Spawning-biomass-per-recruit proxies for fisheries reference points under multiple axes of uncertainty

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Biological reference points provide a metric against which the effects of fisheries management can be measured and have been integral in fisheries reform globally. Reference points are predicated on the idea that a relationship between spawning biomass and recruitment exists, but this relationship has not been observed for a majority of stocks for which assessments are available. Spawning-biomass-per-recruit (SBPR) proxies were developed to address this issue and identify reference points that perform well across a range of stock-recruit relationships. These proxies are used widely, including in Bering Sea crab fisheries. However, in the snow crab fishery, the fraction of morphometrically mature males that participate in reproduction is an additional axis of reproductive uncertainty. Here we present a methodology for identifying SBPR proxies under multiple axes of uncertainty using eastern Bering Sea snow crab as an example. In addition to the lack of a stock recruit relationship, there is also uncertainty around the size at which mature crab become reproductively active. Incorporating this uncertainty into the calculation of reference points triples the target amount of biomass retained in the water. This methodology could be easily extended to other species and sources of uncertainty, but care must be taken to define plausible realities to be considered in the axes of uncertainty because the most conservative scenario can play a large role in determining reference points.

INTRODUCTION

Biological reference points associated with maximum sustainable yield are key tools used to manage data rich fisheries globally (Melnychuk et al., 2023). The theory of maximum sustainable yield suggests that, for a given life history and fishery characteristics (e.g. growth rates, mortality rates, maturity schedules, reproductive dynamics, fishery selectivity), a fishing mortality (F_{MSY}) exists that will deplete a population to the biomass level (B_{MSY}) that will produce maximum sustainable yield at equilibrium (REF). If all other life history characteristics are held constant, reproductive dynamics (specifically the relationship between spawning biomass and recruitment) directly determine F_{MSY}. Populations that produce similar amounts of recruitment over a large range of spawning biomasses have a higher F_{MSY} than populations that have a more linear relationship between spawning biomass and recruitment. The idea of maximum sustainable yield underpins much of the legislation that determines fisheries management in North America and Europe and is arguably responsible for the reversal of overfishing observed prior to and during the 1990s in intensely managed fisheries around the globe (Hilborn et al., 2023).

However, a majority of stocks for which assessments exist do not exhibit a relationship between recruitment and spawning biomass over the observed range of spawning biomass (Szuwalski et al., 2015; Sellinger et al. 2024). For many of these stocks, spawning-biomass-per-recruit (SBPR) proxies for F_{MSY} and B_{MSY} developed by Clark (1991) are used in management. SPBR proxies are based on the simple, but clever idea that simulations can be used to find a fishing mortality that produces close to maximum sustainable yield for a range of relationships between spawning biomass and recruitment. So, even though an underlying stock-recruit relationship is unknown, a manager can produce close to MSY over time by using SPBR proxies as reference points.

Calculating SPBR proxies for F_{MSY} and B_{MSY} can be accomplished by coding a population dynamics model that has the life history and fishery characteristics specific to the population for which reference points are needed. An equilibrium yield curve is calculated by projecting the population to equilibrium under a wide range of fishing mortalities. This process of calculating yield curves is repeated with different parameters defining plausible stock-recruit relationships. Each of these yield curves has its own maximum sustainable yield and associated biomass and fishing mortality levels. The SBPR proxies are identified by **maxi**mizing the **min**imum yield across yield curves (figure 1). So, in figure 1, the 'maximin' value for this hypothetical example is ~0.47 (i.e. 47% of unfished spawning biomass per recruit).

The snow crab population in the eastern Bering Sea is managed using SBPR proxies calculated using a size-based stock assessment model (Szuwalski, 2023). The snow crab population is widely distributed across the Bering Sea shelf and catches have been historically variable (figure 2). The biology of snow crab and the fishery for them have a few uncommon characteristics compared to many finfish fisheries. For example, somatic growth in juvenile snow crab occurs via a yearly molt and they undergo a 'terminal molt' to maturity after which growth ceases and the crab are termed 'morphometrically mature' (Tamone et al., 2005). Male crab begin undergoing the terminal molt at 50 carapace width with a probability of ~0.1 (figure 3), but only male crab larger than 101 mm carapace width are retained in the snow crab fishery (figure 3). The discrepancy between maturity and vulnerability in the fishery (which were assumed to be identical in Clark's analyses) results in SBPR reference points that would allow for very high fishing mortalities on the portion of the stock selected in the fishery (Szuwalski, 2023).

Although male snow crab can mature over a large range of sizes, there is uncertainty around what fraction of the morphometrically mature male crab participate in reproductive dynamics. Laboratory studies show that small males can mate with larger females when larger males are not present (Watson, 1972). However, when larger males were present, they always outcompeted smaller males (Comeau et al., 1998). In the few in situ observations available in eastern Canada, only males larger than 95mm carapace width appeared to be participating in mating (i.e. 'functionally mature'; Conan and Comeau, 1986;). The lack of a stock recruitment relationship is the key uncertainty in reproductive dynamics for snow crab in Alaska that drove the decision to use SBPR proxies for reference points in management. However, the additional uncertainties around what fraction of the morphometrically mature biomass actively engages in reproduction has made defining the 'spawning biomass' in SBPR difficult. Further, it is unclear if the figures of 35-40% of unfished SBPR recommended in Clark's analyses is appropriate for snow crab given updates in the biological information used in the assessment, in spite of previous analyses suggesting they were appropriate (Punt, Szuwalski, and Stockhausen; 2013).

Here we investigate three questions. First, how can the uncertainty in reproductive participation of morphometrically mature males be incorporated into the reference points? Second, what is an appropriate percentage of unfished SBPR to set as a management target for snow crab? Third, what is the most appropriate measure of biomass to be used in harvest control rules to determine status when the true fraction of morphometrically mature biomass participating in mating is unknown? To facilitate answering these questions, we extend Clark's SBPR analyses to incorporate more than one axis of uncertainty around reproductive dynamics. We project size-structured models based on the assessment used for snow crab in the eastern Bering Sea under a range of stock-recruit relationships and fishing mortalities to calculate equilibrium yield curves for two scenarios that differ in what portion of population contributes to reproduction. We compare the maximin solutions for SBPR reference points (i.e. the fishing mortality that maximizes the minimum yield across uncertainty) under each scenario to the joint maximin solutions and discuss the potential uses of this methodology in management.

METHODS

The population dynamics model used here is based closely on the stock assessment model used for snow crab in the Bering Sea (Szuwalski, 2023). The model tracks numbers of male crab at size s by maturity state m over time t ($N_{t,s,m}$) with size bins ranging from 30-135 mm carapace width with 5 mm bin widths. Mortality is the only population process that occurs in the first seven months of a given year (the crab year begins in July with the bottom trawl survey):

$$N_{t=y+0.59,s,m} = N_{t=y,s,m}\, e^{-\frac{7}{12}M_{t,s,m}}$$

Fishing occurs as a pulse fishery on February 15 in which the crab captured and brought on deck of fishing vessels, C_{cap}, are a function of capture selectivity, S_{cap}, the number of crab in the Bering Sea at the time of fishing, and the fishing mortality applied, F_t. A retention ogive, S_{ret}, is applied to the captured crab to determine what fraction of crab at a given size are retained, $C_{ret,y}$, and what fraction are discarded back into the ocean. A discard mortality, d_{mort}, of 30% is applied to the crab returned to the ocean.

$$C_{cap,y} = n_{t=y+0.59,s,m} 1 - e^{-F_t * S_{cap}}$$

$$C_{ret,y} = C_{cap,y} S_{ret}$$

$$n_{t=y+0.59,s,m} = n_{t=y+0.59,s,m} e^{-F_t S_{cap}}$$

$$n_{t=y+0.59,s,m} = n_{t=y+0.59,s,m} + d_{mort} C_{cap,y}(1 - S_{ret})$$

Equilibrium yield curves presented here are based on the retained portion of total catch. Spawning biomass is calculated after the fishery. Growth also occurs after the fishery for immature crab and is represented in the model by multiplying the vector of immature crab at size by a size-transition matrix, $X_{s,s'}$, that defines the size to which crab grow given an initial size (figure 3). All immature crab are assumed to molt and no mature crab molt in the model. Newly molted crab are assigned to a maturity state based on the median observed ogives of the proportion of mature new shell males by size calculated from chelae height measured in the NMFS survey data, ρ_s; Richar and Foy, 2022; figure 3). This process results in two temporary vectors of numbers at size:

$$n_{t=y+0.59,s,m=1} = (1 - \rho_s) X_{s,s'} n_{t=y+0.59,s,m=1}$$

$$n_{t=y+0.59,s,m=2} = \rho_s X_{s,s'} n_{t=y+0.59,s,m=1} + n_{t=y+0.59,s,m=2}$$

The size transition matrix $X_{s,s'}$ used here is estimated in the stock assessment and is based on growth increment data collected over several years (Szuwalski, 2024). Beverton Holt curves parameterized in terms of steepness (h), unfished spawning biomass (SB_0), and unfished recruitment (r_0) are used to determine recruitment in the projections.

$$r_y = \frac{4 r_0 h SB_y}{(1 - h) r_0 \left(\frac{SB_0}{r_0}\right) + (5h + 1) SB_y}$$

The spawning biomass (SB_y) from which recruitment is calculated differs among scenarios: SB_y includes all morphometrically mature biomass in one scenario and SB_y includes only morphometrically mature biomass larger than 95 mm carapace width in the other scenario. Recruitment enters the model in the first three size bins with relative proportions allocated to a give size bin ($\theta_{1,2,3}$) derived from stock assessment estimates:

$$n_{t=y+0.59,s=1,2,3,m=1} = n_{t=y+0.59,s=1,2,3,m=1} + r_y\theta_{1,2,3}$$

Finally, the last half of the year of natural mortality is applied to the population after growth, molting, recruitment, and fishing occurs. Note that this allows a crab to experience two different mortalities within a given year as it undergoes terminal molt.

$$N_{t=y+1,s,m} = n_{t=y+0.59,s,m}\, e^{-\frac{5}{12}M_{t,s,m}}$$

All parameter values aside from those associated with recruitment or fishing mortality are drawn from the 2023 assessment for snow crab (figure 3 & table 1). Fishing mortality specified to calculate the yield curves range from 0 to 5 incremented by 0.05. Five steepness values are used ranging from 0.4 to 0.9 in increments of 0.1. The simulated populations are projected 200 years and the relevant equilibrium metrics (e.g. yield, morphometrically mature biomass, functionally mature biomass, vulnerable biomass, fishing mortality, recruitment) are saved after the fishery, but before growth and recruitment. The percentage of unfished biomass per recruit to be used as a reference points is identified by maximizing the minimum value of relative yield across considered spawner-recruit relationships. Yield curves are calculated for three different currencies of management (i.e. morphometrically mature biomass, functionally mature biomass, and vulnerable biomass) to understand how the SBPR proxies change based on the chosen currency.

RESULTS

The yield curves produced when morphometrically mature biomass determines recruitment are very different from the yield curves produced when functionally mature biomass determines recruitment (figure 4). When morphometrically mature biomass determines recruitment, the optimal fishing mortality is very high because much of the morphometrically mature biomass is protected from fishing pressure by the selectivity of the fleet (figure 4a). Even under the highest fishing mortalities that remove ~100% of fully selected crab, the morphometric biomass can only be depleted to ~35% of unfished levels under the least productive recruitment scenarios (figure 4b). The optimal fishing mortality results in nearly all of the males larger than 95 mm carapace width being removed (figure 4c) and this follows from the assumption that smaller mature males are interchangeable with the larger mature males. However, when functional maturity determines recruitment, distinct maximas for yield relative to fishing mortality occur and there are clearly levels of fishing mortality that would drive the population to very low levels (figure 4d). This follows from the assumption that only males larger than 95 mm carapace width participate in reproduction and removing them would impair recruitment.

A very similar, but not identical pattern appears when examining these metrics on a per recruit basis (as Clark does in his original analyses and as the reference points are defined in management; figure 5). Differences among steepness scenarios become more pronounced when examining biomass per recruit. For example, the relative morphometric biomass yield curves are nearly indistinguishable across steepness scenarios (figure 4e), but when looked at from a per recruit standpoint, lower steepnesses are depleted to lower relative biomass per recruit (figure 5e). The relative functional biomass per recruit when functional maturity determines recruits are also more separated and result in a higher proportion of unfished functional biomass per recruit at which maximum sustainable yields occurs compared to the results for functional biomass.

The key contribution of this manuscript is overlaying panels from figure 5 so that maximin comparisons can be performed over both uncertainty in the stock recruit relationship (i.e. the steepness scenarios), but also uncertainty in the contribution to reproduction at size by male crab (figure 6). If functional biomass drives recruitment, the maximin solution to the proportion of unfished functional biomass per recruit to use as a management target is ~48% (figure 6b; square). If morphometric biomass drives recruitment, the maximin solution to the proportion of unfished functional biomass per recruit to use as a management target is ~13% (figure 6b; triangle). If both sets of yield curves are considered in the comparison, the maximin solution is ~45% (figure 6b; circle). Accordingly, the fishing mortality (F) that maximizes the minimum yield when morphometric maturity drives reproductive dynamics is ~4, the maximin F is ~0.5 when dynamics are driven by functional maturity, and the maximin F is 0.55 when the uncertainty around the reproductive contribution of smaller crab is considered.

Determining an appropriate management currency is more difficult when the true contribution of different portions of the morphometrically mature biomass is unknown. It is clear that morphometrically mature biomass is not an appropriate currency because many of the yield curves do not cross, so identifying a maximin solution that represents all scenarios is difficult. Using vulnerable biomass (i.e. the product of total and retained selectivity) instead of functional biomass shifts the yield curves (and the corresponding maximin solutions) to the right (figure 7a and 7c). The fishing mortality that produces the maximin solution does not change when changing between currencies, but the inferred status (i.e. the ratio of the observed biomass to the biomass that corresponds to the SBPR proxy for B_{MSY} that is used in a harvest to control rule to determine the fraction of the SBPR proxy for F_{MSY} to apply to the stock) does. When functional biomass is used as the currency, the status of the stock is less than the status determined by vulnerable biomass when the stock is above the B_{MSY} proxy. When the stock is below the B_{MSY} proxy, status determined by functional biomass is greater than that determined by vulnerable biomass (figure 7b and 7d). This is likely related to the incorporation of biomass in the 'functional biomass' that is not vulnerable to the fishery (figure 3).

DISCUSSION

Our analysis demonstrates a methodology to incorporate multiple axes of uncertainty into the calculation of SBPR proxies for biological reference points used in fisheries management. The key uncertainty this addresses for snow crab is the contribution of differently sized mature crab to reproduction. If males are equally competent in reproduction regardless of size, the optimal strategy would be to harvest nearly all large males and let the small males reproduce (similar to Dungeness crab on the West coast of North America; Richarson et al., 2017). However, if only large males are participating in reproduction, much stricter management would be necessary to protect them. Our analyses identify a compromise in terms of biomass targets that will produce a large fraction of maximum sustainable yield (~63%) regardless of the underlying reproductive dynamics.

The inclusion of an additional axis of uncertainty comes at the cost of yield, however. The fraction of MSY achieved when incorporating stock-recruit steepness and male maturity as axes of reproductive uncertainty (63%) is only slightly smaller than that produced by the maximin solution when functional biomass is the true driver of recruitment (~73%), but considerably smaller than that if morphometric maturity is the true driver of dynamics (~98%). Presumably, no matter the axis of uncertainty incorporated, the proportion of

MSY provided by a proxy can only decrease as additional uncertainty is incorporated. Further, the more conservative hypothesis about the additional axis of uncertainty may be a strong driver of the maximin solutions. In the case of snow crab, the maximin solution over both morphometric and functional maturity is much closer to the maximin solution over functional biomass (which is more conservative) than the solution for when morphometric biomass drives recruitment. Given these results, understanding the true reproductive contribution by size is could have large implications for snow crab management and recommended acceptable biological catches. This result also underscores the importance of identifying realistic ranges for the uncertain processes incorporated in the analysis.

Our analysis identified a target fishing mortality that maximizes the minimum yield over the range of steepness values and potential reproductive contribution of mature male crab by size. Harvest control rules used in fisheries management are often based on three quantities: a target fishing mortality, a target biomass, and an estimate of the current biomass. Sloped harvest control rules are often used in management in which the ratio of the current biomass to the target biomass (i.e. 'status') modifies the proportion of the target fishing mortality to apply to the population. When the current biomass is greater than or equal to the target, the full target fishing mortality is applied, and when the current biomass is less than the target biomass some fraction of the target fishing mortality is applied. The differences in 'status' between vulnerable and functional biomass suggests that for a given fishing mortality, reductions in fishing mortality would be smaller when vulnerable biomass is used as a currency for management. Given the target fishing mortality does not change when changing currencies, the practical impact of these differences in status are likely small. However, simulation studies to understand how large these differences are would be useful.

We demonstrated a method to incorporate multiple axes of uncertainty into the calculation of SBPR reference points using an example of the uncertainty in the size of reproductively active snow crab in the Bering Sea. However, these methods could be extended to uncertainty in other processes. For example, natural mortality is one of the most important, but poorly known parameters in population dynamics modeling because mis-specifying natural mortality has an outsized impact on the calculation of reference points when compared to other processes (Thorson et al., 2015). Specifying two plausible natural mortalities, calculating yield curves, and then identifying maximin solutions across these hypotheses could be a useful way to consider this uncertainty in the management process. Uncertainty in other processes like growth or selectivity could also be addressed in this way.

Our extension of Clark's seminal work aligns well with the classical literature and the currently implemented management for snow crab and other species that use SBPR proxies for reference points. However, SBPR proxies and the concept of maximum sustainable yield are still couched in an equilibrium worldview and non-stationary dynamics are increasingly observed in fisheries (Szuwalski and Hollowed, 2016). For example, Alaska snow crab recently underwent a mortality event in which 90% of crab died during an extended marine heatwave (Szuwalski et al., 2023) and recruitment dynamics are strongly related to environmental drivers like ice (Szuwalski et al., 2021). Equilibrium based reference points may have limited use as we delve deeper into a non-stationary world in which population processes vary strongly from year to year (Szuwalski et al., 2023). Methods like multi-dimensional SBPR reference points may be a useful stopgap to incorporate uncertainty into the existing management frameworks while non-equilibrium management frameworks are developed and tested.

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Table 1. Parameter values by size used in the population dynamics model.

Size	*Mature M*	*Immature M*	*p(capture)*	*p(retained)*	*p(terminal molt)*	*p(recruit)*
27.5	0.29	0.24	0	0	0	0.32
32.5	0.29	0.24	0	0	0	0.42
37.5	0.29	0.24	0	0	0.01	0.26
42.5	0.29	0.24	0	0	0.03	0
47.5	0.29	0.24	0	0	0.07	0
52.5	0.29	0.24	0	0	0.12	0
57.5	0.29	0.24	0	0	0.18	0
62.5	0.29	0.24	0	0	0.25	0
67.5	0.29	0.24	0	0	0.32	0
72.5	0.29	0.24	0	0	0.4	0
77.5	0.29	0.24	0	0	0.44	0
82.5	0.29	0.24	0	0	0.47	0
87.5	0.29	0.24	0.01	0	0.5	0
92.5	0.29	0.24	0.03	0.05	0.55	0
97.5	0.29	0.24	0.08	0.5	0.65	0
102.5	0.29	0.24	0.22	0.95	0.8	0
107.5	0.29	0.24	0.47	1	0.89	0
112.5	0.29	0.24	0.74	1	0.94	0
117.5	0.29	0.24	0.9	1	0.97	0
122.5	0.29	0.24	0.97	1	0.98	0
127.5	0.29	0.24	0.99	1	0.98	0
132.5	0.29	0.24	1	1	1	0

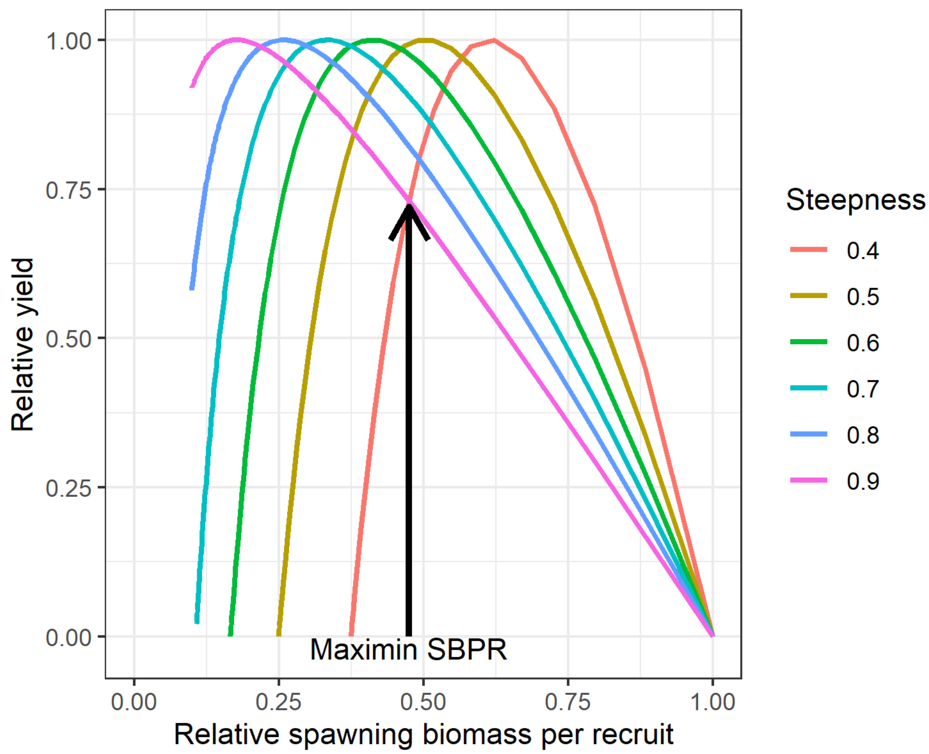

Figure 1. Conceptual example of yield curves over steepness space (colored lines) to identify spawning biomass per recruit proxies by maximizing the minimum relative yield. In this example, the maximum of the minimum of the yield curves occurs at ~47% of unfished spawning biomass per recruit.

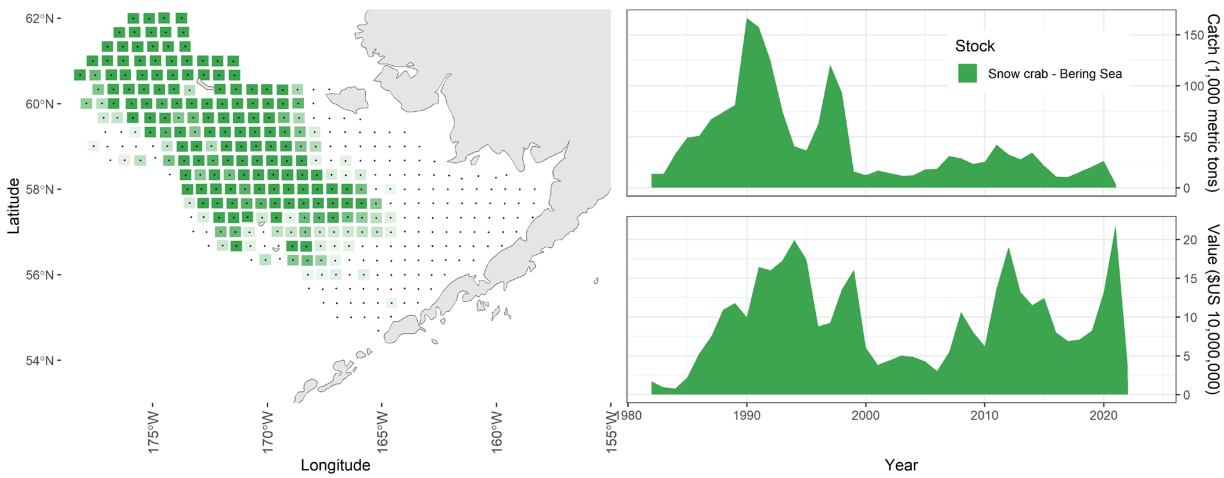

Figure 2. Average distribution of snow crab in the eastern Bering Sea (left). Each colored square represents a survey location by the NMFS bottom trawl survey, with the shading representing the average density in a square over time relative to the maximum average density (darker square have higher densities). Dots are locations where the survey occurs, but the average snow crab catch is less than 1% of the maximum density observed (including zero catch stations). Snow crab catches and ex-vessel values are at the right. The fishery was closed 2022-2024.

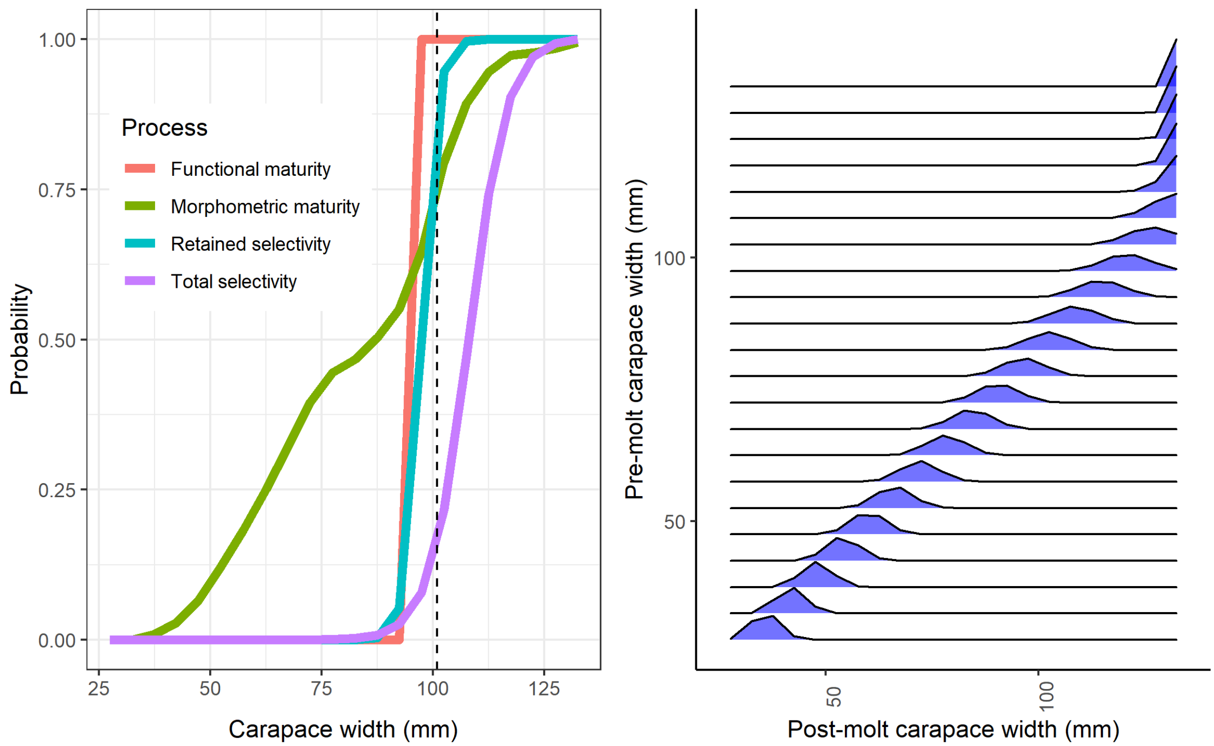

Figure 3. Key population processes used in projections. Total and retained selectivity refer to the directed fishery for snow crab. Morphometric maturity refers to the probability of having undergone terminal molt, after which growth ceases. Crab larger than the vertical dashed line are the industry preferred size. The right panel is the size transition matrix used in projections that determines the distribution of the post-molt size (blue polygons) given a pre-molt size (y-axis).

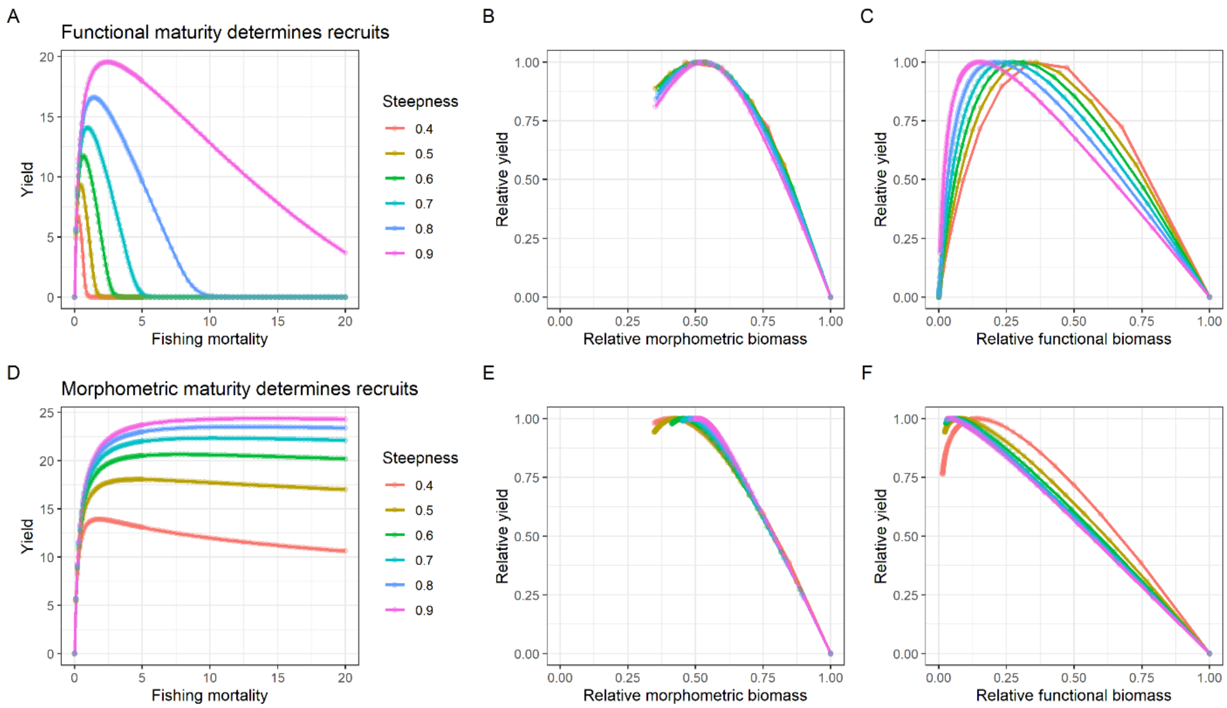

Figure 4. Equilibrium yield curves against fishing mortality (left), morphometric biomass (center), and functional biomass (right) for a range of steepness values. The top row represents population dynamics in which functionally mature biomass (i.e. >95 mm) is used in the stock recruit relationship to determine recruitment; the bottom row uses morphometrically mature biomass.

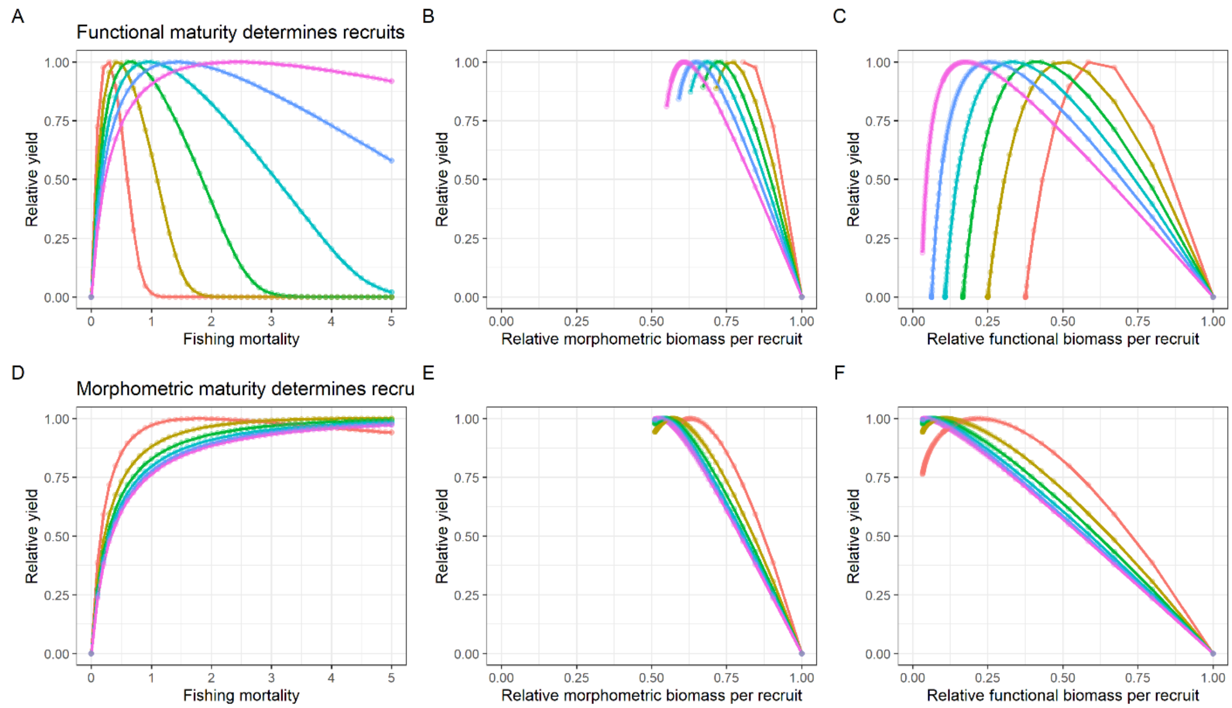

Figure 5. Relative yield curves against fishing mortality (left), morphometric biomass per recruit (center), and functional biomass per recruit (right). The top row represents population dynamics in which functionally mature biomass (i.e. >95 mm) is used in the stock recruit relationship to determine recruitment; the bottom row uses morphometrically mature biomass. (fix title)

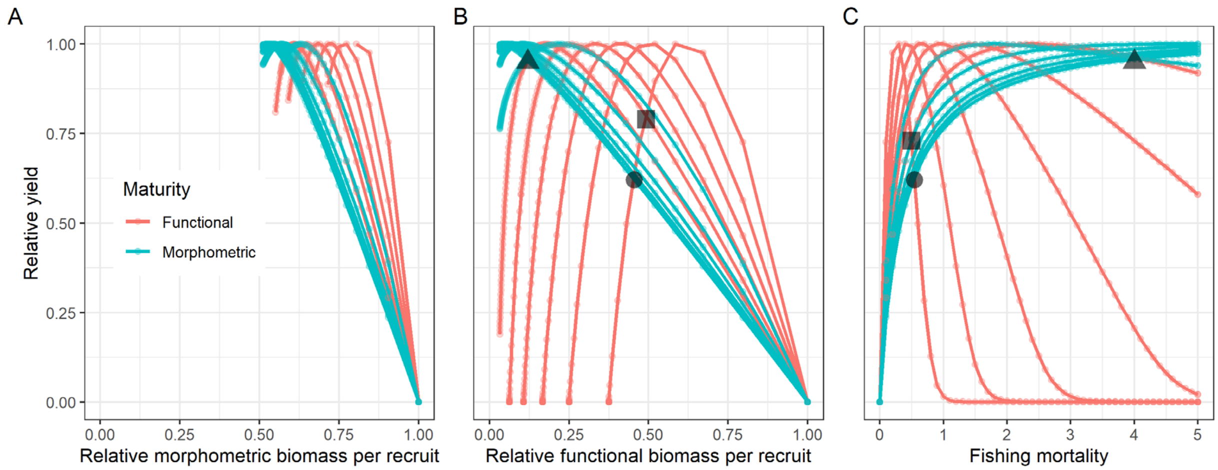

Figure 6. Relative equilibrium yield for scenarios in which recruitment is determined by morphometric biomass (blue) overlaid on scenarios in which recruitment is determined by functional biomass (red) for morphometric biomass per recruit (left), functional biomass per recruit (middle), and fishing mortality (right). Each line represents a different value for steepness (see figure 3 for reference). The triangles in panel B and C represent the maximin solution for the percentage of functional biomass per recruit over steepness space; the squares represent the maximin solution for the percentage of morphometric biomass per recruit. The circles represent the maximin solution over both uncertainty in steepness and the reproductively active portion of the biomass.

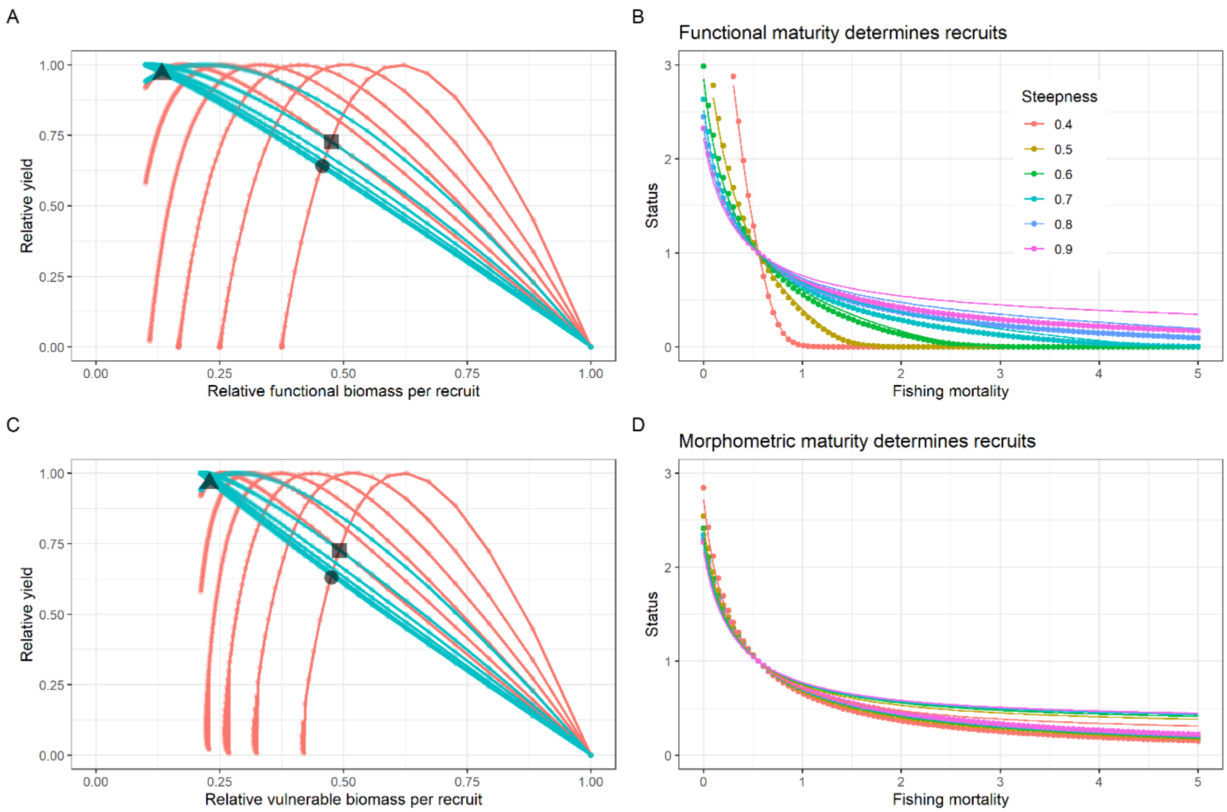

Figure 7. Per recruit reference points over multiple axes of uncertainty (red is functional biomass determines recruitment; blue is morphometric biomass determines recruitment) under different currencies of management (panel A is functional biomass per recruit; panel C is vulnerable biomass per recruit). Panels B and D show the status over steepness (color) and currency (lines are vulnerable biomass; points are functional biomass) for scenarios in which functional maturity determines recruitment (panel b) and morphometric maturity determines recruitment (panel d).