery if nothing else was available. In a few cases the starting and ending values of the index were not reported and had to be derived by eye from examination of a plot in the stock assessment report (Table S1). We then used the level of depletion, d, originally reported in, or inferred from, the stock assessment (n=24). In cases where d could not be obtained (n=9), we assumed a value that we felt was reasonable based on knowledge about the development of the specific fishery (Table 1).

Because the hypothesis about d can impact the conclusion on overfished status, we further computed the initial value of depletion, $d_{critical}$, that would result in a change of status from our limit reference point (pB_{MSY}/B_0 or pB_{MER}/B_0) and determined whether the magnitude of the change was reasonable based on the prevailing knowledge of the fishery. This allowed us to determine whether our data-limited approach to assessing overfished status was robust to assumed initial depletion. For example, for the North Atlantic blue shark (*Prionace glauca*, Carcharhinidae) stock assessment (ICCAT 2009), the assumed depletion at the beginning of the index in 1957 was 0.90. In order for conclusions on stock status to have changed from not overfished to overfished, initial depletion in 1957 would have had to be 0.25 or less. We conclude that 0.25 is unreasonably low, considering the fishery started *ca.* 1950, and therefore the method was deemed robust in this case. In contrast, for the Gulf of Mexico blacktip shark (*Carcharhinus limbatus*, Carcharhinidae) stock assessment (NMFS 2012), the assumed depletion at the beginning of the index in 1982 was 0.65 and the depletion that would result in a change of status was 0.50. Considering that the blacktip shark stock was already rather heavily exploited, the initial depletion would not have to change substantially for stock status to change from not overfished to overfished, and therefore the method was not deemed to be robust in this case.

To summarize the degree of agreement in overfished status determination between the assessments and our data-limited approach we computed several performance measures. These include true positives (TP), false positives (FP), true negatives (TN), false negatives (FN), accuracy rate ((TP+TN)/(P+N)), error rate ((FP+FN)/(P+N)), sensitivity (= true positive rate; TP/P), and specificity (= true negative rate; TN/N), obtained with the R library "ROCR" (Sing *et al*. 2005).

Derivation of overfishing reference points

Overfishing reference points are usually expressed in terms of an instantaneous rate of fishing that produces optimal yield, F_{MSY}. This is typically derived within a stock assessment, and in age-structured models it depends on the stock-recruit function. When a stock-recruit function cannot be fit, or when information is insufficient to conduct a stock assessment, a proxy value is often used for F_{MSY} (Froese *et al*. 2016). For the 33 stock assessments we assembled, we calculated the ratio of F_{MSY} to M where that information was available (n = 29). We refer to this as the assessment-based proxy for F_{MSY}. For age-structured models, the M value used was the mean of ages 1 to maximum; for production models, the value of M was obtained iteratively by solving for the value of r_{max} used in the stock assessment (e.g., as a Bayesian prior) through the Euler-Lotka equation (Lotka 1907) while fixing the other published life history inputs (i.e., growth, maturity, lifespan, and fecundity) for that stock.

Evaluating overfishing status

To evaluate whether overfishing is occurring, an estimate of current fishing mortality (F_{CUR}) is needed to compare against F_{MSY}. We determined overfishing status in two ways. First, we evaluated how consistent conclusions about overfishing status were between the stock assessment and when comparing F_{CUR} from the stock assessment to the F_{MSY} proxies (assessment-based proxy, Au *et al.*'s (2008) $F_{\mathrm{MSY}}=0.50M$ proxy, and Zhou *et al.*'s (2012) $F_{\mathrm{MSY}}=0.41M$ proxy) calculated by multiplying the F_{MSY}/M ratio by the assessment estimate of M). Agreement was summarized by computing performance measures with the "ROCR" R package (Sing *et al*. 2005).

We also searched for estimates of F that were derived independently of a stock assessment to compare with the F_{MSY} proxies. We only found four estimates for the stocks that had been assessed: three derived using mark-recapture methods for Gulf of Mexico blacktip shark (Swinsburg 2013), North Atlantic blue shark (Aires-da-Silva *et al*. 2009), and North Atlantic shortfin mako (*Isurus oxyrinchus*, Lamnidae) (Wood et al. 2007), and the other for the bonnethead shark (*Sphyrna tiburo*, Sphyrnidae) (Cortés and Parsons 1996) obtained with a length-converted catch curve. The four studies provided estimates of Z (total instantaneous mortality rate) from which F was obtained by subtracting the value of M used in the stock assessment. We then compared the estimated F value from each study to the three F_{MSY} proxies and determined whether overfishing was occurring or not. To determine consistency of status determination for this approach, we compared our result to that from the stock assessment, where the assessment estimate of overfishing was determined from the estimate of F for the same year as the independent study and the assessment estimate of F_{MSY}. For the Gulf of Mexico blacktip shark and North Atlantic shortfin mako the mark-recapture studies spanned 1964-2011 and 1962-2003, respectively, but only provided a single value of F for the entire time period. We opted to compare that single F value to the median F value from the stock assessment for the years that overlapped, 1981-2010 and 1971-2003, respectively.

Simulation study

The rules of thumb derived by Au *et al*. (2008) and Zhou *et al*. (2012) are simple ratios to derive F_{MSY} proxies from M. As such, these proxies do not consider the effect of selectivity on the estimates of F_{MSY} or the variation in life history. We extend simulation work in Brooks *et al*. (2010) to examine the ratio of F_{MSY} / M and F_{MER} / M for a range of productivity values and for several relationships between median selectivity age and median age at maturity. To simulate productivity ($\hat{\alpha}$), we need to specify values for the following life-history parameters: natural mortality, maturity, fecundity, and pup survival (Equation 1). Below, we define empirical relationships to calculate maturity, fecundity, and pup survival for a given value of natural mortality based on the stock assessments that we reviewed. Values for weight at age were also needed to calculate MSY and depletion in terms of biomass, and we also describe those relationships to natural mortality. All simulation parameters and their values are described in Table 2.

A relationship for age at 50% maturity was derived by examining cumulative survival to a_{50} from the stock assessments assembled for this study. On average, cumulative survival was 0.35, with a standard deviation of 0.12, and ranged from 0.16 for one of the slowest growing, least productive species we examined (sandbar shark (*Carcharhinus plumbeus*, Carcharhinidae)) to 0.71 for one of the fastest growing, most productive stocks (Atlantic sharpnose (*Rhizoprionodon terraenovae*, Carcharhinidae)). To reflect this variability in cumulative survival as a function of longevity, a_{50} in our simulation was calculated as

$$a_{50} = \frac{-\ln(x)}{M} \quad (6)$$

where x ranged from 0.21 to 0.35 in 25 equal increments (to match the number of different M values). This range contributed to the contrast we sought in our simulation for overall productivity, and was supported by the observed range from stock assessments. Our mean estimate for survival to a_{50}, and also the relationship between M and K, are similar to values reported by Frisk *et al*. (2001) for elasmobranchs.

Fecundity in our simulation was defined as the annual production of pups. Gestation periods ranged from 9-24 months for the species included in our review. Calculating the number of pups produced in a given year (total pups produced/gestation period) yielded an observed range of 2.25-37.26, or 1.12-18.63 female pups per year. The lower range corresponded to long-lived, late maturing species, while the shorter-lived, earlier maturing species were on the higher end of that range. We specified annual pup production to range from 1.15-16 female pups per year in 25 equal increments to pair with the range of natural mortality in our simulation.

Pup survival was calculated as $S_0 = \exp(-M)/c_0$, where c_0 ranged from 1.1 to 1.5 in increments of 0.01. This scales adult survival (i.e., $\exp(-M)$) to be 1.1-1.5 times greater than pup survival.

Length at age was also derived from the value of M, such that the von Bertalanffy growth coefficient (K) was a scalar multiple:

$$K = 1.15M \quad (7)$$

This functional form was motivated by life-history invariant relationships from Charnov (1993) and Jensen (1996) who found that $K \approx 0.61M$ and $K \approx 0.67M$, respectively, across a wide range of taxa.

While the value 1.15 was representative for the studies we examined, we note that the value of M in these studies was derived from empirical relationships, some of which used parameter estimates from the von Bertalanffy growth function (e.g., Pauly (1980), Jensen (1996), Chen and Watanabe (1989)), while others were length- or mass-based (e.g., Lorenzen (1996), Peterson and Wroblewski (1984)). Thus, rather than claim this as a new paradigm for sharks, we simply note that using this scalar within our simulations will result in relationships between life history parameters that are consistent with the stock assessments.

The remaining parameters for the von Bertalanffy growth curve, asymptotic maximum size (L_∞) and age at zero length (t_0), were fixed at 200 and 0, respectively. Length (L) at age is converted to weight (W) at age as $W = aL^b$, where a = 1E-6, and b = 3.0. These are arbitrary constants that might be expected to vary across life history. However, the only use in the simulation is to calculate spawning biomass depletion at MSY or MER, which is expressed on a relative scale. Furthermore, selectivity is age-based rather than length-based, so these constants have no bearing on the fishing component of the simulation.

We considered four cases to explore the effect of selectivity on F_{MSY} proxies: 1) only immature sharks are selected, i.e. selectivity = (1-maturity); 2) median selectivity age (s_{50}) = one-half the median age at maturity (a_{50}); 3) $s_{50} = 1.0a_{50}$; and 4) $s_{50} = 1.25a_{50}$. The slope of the selectivity ogive was moderately steep (1.5), while the maturity ogive either had a gradual (0.5) or knife-edged slope (100). For cases (2)-(4), we also considered two shapes for the selectivity at age, logistic and dome-shaped, for a total of 14 selectivity cases (Fig. 1). When selectivity was dome shaped, the age at 50% selectivity on the descending limb of the dome was paired with the ascending s_{50}, yielding median ascending and descending selectivity of 1) [$0.5a_{50}$, $1.50a_{50}$], 2) [$1.0a_{50}$, $2.0a_{50}$], and 3) [$1.25a_{50}$, $2.25a_{50}$]. Each of these selectivity combinations was evaluated for 25 different values of M [0.08, 0.09, …, 0.32] and 41 values for pup survival (S_0) for a total of 12 × 25 × 41 = 12,300 cases + the immature-only selectivity cases (2050 cases).

By separately specifying M and S_0, and the other biological parameters described above, we were able to calculate $\hat{\alpha}$ directly for all 14,350 simulation cases ($\hat{\alpha}$ ranged from 1.504 to 12.968). An alternative parameter for describing productivity or resilience to exploitation, which incorporates both survival and reproduction, is steepness (h). Steepness is a unitless parameter, and measures the proportion of unfished recruitment that can be expected from a population that has been reduced to

20% of unfished spawning abundance (Mace and Doonan 1988). Steepness ranges from 0.2 (indicating replacement only, i.e. "lowest" productivity) to 1.0 (indicating no reduction in recruitment as spawners decrease, i.e. "highest" productivity), and can be calculated from $\hat{\alpha}$ as $h = \hat{\alpha}/(4 + \hat{\alpha})$ (Myers *et al*. 1999). The range of $\hat{\alpha}$ in the simulations corresponds to a steepness range of 0.27-0.76.

Our choice of cases relating s_{50} to a_{50} in the simulation was motivated in part by examining values from the 33 stock assessments and also to explore the effect of increased exploitation or escapement on different segments of the population. In assembling the empirical values, we took a_{50} directly from the stock assessment when age-structured models were used or from the inputs to the Euler-Lotka equation used to develop an estimate of r_{max} with production models. Similarly, s_{50} was extracted directly from the age-structured models or from information available about the fishery (e.g., gear, fishing location, size frequency) in the stock assessment otherwise. The shape of the selectivity curve, i.e. logistic or dome-shaped, for the predominant gear type was used, except in a few cases where a predominant gear could not be identified and both a logistic and a dome-shaped curve were used. We were able to extract data on a_{50} and s_{50} for 19 out of the 33 stock assessments examined. The median ratio between s_{50} and a_{50} for the stocks examined was 0.48 (IQR = 0.19-0.75, n = 12) for dome-shaped selectivity and 0.51 (IQR = 0.29-0.67, n = 10) for logistic selectivity (Fig. 2).

Results

Consistency of overfished status

The analytical method accurately replicated the results of stock assessments on overfished status in 31 out of 33, or 94%, of the cases (Tables 1 and 3). There was only disagreement with two stock assessments which used age-structured models. The sensitivity (probability of correctly predicting that the stock was overfished when it was indeed overfished), was 83% and the specificity (probability of correctly predicting that the stock was not overfished when it was not overfished) was 100% (Table 3). The mean difference between the analytically predicted optimum depletion (B_{MER}/B_0) and B_{MSY}/B_0 values from age-structured stock assessments was 15% (SD = 0.11, n = 15; Table 1).

We deemed that the analytical method was robust to changes in assumed initial depletion, *d*, in 70% of the cases (the difference between *d* and $d_{critical}$ ranged from 0.36 to 0.84, or 55-96%, in the cases where it could be calculated, n = 16). This range for the hypothesized depletion difference was not realistic given knowledge of the fishery operation, species biology, and/or details about available indices. In the 10 cases where it was not robust, the hypothesized value for *d* needed to vary from 0.04 to 0.23 (or 8-31%) for the status estimate to change from not overfished to overfished (n = 7) or vice versa (n = 3; Table 1) indicating that we could not make meaningful distinctions about initial depletion.

Assessment-based F_{MSY} *proxy*

The mean ratio of F_{MSY} and *M* for all stock assessments was 0.74 (median = 0.64; interquartile range (IQR) = 0.39-1.00, n = 29; Fig. 3). We used the median value to calculate the assessment-based F_{MSY} proxy and evaluate overfishing status. The relationship between the F_{MSY}/M ratio and productivity (expressed as $\hat{\alpha}$) was not significant (r_s = 0.34, df = 26, *P* = 0.076), but it became highly significant (r_s = 0.80, df = 22, *P* = 2.17E-06) after removing four stocks that had F_{MSY}/M ratios >1. The mean ratio was 0.60 (median = 0.46; IQR = 0.24-1.00; n = 11) for surplus production models, 0.81 (median = 0.79; IQR = 0.52-1.09; n = 9) for age-structured production models, 0.62 (median = 0.57; IQR = 0.48-0.80; n = 6) for age-structured models, and 1.31 (median = 0.83; IQR = 0.65-1.74; n=3) for stock reduction models (Fig. 3).

The predictions on overfishing status from stock assessments and those based on comparing F_{CUR} from the assessment with the F_{MSY} proxies (assessment-based value of 0.64 and the two published empirical values of 0.41 and 0.50) agreed well, with the assessment-based F_{MSY} proxy we derived producing the highest agreement (Tables 3 and 4). The overfishing status did not match in several cases where the assessment determined there was no overfishing occurring, while the proxies suggested overfishing was occurring, particularly for Indian Ocean blue shark, Atlantic sharpnose in the Gulf of Mexico, and Atlantic smooth dogfish (*Mustelus canis*, Triakidae). Most of these cases corresponded to productive stocks where the fishery selectivity was dome shaped, with some fraction of the adult population not subject to full exploitation, a distinction that was not captured by the F_{MSY} proxies, which ignore selectivity. In all, the assessment-based F_{MSY} proxy had the highest accuracy and specificity, with the three F_{MSY} proxies being able to correctly predict overfishing when overfishing was occurring in all cases (Table 3).

Overfishing status calculated from four estimates of F obtained from available tagging studies and a catch curve and the F_{MSY} proxies was inconsistent with the estimated status from the stock assessments. There was good agreement for bonnethead shark, where the estimate of F from the catch curve was 0.152 and the F_{MSY} proxies ranged from 0.091 to 0.142, indicating overfishing in all cases. The assessment estimate of F during the year when data for the catch curve were collected (1992) also estimated overfishing. However, for the three other cases, where F was obtained from tagging studies, proxy-based overfishing status and that derived from the stock assessment did not match. For the Gulf of Mexico blacktip shark and the North Atlantic shortfin mako, the estimate of F from the tagging studies was 0.168 and 0.10, while the F_{MSY} proxies ranged from 0.063 to 0.099 and 0.041 to 0.064, respectively, indicating overfishing. However, the median as well as the annual F estimated from the stock assessment for the period 1981-2010 and 1971-2003, respectively, which included years during which the tagging studies took place (1964-2011 for blacktip shark and 1962-2003 for shortfin mako), was well below F_{MSY}, thus indicating that overfishing was not occurring. For the North Atlantic blue shark, mean F in 2000 from the tagging study from four subareas of the North Atlantic was 0.136, whereas the F_{MSY} proxies ranged from 0.062 to 0.096, indicating overfishing. However, the F from the stock assessment for the year 2000 was well below F_{MSY}, indicating that overfishing was not occurring.

Simulation results

We evaluated variability in the estimates of F_{MSY} and F_{MER} reference points due to the factors explored in the simulation (M and S_0 values, relationship between a_{50} and s_{50}, gradual versus knife-edged slope of the maturity ogive, and logistic versus dome-shaped selectivity). All factors were significant (ANOVA, $P << 0.001$), but M explained almost half of the variability in F_{MSY} and F_{MER}, and the trend was nearly linear (Fig. 4; results for F_{MSY} shown only). The next most important factor was the relationship between a_{50} and s_{50}, explaining almost 40% of the variability. Lower values of F_{MSY} and F_{MER} were associated with lower values of M and $s_{50} < a_{50}$. Also, logistic selectivity had lower F_{MSY} and F_{MER} than dome-shaped selectivity because the dome allowed greater survival and additional spawning opportunities. The slope of the maturity ogive made a slight difference, with the gradual slope having slightly higher F_{MSY} and F_{MER} compared to the knife-edged slope (Fig. 4).

Noting that $\hat{\alpha}$ reflects the combined effect of M, S_0, maturity, and fecundity, we grouped results for the F_{MSY} / M scalar into three productivity categories as follows: "low" corresponds to $\hat{\alpha}$ = [1.50 - 2.67]; "medium" corresponds to $\hat{\alpha}$ = [2.671 - 6.00]; "high" corresponds to $\hat{\alpha}$ = [6.01 - 13.00]. When selectivity was dome-shaped, we found that across all s_{50} cases for low productivity the median F_{MSY}/M ratio was 0.39 (IQR = 0.29-0.57; "Combined" column in Table 5a). At medium productivity, the median ratio was 1.03 (IQR = 0.67-1.52), and at high productivity the median ratio was 1.74 (IQR = 1.05-2.67). If selectivity was logistic instead of domed, these values all decreased by 0.07-0.23, depending on productivity.

Regardless of the shape of the selectivity curve (logistic, dome, or combining both sets of results—"All" in Table 5), the median F_{MSY}/M ratios for the case where $s_{50} = 0.5{*}a_{50}$ were only 67% at most of the median result for the "Combined" ratios. Similarly, if only immature sharks are harvested ("Immature" row, Table 5), then the F_{MSY}/M ratios were the lowest estimated, with median values of 0.22, 0.51, and 0.96 for the low, medium, and high productivity categories, respectively.

The median ratios for F_{MER} / M were very similar to F_{MSY} / M at low and medium productivity, and were greater by about 0.5 at high productivity (Table 5b). This is consistent with the result described in Brooks et al. (2010), i.e., that F_{MER} is a good proxy for F_{MSY} for stocks on the lower end of the productivity scale, as many sharks are. However, for more productive stocks, the fishing mortality that maximizes yield in number becomes non-negligibly larger than the F that maximizes yield in biomass. We summarize additional results for F_{MSY} / M below, and note that the pattern was identical for F_{MER} / M.

The pattern of optimal depletion at MSY (B_{MSY}/B_0) and $SPR_{MSY} = SPR_{F=FMSY}/SPR_{F=0}$ is also associated with productivity, and follows naturally from the fact that higher productivity stocks can support higher F_{MSY} (Fig. 5). For our three productivity categories, optimal depletion ranged from 0.38-0.47 (low), 0.30-0.39 (medium), and 0.26-0.33 (high), indicating that stocks with higher productivity can sustain greater depletion (Fig. 5a). Similarly, the range for SPR_{MSY} by productivity category was 0.61-0.82 (low), 0.42-0.62 (medium), and 0.33-0.44 (high), reinforcing that more productive stocks are able to sustain a greater reduction in reproductive capacity and still remain sustainable (Fig. 5d). Not unexpectedly, when only immature sharks are selected, the fraction of the population remaining at optimal depletion is the highest, SPR_{MSY} estimates are higher, F_{MSY} / M ratios are the lowest, and the fraction of total population biomass that can be sustainably harvested (MSY / B_0) is the lowest.

Discussion

Evaluating overfished status

The Brooks *et al.* (2010) analytical method for deriving overfished reference points performed well in the vast majority of cases, and conclusions about overfished status were generally robust to hypotheses about initial depletion of the stock. The ability of this method to replicate results of more complex stock assessments is encouraging and suggests that it could be applied to stocks that have not been assessed as a first indication of the overfished status of the population. Choice of a representative and credible index of abundance, however, often remains a challenging issue. Formulating a hypothesis about the depletion at the beginning of the index of abundance is also challenging, particularly when a stock is near the overfished reference point where the method is more sensitive to the assumed value of depletion. This is a limitation that also affects other data-poor methods based on catch, such as the Depletion-Corrected Average Catch (DCAC; MacCall 2009), the Catch-MSY (Martell and Froese 2013), or the CMSY (Froese *et al.* 2017) methods.

The analytical method is able to replicate results from more complex stock assessment models on a relative scale only because it does not use total catch. This emphasizes the role that different data play in a stock assessment: in general, life history parameters determine vulnerability to exploitation, indices of abundance inform about the trend over time, and catch provides absolute scale. In order to provide advice about sustainable catch, one would need data that allows estimation of scale.

Evaluating overfishing status

Whereas previous studies attempted to estimate a single value reflecting the "best" ratio of F_{MSY} to M, we found that there is no single "best" value for that ratio. It depends first on the productivity of the stock, and then on the relationship between selectivity and maturity, with the F_{MSY} / M ratio becoming larger if fish are harvested after they become mature. Other factors related to the shape of the selectivity function and the slope of the maturity ogive had a smaller, but still significant impact on F_{MSY} /M ratios. Dome-shaped selectivity results in larger F_{MSY} /M ratios because it allows some mature adults to avoid exploitation.

The median of simulation results, aggregated across selectivity shape and age at 50% selectivity, suggests that for low productivity stocks F_{MSY} / M < 0.36 should be an upper threshold, which is just below the 0.41 value proposed in Zhou et al. (2012) for chondrichthyans. In contrast, upper thresholds for shark stocks with medium productivity would be F_{MSY} / M ≈ 1.0, and for stocks with high productivity, F_{MSY} / M ≈ 1.6. However, empirical evidence showed that in most situations immature individuals are harvested (s_{50}/a_{50} < 1) and therefore an approximate rule of thumb is that F_{MSY} should not exceed ≈0.2M for low productivity stocks, ≈0.5M for stocks of intermediate productivity, and ≈0.8M for the most productive shark stocks (Table 5). These recommended ratios were consistent (medians and interquartile ranges) for the case when only immature sharks are selected and also when aggregating dome and logistic results for the case when s_{50}=0.5a_{50}. Although we have summarized our results into discrete productivity categories, we emphasize that there is a continuum of F_{MSY} / M ratios, and the appropriate ratio will depend on a shark's productivity and the degree to which immature sharks are harvested and/or there is escapement of mature sharks.

These simulation results have implications for data-limited methods that rely on predetermined reference points based on F_{MSY} /M ratios (MacCall 2009; Moore *et al.* 2013; Carruthers *et al.* 2014; Newman *et al.* 2014). Froese *et al.* (2016) noted that $F = M$ should be considered a limit, rather than a target, reference point and that candidate values of F should not exceed M. Walters and Martell (2004) found the F_{MSY} / M ratio to be 0.6 or less for vulnerable stocks. As we have shown, there is no single ratio that can be specified for all stocks, whether they be fish or sharks, because the appropriate ratio depends on the life history of the stock and selectivity of the fishery, just as with other reference points (e.g. SPR_{MSY} and B_{MSY}/B_0).

Our finding that harvesting immature sharks results in a lower level of sustainable exploitation than when fishing mature individuals is in contrast to the gauntlet fisheries hypothesis (Walker 1998; Prince 2005; Smart *et al*. 2017), which advocates harvesting one or more age classes of juveniles because natural mortality is high at young ages and one would just be replacing natural with fishing mortality. Accordingly, the hypothesis suggests that protecting older females that have already been through the "gauntlet" and are exposed to lower levels of M is preferable because they can immediately contribute to the population. In contrast, elasticity analyses of sharks have consistently shown that the juvenile stage for species with delayed onset of maturity has the greatest influence on population growth (Cortés 2002). This is also supported by several studies that have shown that preservation of reproductive potential or reproductive value—which peaks shortly after maturity—is the preferred management strategy for sharks (Gallucci *et al*. 2006; Cortés *et al*. 2012). Indeed, increasing age at first capture so that all fish have had a chance to spawn is a well-known precautionary approach to fisheries management (Froese 2004; Forrest and Walters 2009). In general, potential responses of populations to changes in cause-specific mortality can be explained by two hypotheses: compensation and additivity (Anderson and Burnham 1976; Nichols *et al*. 1984). Compensation, to which the gauntlet hypothesis conforms, implies that if mortality from one source is reduced, the surviving individuals will die from other causes. In contrast, the additivity hypothesis predicts that individuals that die from the additive cause would have survived if this cause were removed. Péron (2013) showed that in reality these two hypotheses are extreme points on a gradient of possible population responses to changes in mortality patterns and that long-lived species and populations under the carrying capacity tend to "compensate" less than short-lived species and populations above carrying capacity. There is also evidence that partial compensation can occur up to some harvest level, after which the additional harvest becomes additive (Skalski et al. 2005).

Identification of F_{MSY} proxies for determining overfishing status will ultimately require specification of the type of selectivity from the main fishing gears affecting the stock. We suggest that our simulation study, which grouped F_{MSY} proxies by productivity level and selectivity versus maturity pattern, may provide a null hypothesis for sharks where very little information is available. These F_{MSY} proxies could be a quantitative alternative to the more qualitative productivity-susceptibility analyses, for example (Milton 2001; Stobutzki *et al.* 2001; Zhou and Griffiths (2008); Patrick et al. 2010; Cortés *et al.* 2010).

Determining whether overfishing is occurring, however, will still require characterization of current fishing rates. The few estimates of F for the assessed shark stocks examined that were obtained independently of stock assessments made it clear that more soundly designed field-based research is needed if we expect to evaluate overfishing in data-limited situations. A factor that complicated comparison of F estimates obtained from mark-recapture data with those from stock assessments is that tagging experiments usually covered a protracted time span making it difficult to compare the resulting single *F* estimate to annual values estimated in stock assessments. Estimates of *F* from mark-recapture studies that span a period of only a few years, such as those derived for several shark species in Australia (e.g. McAuley *et al.* 2007; Harry *et al*. 2016), would be more amenable to using F_{MSY} proxies for determining overfishing status. Another factor that may explain the discrepancy between *F* values obtained from mark-recapture studies and those estimated from stock assessments is that in the tagging studies we found, the *F* values were obtained by subtraction of *M* from *Z*. Methods that directly estimate *M* or *F*, such as known-fate models, hold more promise, especially with the growing availability of satellite-tag data (Byrne *et al*. 2017)

A triage method

Shark and other chondrichthyan fish stocks worldwide are generally data poor. Following the development of the International Plan of Action (IPOA) for the Conservation and Management of Sharks (FAO 1999), at least 18 of the top 26 shark fishing countries have developed a National Plan of Action (NPOA) for shark management (Fischer *et al*. 2012). While the greatest progress has been in terms of improved reporting of catch and management measures related to shark fins (Fischer *et al*. 2012), determination of stock status and assessment are much less developed. The objective of the IPOA for Sharks was "to ensure the conservation and management of sharks and their long-term sustainable use," and one of the guiding principles was that "management and conservation strategies should aim to keep total fishing mortality for each stock within sustainable levels by applying the precautionary approach" (FAO 1999). A recent study (Simpfendorfer and Dulvy 2017) concluded that sustainable fishing of chondrichthyans is feasible, a view first expressed by Walker (1998), but that management in general is insufficient. We suggest that a triage approach to perform an initial assessment could be used to evaluate stock status and sustainability, and then management action could be focused on stocks needing the most urgent attention.

This triage approach would focus on three key elements: 1) life history; 2) abundance trends; and 3) fishing métier. If detailed life history information on age, growth, maturity, reproduction, and mortality is available, then quantitative estimates of productivity (e.g. $\hat{\alpha}$) and appropriate reference points for overfished status, such as those in Brooks et al. (2010), can be made. If detailed vital rate data are not available, we suggest that if some general biological knowledge about the stock in question exists, then it could be categorized by productivity, similar to the low-medium-high categories we defined. Alternatively, a stock could be assigned to a productivity category based on biological similarities with better-known stocks.

The second element, abundance trends, could then be used in concert with the productivity estimate from the first element for determining overfished status. Abundance trends would be ideally in the form of a fisheries-independent index of relative abundance, or alternatively, a fisheries-dependent index for the stock of interest.

The third element, fishing métier, would provide essential information for understanding the fishery affecting the stock, including the duration of the fishery, the trend in effort over time, the spatial distribution of the fleet, and the size selectivity of the gear. Information on the length of time a fishery has operated, and the trend in effort over time, can give insight into reasonable hypotheses of depletion at the start of an abundance trend (*d* in Equation 4) and a sensitivity analysis can be carried out to identify d_{crit} and evaluate the robustness of stock status results.

Being able to categorize productivity in the first step would also allow specification of appropriate proxies for F_{MSY}, and identification of sustainable fishing rates. We provide guidance based on our simulation results (Table 5, Figure 5) for common reference points (relative depletion, B_{MSY} / B_0, spawning potential ratio, SPR_{MSY}, harvestable fraction of total biomass, MSY/B_0, and F_{MSY} / M) relative to $\hat{\alpha}$ of a Beverton-Holt function. This could help identify overfishing reference points if one is able to assign a stock within one of our broad categories of productivity and selectivity relative to maturity (see Brooks *et al*. 2010 for analytical derivation of relative depletion and *SPR* at MSY or MER relative to $\hat{\alpha}$). Information on maturity from the life history component together with size selectivity data from the fishing métier component could be used to categorize selectivity relative to maturity and specify adequate reference points.

Hordyk *et al*. (2015) noted that individual life-history parameters may be difficult to obtain for data-poor stocks, and suggested that life-history ratios may be an easier alternative. They identified a relationship between SPR and the quantities M / K, F / M, fraction of asymptotic length where knife-edged maturity begins (L_m / L_∞), and fraction of asymptotic length where knife-edged selectivity begins (L_c / L_∞). Similar to our results, they found that *SPR* decreased with increasing F / M ratio and that the decrease was more severe when immature individuals were harvested (*cf*. their Figure 5b to our Figure 5d). An important distinction between the work herein and that of Hordyk *et al.* (2015) is that they varied F / M across a range of values to explore the impact on SPR, whereas our work estimated a value for F_{MSY} / M that corresponded to each combination of life-history parameters and selectivity pattern. If it is possible to relate the M / K and L_m / L_∞ ratios to productivity, one could use the Hordyk *et al.* (2015) approach to approximate $\hat{\alpha}$, and then use knowledge about the fishery selectivity to determine appropriate reference points and F_{MSY} / M proxies as we have outlined.

Finally, information on the spatial distribution of the fleet from the fishing métier component could help identify potential overlap with nursery areas of the stock and determine whether young, immature sharks are likely to be caught. As we demonstrated with simulation, catching fish before the age of maturity results in a much lower rate of fishing that can be considered sustainable.

Summary

The Brooks *et al.* (2010) analytical method can identify overfished reference points when sufficient life history information is available to calculate productivity, which in turn allows specification of proxy overfishing reference points. An index of relative abundance that adequately represents the population is also needed along with knowledge of the fishery and exploitation history of the stock to formulate credible hypotheses about initial depletion.

The long-held view in fisheries science that the fishing mortality rate that results in the maximum sustainable yield of a stock should not exceed the natural mortality rate of that stock seems too liberal for stocks with low productivity. Our results indicate that productivity is the main driver of the F_{MSY} /M ratio, which is also influenced by the relationship between median age at maturity and selectivity, and the shape of the selectivity ogive. Our finding is in line with García-Carreras *et al.* (2015), who found that F-based reference points and associated uncertainty were more affected by plausible changes in selectivity than by incremental addition of more comprehensive data. We suggest that for low productivity species, such as many shark stocks, the F_{MSY} /M ratio should not exceed ≈ 0.4. Furthermore, for this group of predators where empirical evidence indicates that most stocks are harvested before reaching maturity, our findings also suggest that as a rule of thumb the F_{MSY} /M ratio should not exceed ≈ 0.2, 0.5, and 0.8 for low, medium, and high productivity stocks, respectively.

In summary, the relatively data-limited approach and triage method we propose seems attractive if only because it is easier, faster, and cheaper to implement than more complicated and data-intensive stock assessment methods (Geromont and Butterworth 2015; García-Carreras *et al*. 2015). It can provide a rapid and cost-effective means to assess the overfished status of unassessed shark stocks and, when combined with an independently derived estimate of F, also assess the overfishing status. This approach could then be augmented with more comprehensive stock assessments when sufficient information becomes available.

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Table 1 Comparison of results from 33 stock assessments to predictions from analytically predicted optimum depletion (B_{MER} / B_0) and depletion in the final year based on a scaled index of abundance (D_t). S_0 is first-year survival; φ_0 is virgin spawners per recruit (or net reproductive rate); $\hat{\alpha}$ is maximum lifetime reproductive rate; B_{MSY} / B_0 is the proportion of virgin biomass at which MSY is reached in age-structured assessment models; I'_t is depletion from an index of abundance; d is initial depletion from an unexploited state of the index of abundance; $d_{critical}$ is initial value of depletion that would result in a change of status; M is the instantaneous rate of natural mortality; "Robust?" indicates whether the method is sensitive or not to the hypothesis on initial depletion; areas were as follows: GOM+US-SA=Gulf of Mexico and U.S. South Atlantic; NA=North Atlantic; SA=South Atlantic; NWA= Northwest Atlantic; GOM=Gulf of Mexico; NP=North Pacific; I=Indian; NEA=Northeast Atlantic; US-SA=U.S. South Atlantic; NEP=Northeast Pacific; WCP=West Central Pacific; SEI=Southeastern Indian; SWP=Southwest Pacific; Shading indicates disagreement between stock assessment and analytical result. Assessments are listed by method (surplus production: 1-12; age-structured production: 13-21; age-structured: 22-29; stock reduction: 30-32; index: 33). See Table S1 for details.

Stock assessment No.	Scientific name	Area	Stock code	S_0	f_0	$\hat{\alpha}$	B_{MER}/B_0	B_{MSY}/B_0	D_t	I'_t	d	$d_{critical}$	M	Robust?	Assessment result	Analytical result
1	*Carcharhinus isodon*	GOM+US-SA	FTH-NWA	0.703 [a]	1.46	1.03	0.50	[d]	0.42	0.53	0.80	0.74	0.214	no	not overfished	not overfished
2	*Isurus oxyrinchus*	NA	SMA-NA	0.88	2.23	1.95	0.42	[d]	0.45	0.65	0.70	0.57	0.100	no	not overfished	not overfished
3	*Isurus oxyrinchus*	SA	SMA-SA	0.88	2.23	1.95	0.42	[d]	7.18	10.26	0.70	0.03	0.100	yes	not overfished	not overfished
4	*Lamna nasus*	NWA	POR-NA	0.88	1.31	1.15	0.48	[d]	0.17	0.26	0.65	[i]	0.150	yes	overfished	overfished
5	*Mustelus spp.*	GOM	SMHD-GOM	0.68 [b]	5.37	3.65	0.34	[d]	1.63	2.33	0.70	0.11	0.231	yes	not overfished	not overfished
6	*Prionace glauca*	NA	BSH-NA	0.71	27.21	19.24	0.19	[d]	0.55	0.61	0.90	0.25	0.150	yes	not overfished	not overfished
7	*Prionace glauca*	SA	BSH-SA	0.71	25.82	18.25	0.19	[d]	2.14	2.38	0.90	0.06	0.150	yes	not overfished	not overfished
8	*Prionace glauca*	NP	BSH-NP	0.71	27.21	19.24	0.19	[d]	0.52	1.04	0.50	0.14	0.177	yes	not overfished	not overfished
9	*Prionace glauca*	SA	BSH-SA2	0.71 [a]	27.21	19.24	0.19	[d]	1.93	3.86	0.50	0.29	0.150	yes	not overfished	not overfished
10	*Prionace glauca*	I	BSH-I	0.71 [a]	27.21	19.24	0.19	[d]	1.20	2.00	0.60	0.07	0.150	yes	not overfished	not overfished
11	*Sphyrna lewini*	NWA	SHH-NWA	0.84	8.04	6.75	0.28	[d]	0.19	0.29	0.65	0.85	0.103	no	overfished	overfished
12	*Squalus acanthias*	NEA	DOG-NEA	0.90	3.07	2.77	0.38	[d]	0.08	0.10	0.80	[i]	0.104	yes	overfished	overfished
13	*Carcharhinus acronotus*	US-SA	BNOS-NWA	0.75	1.76	1.32	0.47	0.45	0.24	0.30	0.80 [h]	[i]	0.197	yes	overfished	overfished
14	*Carcharhinus acronotus*	GOM	BNOS-GOM	0.75	2.59	1.94	0.42	0.36	1.25	1.78	0.70 [h]	0.19	0.213	yes	overfished	not overfished
15	*Carcharhinus limbatus*	GOM	BTIP-GOM	0.79	1.64	1.30	0.47	0.34	0.51	0.79	0.65	0.50	0.154	no	not overfished	not overfished
16	*Carcharhinus limbatus*	US-SA	BTIP-NWA	0.85	1.91	1.62	0.44	0.44	4.23	7.04	0.60 [h]	0.05	0.123	yes	not overfished	not overfished
17	*Carcharhinus plumbeus*	NWA	SAN-NWA	0.85	1.34	1.14	0.48	0.43	0.25	0.42	0.60 [h]	0.99	0.136	yes	overfished	overfished
18	*Carcharhinus obscurus*	NWA	DUS-NWA	0.81	2.40	1.94	0.42	0.35	0.37	0.42	0.87	[i]	0.067	yes	overfished	overfished
19	*Rhizoprionodon terraenovae*	GOM	ATSH-GOM	0.66	3.45	2.28	0.40	0.36	0.71	0.89	0.80	0.33	0.259	yes	not overfished	not overfished
20	*Rhizoprionodon terraenovae*	US-SA	ATSH-NWA	0.79	4.48	3.54	0.35	0.45	2.27	2.84	0.80	0.09	0.232	yes	not overfished	not overfished
21	*Sphyrna tiburo*	GOM+US-SA	BH-GOM+SA	0.79	5.19	4.10	0.33	0.30	0.30	0.38	0.80	0.68	0.223	no	not overfished	not overfished
22	*Alopias vulpinus*	NEP	THR-NEP	0.84	3.71	3.10	0.36	0.49	0.33	0.54	0.60	0.54	0.179	no	not overfished	not overfished
23	*Carcharhinus falciformis*	WCP	SIL-WCP	0.84	3.28	2.74	0.38	0.39	0.03	0.06	0.41 [h]	[i]	0.180	yes	overfished	overfished

24	*Carcharhinus longimanus*	WCP	OCW-WCP	0.84	3.28	2.74	0.38	0.42	0.06	0.12	0.47 [h]	[i]	0.180	yes	overfished	overfished
25	*Furgaleus macki*	SEI	WHIS-SEI	0.76	4.39	3.35	0.35	[e]	0.21	0.21	1.00	[i]	0.270	yes	overfished [j]	overfished
26	*Galeorhinus galeus*	SWP	SCHO-SWP	0.86	5.83	5.02	0.31	0.28	0.26	0.52	0.50 [h]	0.54	0.100	no	overfished [k]	overfished
27	*Mustelus canis*	NWA	SMD-NWA	0.82	8.10	6.62	0.28	0.32	1.15	1.64	0.70 [h]	0.13	0.202	yes	not overfished	not overfished
28	*Mustelus lenticulatus*	SWP	RIG-SWP	0.78 [c]	2.90	2.26	0.40	[e]	0.35	0.55	0.65	0.54	0.250	no	overfished	not overfished
29	*Prionace glauca*	I	BSH-I3	0.51 [a]	7.83	3.99	0.33	0.46	0.30	0.51	0.60	0.55	0.159	no	not overfished	not overfished
30	*Carcharhinus sorrah*	SWP	SPOT-SWP	0.73 [c]	1.37	1.00	0.50	[f]	0.74	0.93	0.80	0.36	0.315	yes	not overfished	not overfished
31	*Carcharhinus tilstoni*	SWP	ABTIP-SWP	0.73 [c]	3.24	2.36	0.39	[f]	0.90	1.12	0.80	0.24	0.315	yes	not overfished	not overfished
32	*Prionace glauca*	I	BSH-I2	0.70 [a]	9.70	6.79	0.28	[f]	1.20	2.00	0.60	0.10	0.260	yes	not overfished	not overfished
33	*Squalus acanthias*	NEP	DOG-NEP	0.95	5.76	5.48	0.30	[g]	0.40	0.50	0.80 [h]	0.57	0.043	no	not overfished	not overfished

[a] Value not reported, but resulted in same productivity as used in stock assessment

[b] Midpoint of values used in Euler-Lotka equation for *Mustelus canis-M.sinusmexicanis* complex and *M. norrisi* (0.74 and 0.63, respectively)

[c] Value not reported, but assumed to be equal to adult survivorship

[d] Stock assessment was surplus production model and result is not comparable to analytically derived optimal depletion

[e] Stock assessment was age-structured model but no value was provided

[f] Stock assessment model was stock reduction analysis and no value was provided

[g] Stock assessment was an index method and no value was provided

[h] Not specified in stock assessment; depletion assumed to have occurred by the time the index of abundance starts (see also Supplementary materials)

[i] Indicates that $d_{critical}$ would have to be above 1 for status to change from overfished to not overfished

[j] Model results expressed in terms of depletion from virgin biomass, but assumed overfished state (B_{1997}/B_0=0.32-0.40)

[k] Model results expressed in terms of depletion from virgin biomass, but assumed overfished state (B_{1995}/B_0=0.25-0.39)

Table 2 Specifications for simulation study. Factors are parameters for which a simulation loop iterated across their values: *M* (25 levels), S_0 (41 levels), maturity slope *s* (2 levels), selectivity shape (2 levels) with median selectivity s_{50} or [$s_{50.a}$, $s_{50.d}$] (3 levels), for 12,300 cases. Parameters (a_{50}, pup production, *K*) were calculated directly from *M*. In the equations for maturity and selectivity, *a* is age.

Parameter	Value	Description
M	[0.08-0.32]	Natural mortality **factor** with 25 levels: [0.08-0.32] (increments of 0.01); constant for ages 1+
S_0	exp(-*M*)/c_0	Pup survival **factor** with 41 levels: c_0 in [1.1-1.5] (increments of 0.01)
Maturity (m_a)	$\frac{1}{1+\exp(-s(a-a_{50}))}$	Logistic maturity; slope **factor** (*s*) with 2 levels: 0.2 or 100
	a_{50} = -ln(x)/*M*	Age at 50% maturity (a_{50}) is calculated directly from *M*, with x ranging from [0.21-0.35] in 25 equal increments (to match *M* levels)
Annual female pup production (p_a)	[1.15-16]	Age invariant, calculated directly from *M* in 25 equal increments (to match *M* levels)
Selectivity (s_a)	$\frac{1}{1+\exp(-0.2(a-s_{50}))}$	Logistic selectivity with slope=0.2 for all cases
	$s_{50} = ca_{50}$	**Factor** age at 50% selectivity (s_{50}) has 3 levels: *c*={0.5, 1.0, 1.25} times a_{50}; additional case for immature only (s_a = 1 - m_a)

	$\left(\frac{1}{1+\exp\left(-0.2(a-s_{50.a})\right)}\right) \times \left(1-\frac{1}{1+\exp\left(-0.2(a-s_{50.d})\right)}\right)$	Double logistic selectivity with slope = 0.2 for both ascending and descending limbs for all cases
	$s_{50.a} = c_a\, a_{50}$ $s_{50.d} = c_d\, a_{50}$	**Factor** age at 50% selectivity for ascending and descending limbs [$s_{50.a}$, $s_{50.d}$] has 3 levels: [c_a, c_d]= {[0. 5, 1.5], [1.0, 2.0], [1.25, 2.25]} times a_{50}
K	1.15M	Von Bertalanffy growth function coefficient
L_∞	200	Arbitrary scalar for asymptotic length
t_0	0	Arbitrary constant for age when length=0
a	1E-6	Arbitrary scalar for converting length (L) to weight (W), $W = aL^b$
b	3.0	Arbitrary exponent for converting length (L) to weight (W), $W = aL^b$

Table 3 Performance measures for prediction of overfished and overfishing status. For overfished status, predictions from the data-poor (analytical) method are compared to those from 33 stock assessments; for overfishing status, predictions from three F_{MSY} proxies are compared to those from 26 stock assessments.

	Overfished status		Overfishing status			
	Assessments	Analytical method	Assessments	F_{MSY} proxies		
				$F_{MSY}=0.41M$	$F_{MSY}=0.5M$	$F_{MSY}=0.64M$
Positives (P)	12		8			
Negatives (N)	21		18			
True positives (TP)		10		8	8	8
True negatives (TN)		21		14	15	16
False positives (FP)		0		4	3	2
False negatives (FN)		2		0	0	0
Accuracy ((TP+TN)/(P+N))		0.94		0.85	0.88	0.92
Error rate ((FP+FN)/(P+N))		0.06		0.15	0.12	0.08
Sensitivity (TP/P)		0.83		1.00	1.00	1.00
Specificity (TN/N)		1.00		0.78	0.83	0.89

Table 4 Overfishing status found in 26 stock assessments compared to predictions from three biological reference points based on *M* (instantaneous natural mortality rate). Shading indicates disagreement between the stock assessment and empirically derived F_{MSY} values.

Stock assessment No.	Stock code	Overfishing?			
		Assessment	F_{MSY}=0.41M	F_{MSY}=0.5M	F_{MSY}=0.64M
1	FTH-NWA	No	No	No	No
2	SMA-NA	No	No	No	No
3	SMA-SA	No	No	No	No
4	POR-NA	No	No	No	No
5	SMHD-GOM	No	No	No	No
6	BSH-NA	No	No	No	No
7	BSH-SA	No	No	No	No
9	BSH-SA2	No	No	No	No
10	BSH-I	No	Yes	Yes	Yes
11	SHH-NWA	Yes	Yes	Yes	Yes
13	BNOS-NWA	Yes	Yes	Yes	Yes
14	BNOS-GOM	Yes	Yes	Yes	Yes
15	BTIP-GOM	No	No	No	No
16	BTIP-NWA	No	No	No	No
17	SAN-NWA	No	No	No	No
18	DUS-NWA	Yes	Yes	Yes	Yes
19	ATSH-GOM	No	Yes	Yes	Yes
20	ATSH-NWA	No	No	No	No
21	BH-GOM+SA	No	Yes	No	No
23	SIL-WCP	Yes	Yes	Yes	Yes
24	OCW-WCP	Yes	Yes	Yes	Yes
27	SMD-NWA	No	Yes	Yes	No
29	BSH-I3	Yes	Yes	Yes	Yes
30	SPOT-SWP	No	No	No	No
31	ABTIP-SWP	No	No	No	No
32	BSH-I2	Yes	Yes	Yes	Yes
% agreement			85	88	92

Table 5 Descriptive statistics (median and interquartile range, IQR) of simulation results of (a) F_{MSY}/M and (b) F_{MER}/M ratios for a given selectivity shape. Results are summarized for three relationships between median selectivity age (s_{50}) and median age at maturity (a_{50}) for stocks with low ($\hat{\alpha}$ = [1.50 - 2.67]), medium ($\hat{\alpha}$ = [2.671 - 6.00]), and high productivity ($\hat{\alpha}$ = [6.01 – 13.00]). The "Immature" selectivity shape specified selectivity at age as s_a = 1-m_a, so only immature individuals were selected. The "All" case includes "Dome" and "Logistic" results.

(a)

			Median selectivity age (s_{50}) vs. median maturity age (a_{50})						
Productivity	Combined		s_{50}=0.5*a_{50}		s_{50}=1.0*a_{50}		s_{50}=1.25*a_{50}		Selectivity shape
Low	Median	IQR	Median	IQR	Median	IQR	Median	IQR	
	0.22	0.18-0.28	--	--	--	--	--	--	*Immature*
	0.32	0.22-0.48	0.19	0.15-0.23	0.35	0.26-0.43	0.55	0.41-0.71	*Logistic*
	0.39	0.29-0.57	0.26	0.2-0.31	0.42	0.32-0.52	0.64	0.48-0.82	*Dome*
	0.36	0.25-0.52	0.22	0.18-0.27	0.38	0.29-0.48	0.59	0.45-0.77	*All*
Medium	0.51	0.43-0.59	--	--	--	--	--	--	*Immature*
	0.89	0.51-1.38	0.44	0.38-0.51	0.9	0.75-1.06	1.69	1.38-2.05	*Logistic*
	1.03	0.67-1.52	0.6	0.52-0.69	1.05	0.88-1.23	1.82	1.51-2.19	*Dome*
	0.96	0.59-1.47	0.51	0.42-0.6	0.97	0.81-1.16	1.76	1.43-2.13	*All*
High	0.96	0.82-1.11	--	--	--	--	--	--	*Immature*
	1.51	0.78-2.5	0.73	0.66-0.78	1.51	1.4-1.62	2.75	2.5-3.04	*Logistic*
	1.74	1.05-2.67	0.99	0.92-1.05	1.74	1.61-1.87	2.92	2.67-3.24	*Dome*
	1.62	0.99-2.58	0.82	0.73-0.99	1.62	1.48-1.76	2.84	2.58-3.15	*All*

Table 5 (cont.)

(b)

Productivity	Combined		Median selectivity age (s_{50}) vs. median maturity age (a_{50})						Selectivity shape
			s_{50}=0.5*a_{50}		s_{50}=1.0*a_{50}		s_{50}=1.25*a_{50}		
Low	Median	IQR	Median	IQR	Median	IQR	Median	IQR	
	0.24	0.19-0.29	--	--	--	--	--	--	*Immature*
	0.32	0.22-0.49	0.2	0.15-0.24	0.36	0.27-0.45	0.57	0.41-0.74	*Logistic*
	0.39	0.29-0.58	0.26	0.21-0.32	0.43	0.32-0.53	0.66	0.48-0.84	*Dome*
	0.37	0.26-0.54	0.23	0.18-0.28	0.39	0.3-0.49	0.61	0.45-0.79	*All*
Medium	0.57	0.48-0.67	--	--	--	--	--	--	*Immature*
	0.96	0.56-1.56	0.49	0.41-0.57	0.98	0.81-1.19	1.93	1.52-2.5	*Logistic*
	1.08	0.71-1.66	0.64	0.54-0.74	1.11	0.92-1.32	2	1.61-2.54	*Dome*
	1.02	0.64-1.61	0.56	0.45-0.66	1.04	0.85-1.27	1.97	1.56-2.52	*All*
High	0.96	0.82-1.11	--	--	--	--	--	--	*Immature*
	2.14	1.08-3.97	0.95	0.81-1.08	2.14	1.8-2.48	4.88	3.97-5.95	*Logistic*
	2.21	1.25-3.97	1.16	1.04-1.25	2.21	1.9-2.51	4.87	3.97-5.93	*Dome*
	2.18	1.19-3.97	1.06	0.9-1.19	2.18	1.85-2.5	4.87	3.97-5.94	*All*

Figure legends

Figure 1 Selectivity cases explored in simulation included dome-shaped (left column) and logistic (right column). Rows indicate an example of low (top panels), medium (middle panels), and high (bottom panels) productivity, corresponding to $\hat{\alpha}$ = 1.61, 6.0, or 11.62, respectively. Median selectivity at age (s_{50}) relative to median age at maturity (a_{50}) is indicated by the color of the dotted line and symbol: s_{50}=0.5 a_{50} (blue with open circles), s_{50}=1.0 a_{50} (medium blue with open squares), s_{50}=1.25 a_{50} (light blue with open triangles). The maturity ogive is indicated by a solid red line.

Figure 2 Ratio of median selectivity age (s_{50}) to median age at maturity (a_{50}) obtained from 19 stock assessments (n = 22) for logistic (black) and dome-shaped (grey) selectivities. See Table 1 for stock codes.

Figure 3 Ratio of F_{MSY} to M from a compilation of 29 shark stock assessments that used surplus production (blue), age-structured production (red), age-structured (green), or stock reduction (grey) models. See Table 1 for stock codes.

Figure 4 Simulation results for F_{MSY} for different levels of instantaneous natural mortality rate (M) when selectivity is dome-shaped (a, c) or logistic (b, d). The maturity ogive had a slope of 100 (protracted ogive; a, b) or 0.2 (knife-edged ogive; c, d). Legends refer to the value of a scalar between median selectivity age (s_{50}) and median age at maturity (a_{50}), $s_{50} = c*a_{50}$, where c = 0.5, 1.0, or 1.25

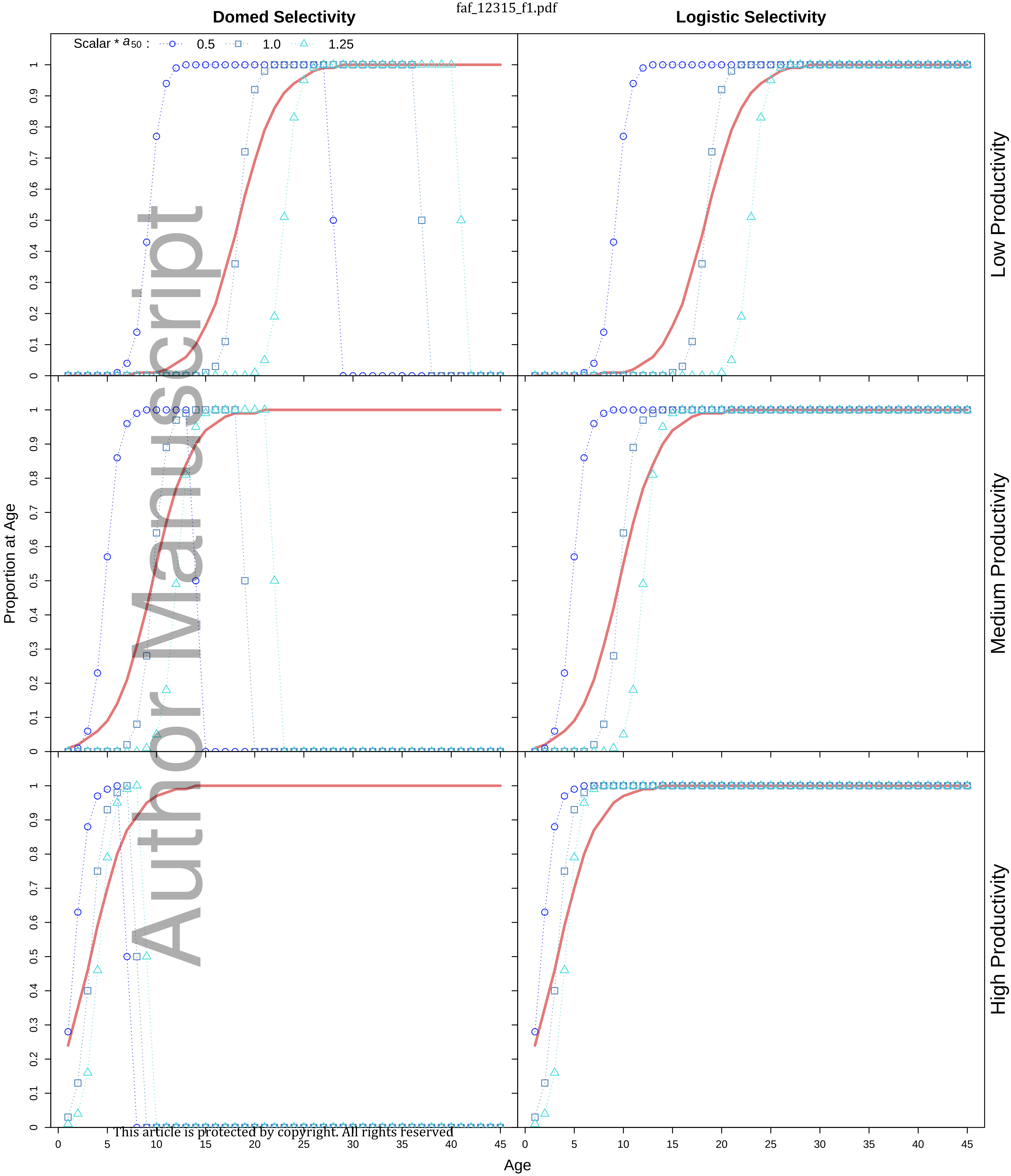
Figure 5 Relationship between maximum lifetime reproduction ($\hat{\alpha}$) of the Beverton-Holt stock recruit relationship and (a) depletion at MSY (B_{MSY} / B_0), (b) harvestable fraction of total biomass (MSY/ B_0), (c) F_{MSY} / M, or (d) SPR_{MSY}. Productivity is delimited by dashed vertical lines: $\hat{\alpha} \leq 2.67$ (low); $2.67 < \hat{\alpha} \leq 6.0$ (medium); $\hat{\alpha} > 6$ (high). The scalar between age at 50% selectivity (s_{50}) and age at 50% maturity (a_{50}) is indicated by symbol: blue circle= 0.5, medium blue square = 1.0, light blue triangle =1.25. The green '+' is when only immature sharks are selected.

Supporting Information

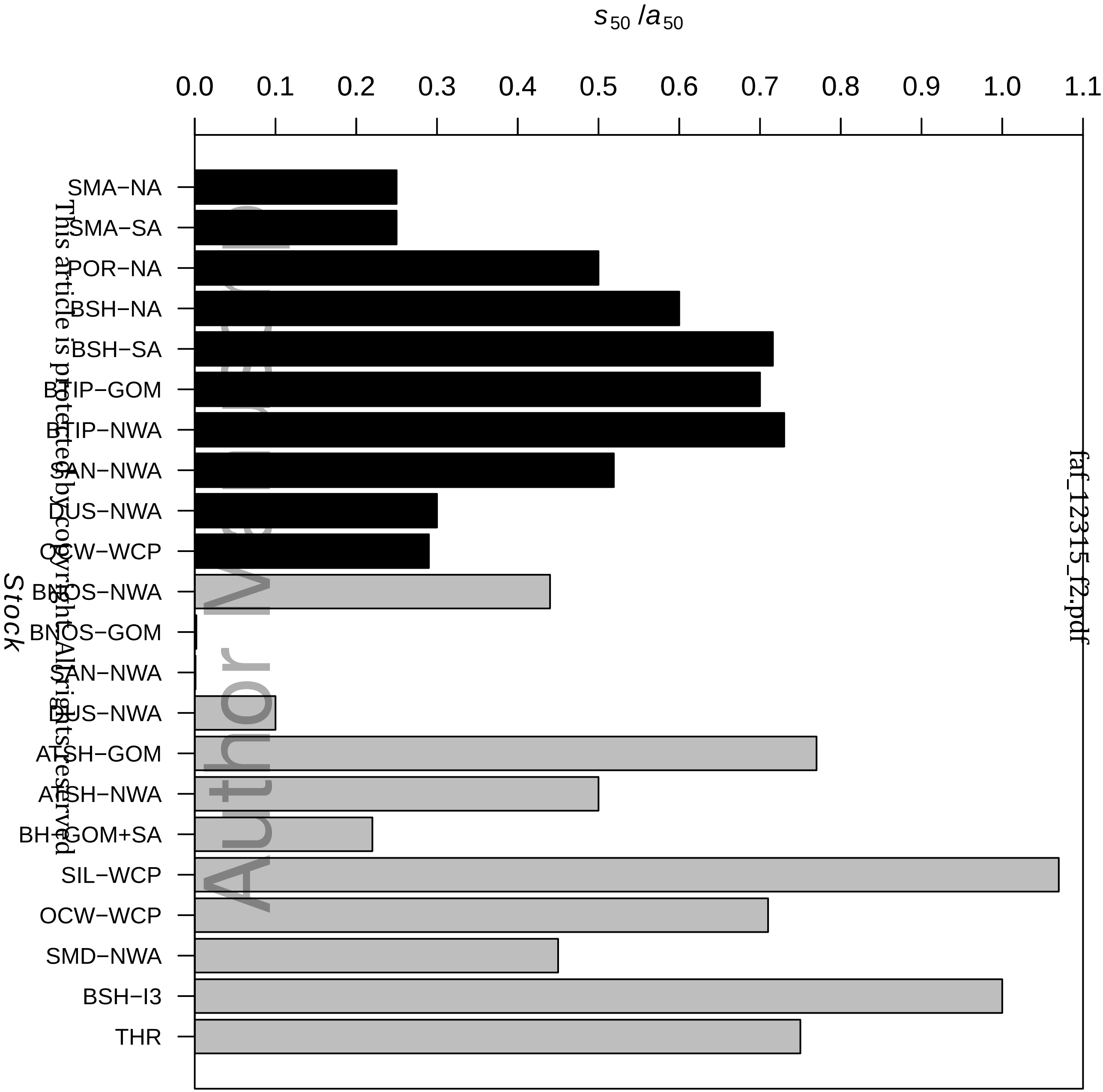
Additional Supporting Information can be found in the online version of this article.

Table S1. Model type and information on the index of abundance used for each stock.

Reference list for Table S1. References of stock assessments cited in Table S1.



Domed Selectivity
Logistic Selectivity
Scalar * a_{50} : 0.5 1.0 1.25
Low Productivity
Medium Productivity
High Productivity
Proportion at Age
Age



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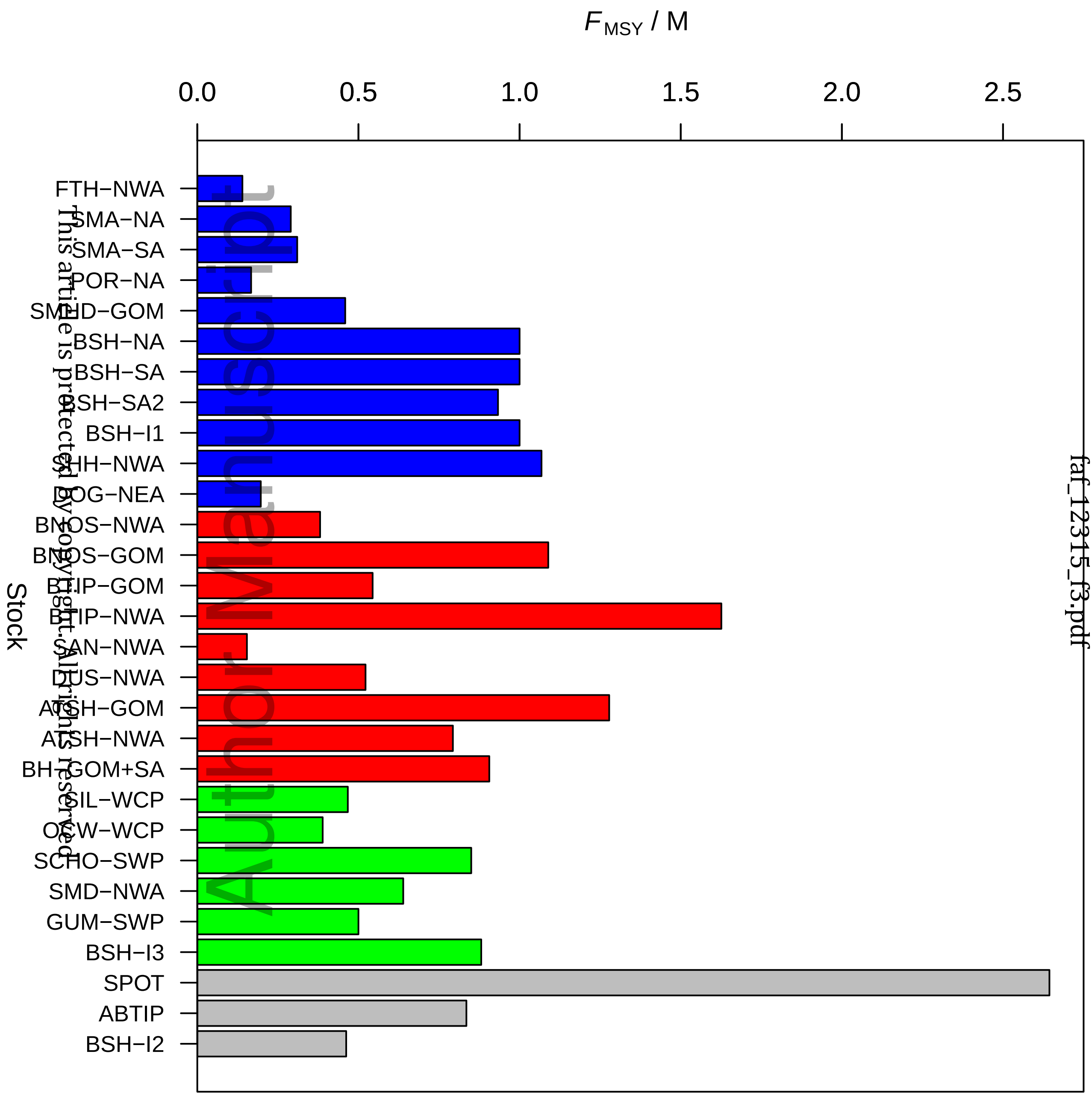
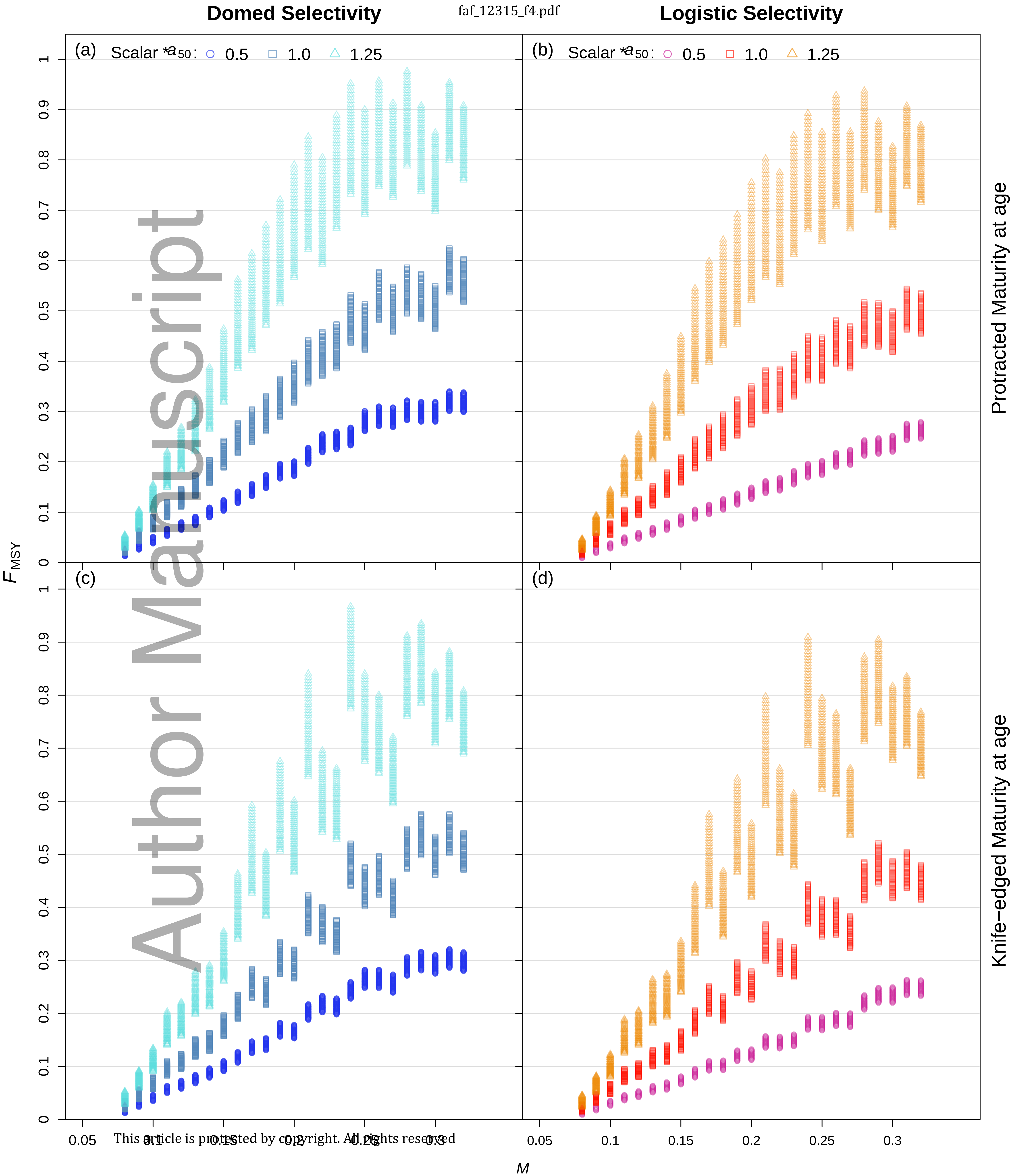
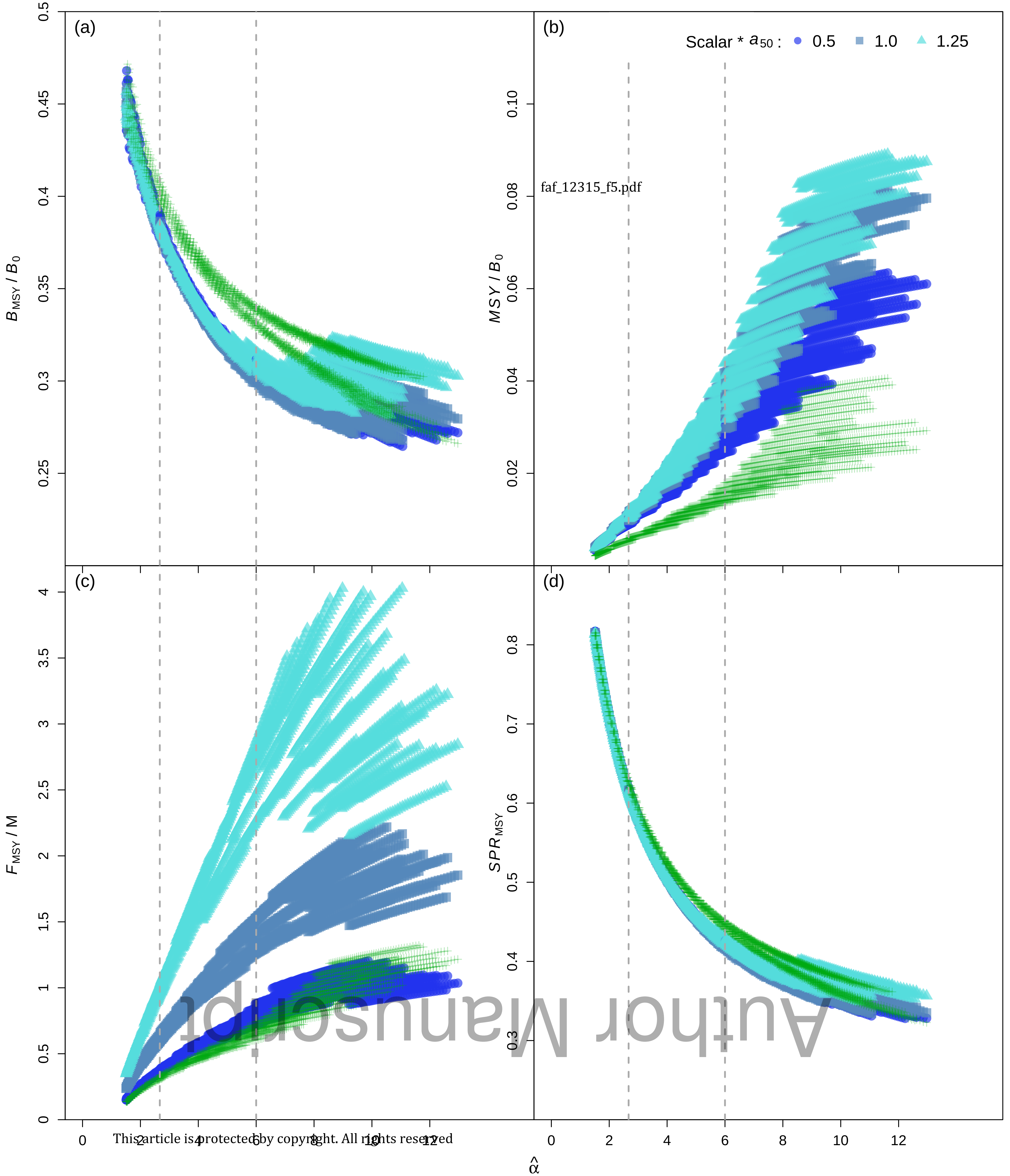

F_{MSY} / M
0.0
0.5
1.0
1.5
2.0
2.5
Stock
FTH−NWA
SMA−NA
SMA−SA
POR−NA
SMHD−GOM
BSH−NA
BSH−SA
BSH−SA2
BSH−I1
SHH−NWA
DOG−NEA
BNOS−NWA
BNOS−GOM
BTIP−GOM
BTIP−NWA
SAN−NWA
DUS−NWA
ATSH−GOM
ATSH−NWA
BH−GOM+SA
SIL−WCP
OCW−WCP
SCHO−SWP
SMD−NWA
GUM−SWP
BSH−I3
SPOT
ABTIP
BSH−I2


Domed Selectivity
Logistic Selectivity
(a) Scalar *a50: 0.5 1.0 1.25
(b) Scalar *a50: 0.5 1.0 1.25
(c)
(d)
Protracted Maturity at age
Knife−edged Maturity at age
FMSY
M
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1
0.05 0.1 0.15 0.2 0.25 0.3



(a)
(b)
(c)
(d)
Scalar * a_{50} : 0.5 1.0 1.25
B_{MSY} / B_0
MSY / B_0
F_{MSY} / M
SPR_{MSY}
$\hat{\alpha}$
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