Effect of bitter crab disease on rebuilding in Alaska Tanner crab stocks

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Eastern Bering Sea (EBS) Tanner crab *Chionoecetes bairdi* stocks were declared overfished in 1996 and were closed to commercial fishing between 1997 and 2004. Subsequent management was based on a rebuilding plan using criteria from the previous US federal fisheries management plan (FMP). Under the revised 2008 FMP, reference points changed for mature biomass (male only vs. total), as well as catch levels (total vs. retained), resulting in different rebuilding criteria. We performed a rebuilding analysis using age-, sex-, and size-structured simulations incorporating recent changes in overfishing definitions. Specifically, we compared the potential effect of additional mortality that bitter crab disease could have on rebuilding performance of lightly infected EBS and heavily infected southeast Alaska Tanner crab stocks. The results suggest that under the assumed recruitment scenario, the new control rules are adequate to rebuild the depleted lightly infected EBS stock, but not the heavily infected southeast Alaska stock.

Keywords: age–sex–size-structured simulations, bitter crab disease, eastern Bering Sea, rebuilding, Tanner crab.

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Introduction

In response to the new statutory requirements under the Magnuson–Stevens Fishery Conservation and Management Act established by US Congress in 2006 (DiCosimo *et al.*, 2010), the Bering Sea and Aleutian Islands (BSAI) crab fishery management plan implemented in 2008 (NPFMC, 2007) defines an overfishing level (OFL; a catch that cannot be greater than the amount that would be taken if the stock were fished at F_{MSY} or its proxy) in terms of a fishing mortality (F_{OFL}), and uses this value as the new limit control rule (CR) for stocks that are not overfished. The F_{OFL} applies to the mature male biomass, MMB, and relates to the total catch removed rather than the fraction landed. The Tier system under the new CR follows the finfish system, but the number of Tiers (5 vs. 6) and Tier structure are different for shellfish and finfish [cf. Table 1 in DiCosimo *et al.*, 2010, and Equation (1)]. Although stock–recruitment (S–R) relationships for major BSAI crab stocks have been established, based on an effective spawning biomass (ESB) that considers female abundance and male-to-female mating ratio (Zheng and Kruse, 2003), their direct use is limited under the new CR, because stock productivity under the new CR is measured in terms of MMB not ESB. Simulations for three major BSAI crab stocks [Bristol Bay red king *Paralithodes camtschaticus* and Tanner *Chionoecetes bairdi* crabs, and eastern Bering Sea (EBS) snow crab *Chionoecetes opilio*] indicate $MMB_{35\%}$ (35% of the unfished level of MMB) and $F_{35\%}$ (the associated F) to serve as adequate proxies for MMB_{MSY} and F_{MSY}, respectively, the defaults for shellfish stocks with adequate information to estimate spawning biomass-per-recruit (Tier 3; no crab stocks have been designated as Tier 1 or 2). For stocks lacking spawning biomass-per-recruit, but for which reliable estimates of MMB and instantaneous natural mortality (M) are available (Tier 4), a constant multiplier (γ) of M should be used as a proxy for F_{MSY} and an average MMB for a selected period as proxy for MMB_{MSY}. For stocks with no biomass and mortality estimates (Tier 5), the average catch is recommended as the OFL (NPFMC, 2007).

The EBS Tanner crab stock was declared overfished from 1997 to 2004 and the direct fishery on this species was closed then because it represents a Tier 4 stock, the OFL is currently determined using the M CR with a default γ value of 1 (Rugolo and Turnock, 2009). We used both $F_{35\%}$ (Tier 3) and M (Tier 4) CRs in forward projections of age-, sex-, and size-structured populations, to investigate the rebuilding capability of the stock component located west of 166°W. This component appears to have a slightly higher prevalence of bitter crab disease (caused by a parasitic dinoflagellate of the genus *Hematodinium*) than its eastern counterpart. Pot-selectivity estimates for retained and discarded crab based on recent fishery and trawl-survey abundance data, as well as biological parameter values from the literature (Zheng and Kruse, 1999; NPFMC, 2007), provided inputs. Rebuilding success under stochastic simulations was evaluated through selected performance statistics (Siddeek and Zheng, 2007). We evaluated the rebuilding success with the new CR under scenarios of absence and presence of bitter crab disease in the lightly infected EBS (west of 166°W) stock. For comparison, we did the same analysis for a local stock of the heavily infected southeast Alaska

(Stephens Passage, SP, 58.2°N 134.5°W) Tanner crab stock (although the fishery on that stock is managed solely by the State of Alaska and does not come under any Tier system prescribed in the new CR, which is applicable only to the EBS crab stocks under joint federal and state management).

Tanner crab fisheries

The EBS Tanner crab fishery is a male-only pot fishery, with a minimum legal size limit. For management purposes, it has been divided into an eastern and western components, with longitude 166°W as the boundary. Comparison of allozyme frequencies between samples from the two areas (Merkouris *et al.*, 1998), different size-at-50% maturity (Somerton, 1981; Zheng, 2008), and recent changes in fishing practices (Rugolo and Turnock, 2009) support this division. Since the reopening of the fishery in 2005, the fishery has been prosecuted under an individual fishing quota programme, with total allowable catches (TACs) set separately for the two areas. The Tanner crab is a major bycatch in the snow crab fishery in the western part of EBS and is also a bycatch in the EBS groundfish trawl and pot fisheries (Rugolo and Turnock, 2009). The crab fisheries are conducted from 15 October to late March. We only deal with the western component here.

The Tanner crab fishery in SP in southeast Alaska is also a male-only pot fishery with a minimum size limit. This is one of many small Tanner crab pot fisheries off southeast Alaska. This fishery is managed under a different management CR from that for EBS stocks. However, here we applied the EBS CR as standardization for purposes of comparison only.

Material and methods

Control rules

The following CR has been defined for stocks (Tiers 3 and 4) lacking reliable estimates of F_{MSY} and $\mathrm{MMB}_{\mathrm{MSY}}$. Proxies for F_{MSY} and $\mathrm{MMB}_{\mathrm{MSY}}$ are identified by subscripts:

$$\begin{aligned} &\text{if } \mathrm{MMB}/\mathrm{MMB}_{\mathrm{MSY}} > 1, && F_{\mathrm{OFL}} = F_{\mathrm{MSY}} \\ &\text{if } \beta < \mathrm{MMB}/\mathrm{MMB}_{\mathrm{MSY}} \le 1, && F_{\mathrm{OFL}} = F_{\mathrm{MSY}} \times (\mathrm{MMB}/\mathrm{MMB}_{\mathrm{MSY}} - \alpha)/(1-\alpha) \\ &\text{if } \mathrm{MMB}/\mathrm{MMB}_{\mathrm{MSY}} \le \beta, && F_{\mathrm{OFL}} = 0, \end{aligned} \tag{1}$$

where β ($0 \le \beta < 1$; default value $= 0.25$) determines the minimum biomass threshold for opening the fishery and α ($0 \le \alpha < \beta$; default 0.1) determines the slope of the ascending part of the CR (NPFMC, 2007).

For Tier 4 CR simulations for EBS Tanner crab, we assumed (following Rugolo and Turnock, 2009) that the average MMB value for 1969–1980 ($\mathrm{MMB}_{69/80}$) from trawl-survey estimates represents a suitable value of $\mathrm{MMB}_{\mathrm{MSY}}$, whereas M was taken as F_{MSY} (i.e. $F_{\mathrm{MSY}} = \gamma \cdot M$ and the default value of $\gamma = 1$) in Equation (1). We also made Tier 3 CR iterations for EBS and SP Tanner crabs, using $F_{35\%}$ as a suitable value for F_{MSY} and the corresponding $\mathrm{MMB}_{35\%}$ for $\mathrm{MMB}_{\mathrm{MSY}}$ in Equation (1).

The target CR, used for determining the TAC that will be below the limit, is similar to Equation (1), but with F_{MSY} replaced by $F_{\mathrm{target}} = 0.75 \times F_{\mathrm{MSY}}$. Performance statistics were calculated for both limit and target CRs.

Simulation models

The age-, sex-, and size-structured population model (Siddeek and Zheng, 2007) used in the rebuilding analysis included individuals in the 20–170 mm carapace width (CW) range for EBS (west of 166°W) and the 60–170 mm CW range for SP for both sexes. The size range for the EBS extended to the smallest size in the trawl catches, to account for the greater prevalence of bitter crab disease encountered among smaller crabs, whereas data for SP run only from 60 mm CW on, the smallest size sampled in the pot fishery. We assumed a constant M of 0.23 for males and 0.29 for females, based on longevity estimates of non-infected crabs and 1% survival at the assumed maximum ages of 20 and 16 years, respectively (NPFMC, 2007). An instantaneous disease mortality rate of 0.05 and 0.02 for sizes <70 mm CW and ≥70 mm CW, respectively, for the EBS, and of 0.68 for all sizes for SP, was added in simulation scenarios with bitter crab disease included. These values were derived from the 1989–2008 time-series of the fraction (x) of bitter crab disease positives (detected by blood smear examination and conventional polymerase chain reaction) converted into instantaneous rates by $-\ln(1-x)$.

The population dynamics model used moult probability, growth increment probability, recruitment distribution probability, maturation probability, length–weight relationship, and selectivity in targeted (retaining vs. discarding) and bycatch (discarding only) fisheries to derive biomasses and yields from a given number of recruits. Immature crabs moult once every year (moult probability = 1), whereas both sexes appear to have a terminal moult upon reaching maturity (moult probability = 0; Tamone *et al.*, 2007; Zheng, 2008). The growth increment, ΔCW, was determined by a linear function of pre-moult size, $\Delta \mathrm{CW}_i = a + b\ \mathrm{CW}_i$ ($a = 15.75$, $b = 0.07$ for males; $a = 25.60$, $b = -0.13$ for females; Zheng and Kruse, 1999) and the growth increment probability was described by a gamma distribution ($\beta = 0.75$ for males, $\beta = 1.00$ for females; Zheng and Kruse, 1999; Siddeek and Zheng, 2007). The recruitment distribution probability to size classes was also described by a gamma function ($\alpha = 82.50$, $\beta = 1.02$ for males; $\alpha = 80.70$, $\beta = 0.96$ for females, Siddeek and Zheng, 2007; NPFMC, 2007). The maturation probability, P_i, for each sex was described by $P_i = 1/(1 + e^{-a(\mathrm{CW}_i - b)})$; $a = 0.12$, $b = 115.0$ for males, $a = 0.13$, $b = 78.25$ for females; NPFMC, 2007 and unpublished data). CW (mm) was converted to weight (W in g) by the relationship $W = a\ \mathrm{CW}^b$ ($a = 0.00019$; $b = 3.1$ for males; $a = 0.004$, $b = 2.56$ for females; NPFMC, 2007).

Because estimates for most biological parameters were lacking for SP, we used as a first approximation the EBS parameter values for this stock, except for the initial number of recruits, which were derived from a catch/survey analysis (Zheng *et al.*, 2006) that was recently updated (by courtesy of Q. Smith of the ADF&G-Douglas). The catch/survey analysis was similar to our full length-based analysis (Siddeek and Zheng, 2007), except that it modelled the male population, using broader size categories as three stages (prerecruit, recruit, and post-recruit) based on relative abundance indices from fishery-independent pot surveys and commercial catch records.

Selectivity (retaining vs. discarding) in the Tanner crab fishery and discard selectivity for Tanner crab in the EBS snow crab fishery were computed by sex, size, and shell condition for males, using 2005–2008 fisheries data and trawl-survey abundance estimates adjusted for trawl selectivity, i.e. absolute abundance (Somerton and Otto, 1999). We estimated selectivity by size, but did not try to fit a function (data are available from the first author). An average instantaneous discard mortality rate of 0.01 was estimated for Tanner crab in the snow crab fishery, based on observer data and absolute abundance estimates from trawl surveys for the years 2005–2008. Following Rugolo and Turnock (2009), a 50% handling mortality was applied to all pot fishery discards. Similarly, an average instantaneous mortality for groundfish discards, assuming a 50 and 80% handling mortality in fixed and trawl gear, respectively (NPFMC, 2007), was estimated as 0.002. For SP, non-directed bycatch selectivity was not considered.

The 2005–2009 trawl-survey estimates of absolute number of recruits were used to determine the maximum number of recruits (R_{max}) for the EBS. The catch/survey analysis of prerecruit absolute abundance, based on catch and pot survey data (2003–2008), was used to determine R_{max} for the SP for the projection models. The R_{max} estimates were 707 million and 0.27 million crabs for the EBS and SP, respectively. A stochastic Ricker (1954) S–R model was used to generate future numbers of recruits for the projection model:

$$R_t = \alpha \mathrm{MMB}_{t-k}\, e^{-\beta \mathrm{MMB}_{t-k}} e^{\varepsilon_t - \sigma^2 \varepsilon/2}, \qquad (2)$$

where

$$\varepsilon_t = \rho^* \varepsilon_{t-1} + \upsilon_t \quad \text{and} \quad \upsilon_t \sim N(0,1),$$

$$\alpha = \frac{(5h)^{1.25}}{\mathrm{MMB}_0/R_0},$$

$$\beta = \frac{\alpha\, e^{-1}}{R_{max}}, \qquad (3)$$

and ρ is the temporal correlation, ε_t the error term at time t, σ_e^2 the associated variance, k the time-lag between spawning and recruitment (4 and 6 years for EBS and SP, respectively), h the steepness parameter, and MMB_0/R_0 the virgin mature male biomass-per-recruit (i.e. MMB/R at $F=0$). α and β are as defined in Siddeek and Zhen (2007) and Mace (1994), respectively.

The 1997–2005 EBS data fitted to the model produced the following parameter estimates: $\alpha = 9.37$, $\sigma_e = 0.80$, $\rho = 0.69$, and $h = 1.95$. Assuming a similar productivity and error regarding recruitment, we adjusted the β parameter for the two areas based on the R_{max} estimates using Equation (3), thereby producing S–R curves with different maxima. We also created a rebuilding scenario with a lower productivity in terms of recruitment, by assuming a value 75% of h.

CR parameters

For CR parameter estimation (Table 1), average $\mathrm{MMB}/\mathrm{MMB}_0$ ratios at F (MMB_0 was determined at $F=0$) were calculated using stochastic simulations of a 100-year (long-term) fishery with the Ricker S–R model for the estimated h, 75% of estimated h, and $F_{35\%}$ for the two stocks (Table 1). $F_{35\%}$ was determined from 100-year deterministic simulations following Clark's method (Clark, 1991; Siddeek and Zheng, 2007), and thereafter the associated $\mathrm{MMB}_{35\%}$ was estimated. Alternatively, M and $\mathrm{MMB}_{69/80}$ were taken from Rugolo and Turnock (2009).

Performance statistics

Given hypothetically overfished simulated populations (50% × MMB_{MSY}; Siddeek and Zheng, 2007) and survey estimates of 2008 MMB, we initiated two separate sets of rebuilding scenarios from the two initial MMB levels (MMB_{ini}) for the EBS stock. For the SP stock, we considered only one rebuilding scenario from $\mathrm{MMB}_{ini} = 50\% \times \mathrm{MMB}_{MSY}$. The stock was considered rebuilt upon reaching the MMB_{MSY} level under a given limit and target F. The following performance statistics (Siddeek and Zheng, 2007) were computed from 1000 iterations of a 30-year fishery with random recruitment and biomass observation errors to evaluate rebuilding success: median and inter-quartile range of rebuilding time (RBT, the number of years for MMB to reach MMB_{MSY}), proportion of years when the stock was overfished (when $\mathrm{MMB} \le 50\% \times \mathrm{MMB}_{MSY}$), proportion of years when the fishery had to be closed (when $\mathrm{MMB} \le 25\% \times \mathrm{MMB}_{MSY}$), 30th year $\mathrm{MMB}/\mathrm{MMB}_{MSY}$ ratio, and mean short-term (year 1–10) and medium-term (year 11–20) yield. A no-fishery ($F=0$) scenario was used to compare performance statistics with those obtained when $F>0$.

In all simulations, lognormal observation errors ($\sigma_1 = 0.2$) were added to estimates of mature biomass for both males and females (i.e. their respective biomasses B were set to $B\, e^{z\,\sigma_1 - \sigma_1^2/2}$, where $z \sim \mathrm{N}(0,1)$). Implementation errors were assumed minimal, because of accurate catch accounting after the introduction of the individual quota system and the fishery achieving near-TAC catches in most years for the EBS stock (NPFMC, 2009). For simplicity, we ignored implementation errors for the SP stock.

Results

The rebuilding simulations considered small- to large-sized crabs for the EBS. Mortality resulting from bitter crab disease (assuming mortality occurs within a year for infected individuals) caused slight changes in all performance statistics for the EBS stock under limit $F_{35\%}$, M, and zero F (Figure 1). Changes in performance statistics for the SP stock under $F_{35\%}$ CR, depending on whether or not the disease was taken into account, were extremely high, because of its high prevalence in the exploitable segment of the stock (Figure 2). Hence, the application of the $F_{35\%}$ CR to a

Table 1. Estimates of CR parameters F_{MSY} (for two steepness parameters of the S–R relationship) and MMB_{MSY} (proxies of F_{MSY} and MMB_{MSY}, respectively), based on stochastic 100-year fishery simulations for EBS and SP Tanner crab stocks and trawl-survey estimates of the 2008 MMB at mating time (15 February) for EBS.

Parameter	EBS	EBS	EBS	SP
F_{MSY}	$F_{35\%} = 2.34$	$F_{35\%} = 2.34$	$M = 0.23$	$F_{35\%} = 2.27$
Steepness parameter (h)	0.98	0.74 (75% reduction)		1.52
MMB_{MSY} ('000 t)[a]	58.1	2.3	58.4	0.096
MMB_{OFL} ('000 t)	29.0	1.2	29.2	0.028
MMB threshold for fishery closure ('000 t)	14.5	0.6	14.6	0.014
MMB_{2008} estimate ('000 t)	21.6			

[a]Based on $\mathrm{MMB}_{35\%}$ for $F_{35\%}$ CR iterations and on $\mathrm{MMB}_{69/80}$ for M CR simulations.

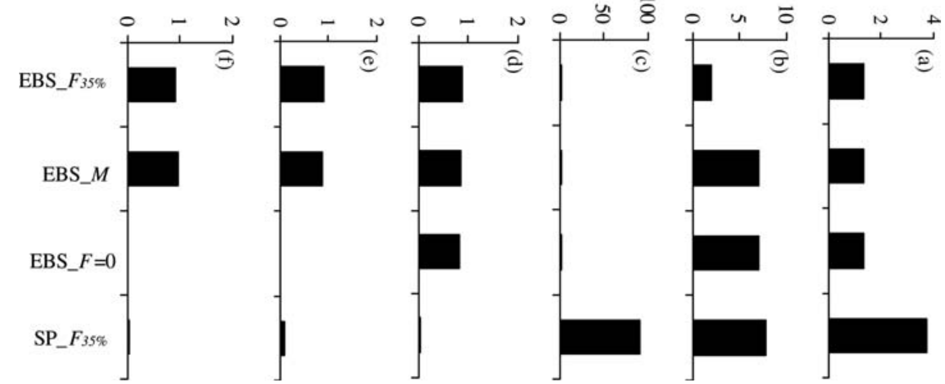

Figure 1. Performance statistics for rebuilding an overfished stock ($MMB_{ini} = 0.5 \times MMB_{35\%}$) infected with bitter crab disease relative to no-infection scenarios under limit $F_{35\%}$, M, and zero F for the EBS and under limit $F_{35\%}$ only for SP: (a) rebuilding time; (b) percentage of years overfished; (c) percentage of years closed for fishing; (d) MMB after 30 years relative to the value for the proxy of MSY (MMB/MMB_{MSY}); (e) short-term (years 1–10) mean yield; and (f) medium-term (years 11–20) mean yield.

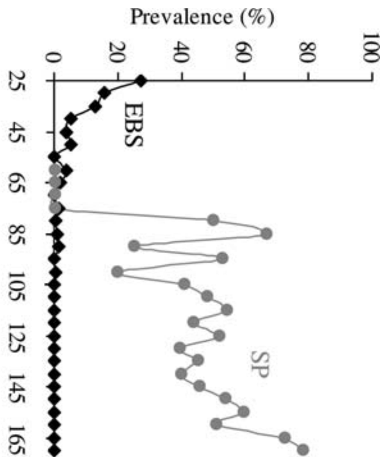

Figure 2. Average prevalence of bitter crab disease in Tanner crab by 5 mm class of CW in the EBS (black, average 1989–2008) and SP (grey, average 2003–2008).

Table 2. Performance statistics (based on 1000 runs) of rebuilding the 2008 male mature biomass (MMB) for EBS Tanner crab under target CRs (CR: 75% of $F_{35\%}$ or M; corresponding F-values given in parentheses) with the steepness parameter of the stock–recruitment relationship (h) as estimated or 75% of this value and for excluding or including bitter crab disease mortality.

Target CR	$0.75 \times F_{35\%}$ (1.76)	$0.75 \times F_{35\%}$ (1.76)	$0.75 \times F_{35\%}$ (1.76)	$0.75 \times F_{35\%}$ (1.76)	$0.75 \times M$ (0.17)	$0.75 \times M$ (0.17)
Multiplier of h	1	1	0.75	0.75	1	1
Bitter crab disease	−	+	−	+	−	+
Rebuilding time (years)	13 (8–19)	13	13 (0–23)	13	9 (6–13)	9
% years >OFL	23 (13–37)	23	43 (30–63)	43	17 (10–23)	17
% years fishery closed	0 (0–3)	0	3 (0–7)	3	0 (0–0)	0
MMB/MMB_{MSY} in year 30	1.26 (0.86–1.97)	1.26	0.70 (0.49–1.03)	0.71	4.48 (2.89–7.10)	4.31
Short-term yield ('000 t)[a]	1.6 (1.0–2.7)	1.5	1.2 (0.7–1.9)	1.1	0.3 (0.2–0.5)	0.3
Medium-term yield ('000 t)[b]	5.8 (4.1–7.9)	5.7	3.1 (2.0–4.5)	3.0	2.4 (1.6–3.4)	2.3

Values in parentheses represent inter-quartile ranges (not illustrated for runs with bitter crab disease included, because the pairwise differences were only minor).
[a]Mean years 1–10.
[b]Mean years 11–20.

heavily infected stock, such as that in the SP, appears not to be sustainable.

Rebuilding of the 2008 MMB for the EBS stock under target *F* (75% of $F_{35\%}$) CR was investigated for base and low (75% *h*) S–R productivity—and also under target *M* CR—without and with bitter crab disease (Table 2). Changes in most performance statistics were minor (and therefore the inter-quartiles for simulations with the disease are not illustrated), except for the mean short- and medium-term yields. Disease-induced mortality slightly reduced the mean yields. The reduction in *F* under low infection rate might have contributed to insignificant effects on most performance statistics. However, low S–R productivity reduced performance in most of the rebuilding statistics. Although several performance statistics under target *M* were better than those under target $F_{35\%}$, the short- and medium-term mean yields were low.

Discussion

The occurrence of the bitter crab parasite is widespread in Alaskan Tanner crab stocks (Meyers *et al*., 1987, 1990, 1996). Our simulation results indicate that under the assumed recruitment scenario, the $F_{35\%}$ CR is adequate for rebuilding the lightly infected EBS stock, which is currently approaching the overfished level (Rugolo and Turnock, 2009), within a period shorter than the maximum age of male crabs (20 years; NPFMC, 2007). However, the $F_{35\%}$ CR might not be appropriate for a stock with a different productivity and disease prevalence. This is clearly demonstrated for the SP stock, which we intentionally selected to explore the sustainability of the EBS CR on other Tanner crab stocks.

Available data suggest that small crabs are infected more frequently and might die more quickly than larger infected crabs. However, the assumed mean time to death of 1 year, applicable to an overall average estimate for all size classes of infected Tanner crabs, is based on information gathered from *Hematodinium* infections in *C. opilio* and *Callinectes sapidus* and this appeared to be the best estimate currently available (Stentiford and Shields, 2005). It is plausible that some crabs could become infected after the survey has been completed and die before they could be sampled by the survey in the subsequent year; hence resulting in underestimation of disease prevalence rates and their effects on mortality. Although studies of *Hematodinium*-infected crabs suggest to us that this is unlikely or rare, such an effect could be tested by estimating infection rates in different seasons.

We used the fisheries and trawl-survey data from the period when the individual quota programme had been implemented (2005–2008), to compute size, sex, and shell condition selectivities. The reasons for this choice were that (i) fishing practices have changed with the introduction of this system (e.g. longer soak time); and (ii) the snow crab fishery in areas west of 166°W longitude reported larger bycatches of Tanner crab in recent years. Using the same selectivity parameters, except for the bycatch in snow crab and groundfish trawl fisheries, in the rebuilding analysis of the SP stock could introduce uncertainty in the results. However, the negative impact of high prevalence of bitter crab disease on the rebuilding capability of this stock under $F_{35\%}$ CR should not be diminished by this uncertainty.

In following the current FMP guidelines (NPFMC, 2007) to choose the CR, we did not test whether other spawning biomass-per-recruit based ($F_{x\%}$ and $MMB_{x\%}$) CRs might perform better than $F_{35\%}$ or *M*. This could be a fruitful topic for future study.

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References

Clark, W. G. 1991. Groundfish exploitation rates based on life history parameters. Canadian Journal of Fisheries and Aquatic Sciences, 48: 734–750.

DiCosimo, J., Methot, R. D., and Ormseth, O. A. 2010. Use of annual catch limits to avoid stock depletion in the Bering Sea and Aleutian Islands management area (Northeast Pacific). ICES Journal of Marine Science, 67: 1861–1866.

Mace, P. M. 1994. Relationship between common biological reference points used as thresholds and targets of fisheries management strategies. Canadian Journal of Fisheries and Aquatic Sciences, 51: 110–122.

Merkouris, S. E., Seeb, L. S., and Murphy, M. C. 1998. Low levels of genetic diversity in highly exploited populations of Alaskan Tanner crabs, *Chionoecetes bairdi*, and Alaskan and Atlantic snow crabs, *C. opilio*. Fishery Bulletin US, 96: 525–537.

Meyers, T. R., Botelho, C., Koeneman, T. M., Short, S., and Imamura, K. 1990. Distribution of bitter crab dinoflagellate syndrome in southeast Alaskan Tanner crabs *Chionoecetes bairdi*. Diseases of Aquatic Organisms, 9: 37–43.

Meyers, T. R., Koeneman, T. M., Botelho, C., and Short, S. 1987. Bitter crab disease: a total dinoflagellate infection and marketing problem for Alaskan Tanner crabs *Chionoecetes bairdi*. Diseases of Aquatic Organisms, 3: 195–216.

Meyers, T. R., Morado, J. F., Sparks, A. K., Bishop, G. H., Pearson, T., Urban, D., and Jackson, D. 1996. Distribution of bitter crab syndrome in Tanner crabs (*Chionoecetes bairdi, C. opilio*) from the Gulf of Alaska and the Bering Sea. Diseases of Aquatic Organisms, 26: 221–227.

NPFMC. 2007. Initial Review Draft: Environmental Assessment for proposed Amendment 24 to the Fishery Management Plan for Bering Sea and Aleutian Islands King and Tanner Crabs to Revise Overfishing Definitions. North Pacific Fishery Management Council, Anchorage, AK, USA.

NPFMC. 2009. Stock assessment and fishery evaluation report for the King and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. 2009 Crab SAFE. North Pacific Fishery Management Council, Anchorage, AK, USA.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada, 11: 559–623.

Rugolo, L., and Turnock, B. 2009. 2009 stock assessment and fishery evaluation report for the Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. Stock assessment and fishery evaluation report for the King and Tanner crab fisheries of the Bering Sea and Aleutian Islands regions. 2009 Crab SAFE. North Pacific Fishery Management Council, Anchorage, AK, USA.

Siddeek, M. S. M., and Zheng, J. 2007. Evaluating the parameters of a MSY control rule for the Bristol Bay, Alaska, stock of red king crabs. ICES Journal of Marine Science, 64: 995–1005.

Somerton, D. A. 1981. Regional variation in the size of maturity of two species of Tanner crab (*Chionoecetes bairdi*, and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. Canadian Journal of Fisheries and Aquatic Sciences, 38: 163–174.

Somerton, D. A., and Otto, R. S. 1999. Net efficiency of a survey trawl for snow crab, *Chionoecetes opilio*, and Tanner crab, *C. bairdi*. Fishery Bulletin US, 97: 617–625.

Tamone, S. L., Taggart, S. J., Andrews, A. G., Mondragon, J., and Nielsen, J. K. 2007. The relationship between circulating ecdysteroids and chela allometry in male Tanner crabs: evidence for a terminal molt in the genus *Chionoecetes*. Journal of Crustacean Biology, 27: 635–642.

Stentiford, G. D., and Shields, J. D. 2005. A review of the parasitic dinoflagellates *Hematodinium* and *Hematodinium*-like infections in marine crustaceans. Diseases of Aquatic Organisms, 66: 47–70.

Zheng, J. 2008. Temporal changes in size at maturity and their implications for fisheries management for eastern Bering Sea Tanner crab. Journal of Northwest Atlantic Fisheries Science, 41: 137–149.

Zheng, J., and Kruse, G. H. 1999. Evaluation of harvest strategies for Tanner crab stocks that exhibit periodic recruitment. Journal of Shellfish Research, 18: 667–679.

Zheng, J., and Kruse, G. H. 2003. Stock–recruit relationships for three major Alaskan crab stocks. Fisheries Research, 65: 103–121.

Zheng, J., Rumble, J. M., and Bishop, G. H. 2006. Estimating southeast Alaska Tanner crab abundance using pot survey and commercial catch data. Alaska Fishery Research Bulletin, 12: 196–211.

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