**ARTICLE**

# When does hypoxia affect management performance of a fishery? A management strategy evaluation of Dungeness crab (*Metacarcinus magister*) fisheries in Hood Canal, Washington, USA

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**Abstract:** Management strategies for fisheries typically do not account for environmental stressors, such as hypoxia (dissolved oxygen < 2 mg·L$^{-1}$). Hypoxia can lead to shoaling of organisms into normoxic habitats, enhancing catchability, which could reduce the performance of fishery management strategies. Here, we conducted a management strategy evaluation of Dungeness crab (*Metacarcinus magister*) fisheries in Hood Canal, Washington, a seasonally hypoxic fjord in Puget Sound. Specifically, we asked whether the current management strategy was robust to hypoxia-induced catchability changes under alternative scenarios of illegal take, incidental capture mortality, and reproductive limitation. We find that the management strategy performed well to changes in catchability when illegal and incidental fishing mortality was low and fishing did not lead to reproductive limitation. However, the performance eroded markedly (reduced long-term catch and (or) population and higher catch variation) under the alternative scenarios. These findings underscore the benefit of applying an ecosystem approach to fisheries management because it identifies potential risks to management strategies in systems subject to environmental change.

**Résumé :** Les stratégies de gestion pour les pêches ne tiennent typiquement pas compte des facteurs de stress environnementaux, comme l'hypoxie (oxygène dissous < 2 mg·L$^{-1}$). Cette dernière peut mener au regroupement d'organismes dans des habitats normoxiques, accroissant leur capturabilité, ce qui peut réduire l'efficacité de stratégies de gestion des pêches. Nous avons réalisé une évaluation des stratégies de gestion des pêches au crabe dormeur (*Metacarcinus magister*) dans le canal Hood (État de Washington), un fjord du Puget Sound caractérisé par une hypoxie saisonnière. Nous nous sommes plus précisément demandé si la stratégie de gestion actuelle était robuste au vu des variations de la capturabilité induites par l'hypoxie dans différents scénarios de prises illégales, de mortalité par capture fortuite et de limitation de la reproduction. Nous constatons que la stratégie de gestion est bien adaptée aux variations de capturabilité quand la mortalité par pêche illégale et fortuite est faible et que la pêche ne mène pas à une limitation de la reproduction. L'efficacité de la stratégie s'érode toutefois de manière marquée (prises ou population réduites à long terme et variations accrues des prises) pour les différents autres scénarios. Ces constatations soulignent l'avantage d'employer une approche écosystémique de gestion des pêches parce qu'elle fait ressortir les risques potentiels pour les stratégies de gestion dans des systèmes assujettis à des changements environnementaux. [Traduit par la Rédaction]

## Introduction

A main challenge for marine resource management is ensuring sustainability in the face of rapid environmental change (Schindler and Hilborn 2015). The pace of change induced by anthropogenic activities (e.g., greenhouse gas emissions, land use, habitat loss) means that systems are being pushed to novel states, challenging our ability to sustain resource systems (Hoegh-Guldberg and Bruno 2010; McCauley et al. 2015). There is already substantial evidence of shifts in species distributions (Perry et al. 2005; Pinsky et al. 2013) and productivity (Blanchard et al. 2012; Britten et al. 2015), both of which likely affect vulnerability to fishing (Poloczanska et al. 2016). For systems and management to successfully mitigate this change requires the development of strategies that are robust to key environmental and harvest uncertainties (Schindler and Hilborn 2015).

Low dissolved oxygen (hypoxia) is a major stressor in coastal marine ecosystems (Diaz 2001). Hypoxic (dissolved oxygen (DO) < 2 mg·L$^{-1}$) events are increasing in frequency, magnitude, and extent in some of the most fished coastal and estuarine systems as a result

of anthropogenic influences (e.g., nutrient loading, climate change) (Diaz and Rosenberg 2008; Altieri and Gedan 2015; Long et al. 2016). Yet, like many environmental parameters, hypoxia is not typically integrated into management frameworks that regulate fisheries (Skagen et al. 2013; Koenigstein et al. 2016). Most understanding of hypoxia impacts on populations has revolved around mortality or secondary, sublethal reduction in growth and (or) reproduction (Rose et al. 2009), with less exploration into interactions with fishing. Low-oxygen conditions can cause mortality events, sometimes leading to immediate, and potentially persistent, declines and even collapse (e.g., cockle and lobster fisheries) of harvested stocks — particularly sessile organisms (Breitburg 1992; Diaz and Rosenberg 1995; Diaz 2001; Rabalais et al. 2002). These events are not the norm, however, because hypoxia more commonly induces an avoidance behavioral response (Pihl et al. 1991; Diaz and Rosenberg 1995; Petersen and Pihl 1995; Eby et al. 2005). Importantly, many organisms often aggregate at the margins of hypoxia (Taylor and Eggleston 2000; Long and Seitz 2008; Craig 2012). Yet, there is little understanding of how fishing and hypoxia might interact to impact a harvested

species beyond the most extreme conditions (Eby et al. 2005; Breitburg et al. 2009).

Hypoxia-induced distributional shifts of harvested species can induce changes in the catchability of fisheries, as fishers may target and (or) increase effort in nonhypoxic areas where motile organisms congregate away from the most severe reaches of hypoxia (Selberg et al. 2001; Craig and Crowder 2005; Breitburg et al. 2009; Craig 2012; Craig and Bosman 2013). Consequently, the behavioral response to hypoxia can indirectly enhance vulnerability to fishing if hypoxia-related aggregations are easily located by fishers (Selberg et al. 2001; Craig and Crowder 2005; Craig 2012; Kraus et al. 2015). Catchability can be affected by fleet response and (or) by shifting distribution of organisms either into or out of areas that are accessible to fisheries. However, there has been limited research into the possible consequences of hypoxia-induced aggregation and fishing pressures (Kraus et al. 2015) and will be the focus of this study.

Here, we evaluate the relative importance of hypoxia in the performance of management strategies used to regulate a Dungeness crab (*Metacarcinus magister*) fishery. Dungeness crab is one of the most important and heavily exploited recreational and commercial species along the west coast of North America (Pauley et al. 1986; Armstrong et al. 2003, 2010). In any one season, upwards of 90% of legal-sized males may be harvested, primarily in trap fisheries (Gotshall 1978; Smith and Jamieson 1991; Armstrong et al. 2010). It is assumed that the combination of Dungeness crab life-history traits — including high fecundity, low maximum age, early maturity and recruitment to the fishery, and high natural mortality — can sustain high levels of harvest (Kruse 1993). Recreational fishing for Dungeness is open-access, while there are entry limits for commercial practices. Notably, all Dungeness crab fisheries are regulated by the 3-S (sex, size, and season) management strategy. Harvestable crabs must be male, have a carapace width greater than or equal to a specific width (154–165 mm, approximately age 4) to help promote at least one successful mating event (mature around age 2), and harvest is closed during the peak of the spring moulting period (Armstrong et al. 2003).

The 3-S restrictions are intended to protect reproductively vulnerable population components, but they may not succeed if the fishery regulations are not followed, particularly if hypoxia changes catchability. One facet is the degree of compliance with the management restrictions (i.e., illegal fishing) (Agnew et al. 2009), which could reduce remaining mature, sublegal male and female numbers. Similarly, another important factor is whether incidentally captured, nonretained individuals (i.e., discards) that are either too small or the wrong sex survive the capture process (Davis 2002). Finally, consideration is required of whether the population can be maintained above levels where reproduction becomes impaired even if the fished segment of the population (e.g., targeted sex and size) is sharply depleted (Sato and Goshima 2006; Kendall and Quinn 2013). The influence of these fishing-related pressures that can and do occur beyond legal harvest thus may be exacerbated under variable environmental conditions; yet, such cumulative impacts are rarely investigated.

To assess potential vulnerabilities of the Dungeness crab 3-S management strategy to hypoxia, we focused our efforts on the Dungeness crab fisheries in Hood Canal, Washington, a 110 km seasonally hypoxic fjord in Puget Sound, where there is growing concern by fishers and managers over the stability of the crab population (Sonntag 2010). In 2013, over half a million pounds of Dungeness crab were harvested in Hood Canal alone (Washington Department of Fish and Wildlife (WDFW), unpublished data). However, Hood Canal landings have been more variable than those in nearby regions, with substantial declines between 2007 and 2010 and a recovery thereafter (WDFW, unpublished data). Although hypoxia has been reported in Hood Canal since the 1950s, oxygen conditions appear to be deteriorating due to a combination of anthropogenic influences, including climate change

and nutrient loading (Newton et al. 1995; Fagergren et al. 2004). Previous work has shown that Dungeness crab shoal into shallower waters during hypoxia intrusion, increasing their overlap to areas where fishing effort is most intense (Froehlich et al. 2014). Such increased overlap could thus result in potential overfishing of shoaling crabs due to increased vulnerability to capture (i.e., catchability) (Kraus et al. 2015).

We conducted a model-based management strategy evaluation (MSE) exercise to examine the performance of the 3-S management system in the face of hypoxia-induced catchability increases, under alternative scenarios of illegal crabbing, incidental mortality of nonharvest crabs, and reproductive limitation arising from skewed-sex ratio. Our intent is not to identify the best policy, but rather to address the environmental and management uncertainty by revealing the conditions under which the current management system is robust to hypoxia and those where management might fail (Punt et al. 2014).

## Methods

### Fishery description

Recreational and tribal fishing are the primary forms of Dungeness crab harvest in Hood Canal, with the latter encompassing commercial, ceremonial, and subsistence practices. Crab fishing is allocated between the state (commercial and recreational) and Native American tribes, with the latter guaranteed 50% of the total allowable catch under treaty rights. Crabbing is permitted to occur during the summer and winter, with catch limits and total summer catch dictating the length of the winter crabbing season. In 2010, a Washington State audit listed the open-access recreational fishery — particularly illegal crabbing — and hypoxia as major risk factors to the sustainability of Dungeness crab populations (Sonntag 2010). There is also concern over the ever-increasing number of recreational crab fishers and what that uncapped future of fishing effort could mean for the resilience of crab stocks in light of the other potential stressors. Yet, there has been no formal attempt to model such concerns.

### Co-managers' objectives and interests

While developing an operating model was a key element of this study, establishing the primary management concerns was the first critical step in effectively creating and testing a meaningful model. Several in-person and remote meetings with Washington State and tribal co-managers were organized to reveal key interests and considerations regarding harvest strategy for testing. The input from the co-managers gave a clearer conceptual understanding of the model content and assumptions.

### Model parameterization and sensitivity

We constructed a model of Dungeness crab population and fishery dynamics to describe possible effects of hypoxia and harvest on Dungeness crab in Hood Canal and the performance of the management system under different assumptions about the fishery and population biology. We developed a deterministic, age-structured operating model and compared steady-state characteristics with and without hypoxia, in concert with other potential demographic impacts. Finally, we evaluated the management performance under a stochastic system. Figure 1 illustrates the conceptual framework of the model.

The model had fixed parameters and those that varied to represent different scenarios. Fixed parameters were those that described natural mortality, fecundity, maturation, and base recruitment (e.g., eggs per recruit). Parameters that we varied for the MSE included the primary parameters of interest, including catchability, probability of illegal retention, incidental mortality, and the effective reproducing population as well as time-varying recruitment and harvest. In both cases, initial values and ranges were determined from information provided in the primary literature, personal correspondence with co-managers, and any existing data (Table 1).

**Fig. 1.** Conceptual framework of the deterministic, age-structured operating model of male (♂) and female (♀) Dungeness crab. Composed of 10 age classes ($N_{s,a,t}$), each yearly age progression has some level of natural mortality, until senescence occurs for the age 10+ proportion of the population. In addition to natural mortality, age classes that can experience fishing mortality (legal, illegal, and incidental) in the model are depicted for males and females. Relative to fishing effort, catchability of both sexes ($q_{s,a,t}$) is dictated by minimum hypoxic depth, where hypoxia expansion (as sampled from the Hood Canal Dissolved Oxygen Program DO profiles) above 30 m linearly increases weekly $q$ (dotted-line box); minimum hypoxic depth below 30 m catchability is held constant. Reproduction corresponds to the possible restriction of mature, older males only able to copulate with younger (assumed smaller), mature females (i.e., the effective reproductive ratio). Egg production ($g_t$) is the summation of the product of mature females in the population, fecundity, and, if induced, the effective reproductive ratio.
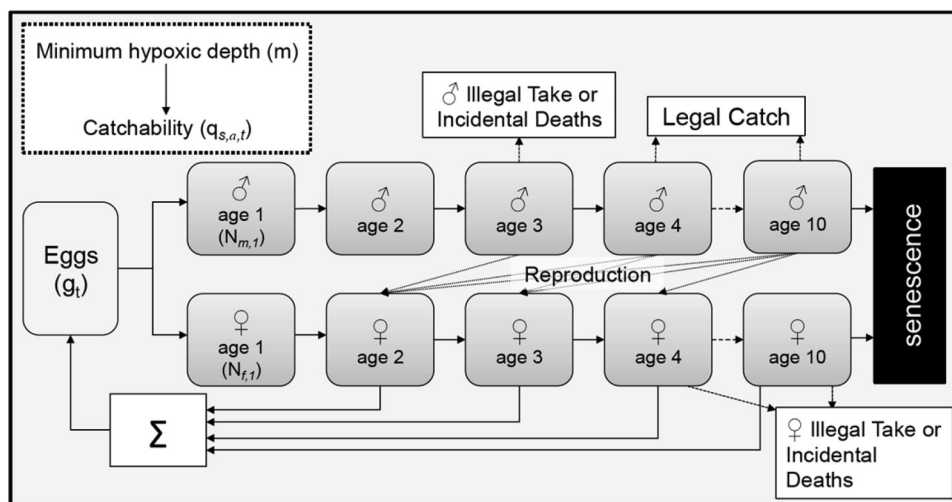


**Table 1.** List of model parameters, range of values, and associated literature or personal correspondence sources.

| Parameter | Value | Source |
|---|---|---|
| $M_a$ = mortality at age $a$ | Age 1–2 (juveniles) = 0.8·year⁻¹<br>Age ≥3 (adults) = 0.3·year⁻¹ | Hankin et al. 1997; Zhang et al. 2004 |
| $\mathcal{F}_a$ = fecundity at age $a$ | Age 1 = 0<br>Age 2 = 1 million<br>Age 3–5 = 2 million<br>Age ≥6 = 1 million | Botsford and Wickham 1978; Higgins et al. 1997; Rasmuson 2013; Toft et al. 2013 |
| $\partial_a$ = proportion of age $a$ mature females | Age 1 = 0<br>Age 2 = 0.2<br>Age ≥3 = 1 | No direct estimates of proportions mature; Butler 1960; Wainwright and Armstrong 1993; Jensen and Asplen 1998; Armstrong et al. 2003 |
| $\Phi_{a,t}$ = effective reproductive ratio | 0–1 | Butler 1960, 1961; Smith and Jamieson 1991; Hankin et al. 1997; expert correspondence |
| $\eta$ = half-saturation constant for "effective reproductive ratio" | 0.1 | |
| $h$ = steepness | 0.5–0.8 | No exact reported measures; Zheng et al. 1995; Zheng and Kruse 2003; Armstrong et al. 2010 |
| EPR = eggs per recruit | 630 222 eggs | Calculated based on natural mortality, fecundity, and proportion mature at age |
| $R_o$ = unfished number of age 1 recruits | 7 000 000 crabs | Butler 1960, 1961; Wild and Tasto 1983; Wainwright and Armstrong 1993; Jensen and Asplen 1998; Armstrong et al. 2003 |
| $\Omega_{s,a,t}$ = probability of capture retention at age $a$ | Males<br>  Age 1–2 = 0<br>  Age 3 = 0–0.8<br>  Age ≥ 4 = 1<br>Females<br>  Age 1–3 = 0<br>  Age ≥ 4 = 0–0.8 | Co-managers' unpublished data and personal correspondence; scales with legal catch rate |
| $\delta_a$ = probability of incidental death at age $a$ | Age 1–2 = 0<br>Age 3–10 = 0–0.8 | Tegelberg 1970; Reilly 1983; Murphy and Kruse 1995; Yochum et al. 2017; correspondence with co-managers |
| $q$ = constant catchability in the absence of hypoxia | 0.00035 | Toft et al. 2013; co-managers' unpublished data and personal correspondence |
| $q_{max}$ = maximum catchability when hypoxic depth is 0 m | 0.005 | Toft et al. 2013; co-managers' unpublished data and personal correspondence |
| $k$ = catchability slope constant | 0.00015 | |
| $E_{rec}$ = state recreational effort | Low = 3000 pots·week⁻¹<br>High = 16 000 pots·week⁻¹ | Co-managers' unpublished data and personal correspondence |
| $E_{com}$ = tribal commercial effort | 4000 pots·week⁻¹ | Co-managers' unpublished data |

**Fig. 2.** (*a*) 2010 mean weekly minimum hypoxic depth (MHD), or the shallowest DO depth < 2 mg·L⁻¹, from the Hood Canal Dissolved Oxygen Program DO profile (ORCA buoy Station 46124: http://orca.ocean.washington.edu/) and (*b*) catchabilities (*q*) calculated from the MHD (see eq. 5). The depicted 2010 levels were used for the equilibrium analysis, while a total of eight similar profiles were randomly sampled for stochastic modelling (not shown). Over the entire 20 weeks of a crabbing season, "summer" crabbing occurs over the first 10 weeks, while "winter" crabbing can occur in the latter half of the season. The broken line depicts the 30 m MHD threshold, below which catchability is held constant (as shown in Fig. 2*b*).
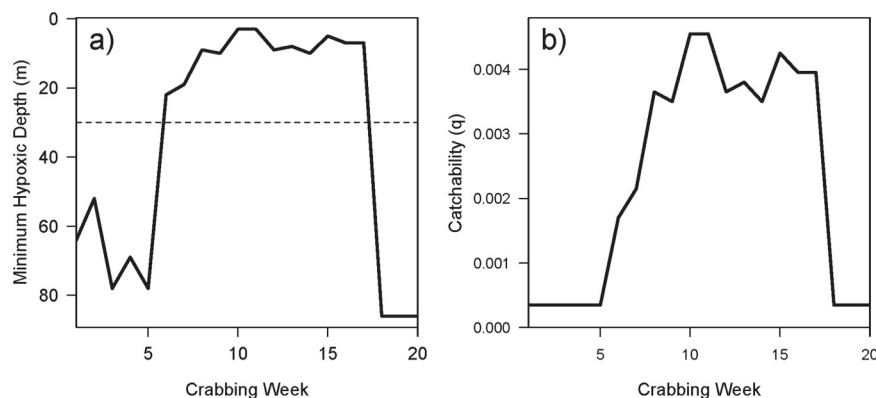
The only crab data available were WDFW legal catch records (1996–2013), nonstandardized survey data (catch per unit effort), and limited tribal patrol records of offenders and illegal possession (composition and number of crabs). Due to the quality and sparse nature of available data, no parameter was formally estimated from these data, but instead, we used these data to ensure that assumed parameter values gave model predictions that were broadly consistent.

We tested the sensitivity of the model to two key assumptions of the biology and harvest: population resilience and fishing effort. First, recruitment to age 1 was assumed to follow a Beverton–Holt stock–recruit relationship where maximum reproductive rate is controlled by steepness (*h*), which indicates the ratio of recrtuitment when spawners are at 20% of unfished to recruitment when spawners are unfished (Lee et al. 2012). Thus, varying the steepness parameter (low versus high) assessed the sensitivity of the deterministic model to population resiliency. Second, the sensitivity of the stochastic model to fishing effort was evaluated by increasing the number of recreational pots per week to levels presumed possible by co-managers. While other static demographic parameters can most certainly influence the response of the population — as amply reported in fisheries literature — our intent was to explore the importance of other, typically overlook and unmeasured factors relative to several standing (but realistically motivated) assumptions.

**Deterministic model overview**

The Dungeness crab population and harvest in Hood Canal were modelled using an age-structured model. Similar modelling approaches have been implemented for Dungeness crab previously (Botsford and Wickham 1978; Higgins et al. 1997; Toft et al. 2013; Zhang and Dunham 2013). The crab population abundance (males and females) and catch were modelled at a weekly time-step with an age structure containing 10 discrete year classes (Pauley et al. 1986; Armstrong et al. 2010):

$$(1) \qquad N_{s,a+1,t+1} = N_{s,a,t}e^{-(M_{s,a}+F_{s,r,a}+F_{s,i,a})}$$

$$(2) \qquad C_t = \frac{M_{m,a,t}F_{m,r,a}}{M_{m,a} + F_{m,r,a} + F_{m,i,a}}(1 - e^{-(M_{m,a}+F_{m,r,a}+F_{m,i,a})})$$

where $N_{s,a,t}$, the number of male (*s* = *m*) or female (*s* = *f*) crabs at age *a* and time *t*, $M_{s,a}$, $F_{s,r,a}$, and $F_{s,i,a}$ are the instantaneous rates of natural mortality, retained fishing mortality, and incidental fish-

ing mortality, respectively, and $C_t$ is the legal catch during week *t*. By separating the fishing mortalities, we were able to explore the population consequences of crabbing and accidental deaths due to capture. Legal catch ($C_t$) each week was calculated based on the Baranov catch equation. Illegal catch was calculated in the same manner. Crabbing was assumed to happen prior to recruitment so that our model year began in June and ended in May of the following calendar year.

The crab fishing mortality was based on age, sex, and other parameters that describe incidental mortality and illegal take so that there was sex- and age-specific mortality from retention ($F_{s,r,a}$) and incidental mortality ($F_{s,i,a}$):

$$(3) \qquad F_{s,r,a} = u_{s,a}\Omega_{s,a}$$

$$(4) \qquad F_{s,i,a} = u_{s,a}(1 - \Omega_{s,a})\delta_a$$

where $u_{s,a}$ represents the probability of a particular sex (*s*) being captured at age *a* at time *t*, $\Omega_{s,a}$ is the probability of a male or female being retained, and $\delta_a$ is the probability of incidental death for crabs that are not retained. The $u_{s,a}$ parameter was calculated as the product of total weekly crabbing effort (tribal and recreational number of pots) and catchability of either sex.

We considered two scenarios for how catchability varies seasonally. First, we considered constant catchability ($q_{s,a}$) — a typical assumption of most fisheries' models — representing no hypoxia effects. Second, we incorporated hypoxia intrusion as a threshold-linear change in catchability ($q_{s,a,t}$). The threshold model assumes no effect of hypoxia on catchability (i.e., constant catchability) unless DO at depths of 0–30 m drops below 2 mg·L⁻¹ — the typical referenced DO level for hypoxia (Diaz 2001) and concentration that appears to induce shoaling in Dungeness crab (Froehlich et al. 2014). When the minimum DO occurs in this portion of the water column — the depth range of most crab pots in Hood Canal (Froehlich et al. 2014) — then catchabilty becomes a linear function of the shallowest depth of hypoxia:

$$(5) \qquad q_{s,a,t} = q_{\max} - kD_t$$

where $D_t$ is minimum hypoxic depth in week *t* and *k* describes the effect size of hypoxic depth (Fig. 2). Thus, the resulting weekly catchabilities directly relate to the minimum hypoxic depth weekly data values.

To generate hypoxia scenarios, we used eight mean weekly (20 weeks) hypoxic (DO < 2 mg·L$^{-1}$) depth profiles spanning 2006–2013 from the Hoodsport, Washington, buoy (Station 46124; Hood Canal Dissolved Oxygen Program) as possible alternative seasonal hypoxia conditions. Over any given simulated fishing period, a DO profile was selected systematically or randomly for the equilibrium and stochastic model runs, respectively.

We also accounted for effects of sexual dimorphism and crab pot escape-rings (diameter = 108 mm) by assigning a catchability of zero to males younger than 3 years and females younger than 4 years. Catchability for all other age classes was assumed to be equal (Table 1).

The probability of retention ($\Omega_{s,a,t}$) after being captured could also be held constant or treated as a function of weekly catch rate of legal males (i.e., functional retention):

(6) $\qquad \Omega_{s,a,t} = \Omega_{max}e^{-c\left(\frac{C_t}{E_t}\right)}$

with a maximum probability of capture retention ($\Omega_{max}$), and a log-linear decline with increasing legal catch rate, with slope $c$; thus, as availability of legal crabs declines, the probability of illegal crabbing increases. This relationship was introduced based on feedback we received from shellfish co-managers indicating that illegal take was likely inversely related to availability of legal-sized males. While the probability of retention for legal males ($a \geq 4$) was assumed 1, the above relationship was applied to sublegal catchable males ($a = 3$). Although females appear to be rarely retained (WDFW, unpublished data), we also explored the illegal retention of older females ($a \geq 4$). Lastly, the incidental mortality parameter ($\delta_a$) was held constant and only applied to catchable ages of both sexes. Increases in $\delta_a$ encompass higher levels of incidental mortality from soft-shell captures, extended air exposure, prolonged soak times, and (or) multiple capture events (Barry 1981; Reilly 1983; Kruse et al. 1994; Van Tamelen 2005; Yochum and Sampson 2015).

Regarding population-level maturation, we presumed that 20% of the estuarine crabs mature at age 2 and all individuals mature by age 3 (Butler 1960, 1961; Tasto 1983; Wainwright and Armstrong 1993; Jensen and Asplen 1998; Armstrong et al. 2003). Additionally, younger ($a < 3$) and older ($a > 5$) female crabs were assumed to exhibit reduced egg production (Botsford and Wickham 1978; Hankin et al. 1997). Older individuals experience reduced fecundity and have been omitted from other Dungeness crab models (Botsford and Wickham 1978; Higgins et al. 1997; Toft et al. 2013), but we included older crabs to explore a more complete representation of illegal crab fishing — particularly on older females.

Males and females were modelled separately and it was assumed that only males of age $a + 1$ or greater could successfully mate with age $a$ females (Butler 1960; Smith and Jamieson 1991; Hankin et al. 1997). Crabs mate in a female post-moult embrace that some suggest require the male to be larger than the soft-shell female (Butler 1960; Smith and Jamieson 1991; Hankin et al. 1997), which we simplify by using age as a proxy for size. This parameterization allowed us to adjust the dependence of fertilized egg production ($g_t$) on male density through a single parameter, the effective reproductive ratio ($\Phi_{a,t}$):

(7) $\qquad g_t = \sum_{i=a}^{n} N_{f,a,t}\mathcal{F}_a\partial_a\Phi_{a,t}$

(8) $\qquad \Phi_{a,t} = \dfrac{\rho}{\eta + \rho}$

(9) $\qquad \rho = \dfrac{\sum N_{m,a+1,t}}{N_{f,a,t}}$

where $N_{f,a,t}$ is the number of age $a$ females at time $t$, $\mathcal{F}_a$ is the fecundity of females at age $a$, and $\partial_a$ is the proportion of mature females at age $a$. The effective reproductive ratio is an asymptotic relationship that takes values between 0 and 1. The relationship depends on $\rho$, the ratio of all age $a + i$ males to age $a$ females at time $t$, and a half-saturation constant ($\eta$). However, inclusion of $\Phi_{a,t}$ reduced the reproductive contribution of older females, making the population effects more similar to models with fewer age classes.

## Equilibrium model scenarios

We first used the deterministic model to explore the expected equilibrium catch versus fishing effort under base-case management when there is no illegal catch, no incidental mortality, and no male limitation to reproduction. We used this as a basis to compare the equilibrium catch versus effort under the different model scenarios, with and without hypoxia-driven seasonal changes in catchability. Seasonal crabbing effort (number of pots) was modelled to occur over a 20 week period, over the "summer" and "winter" seasons. As is the case in Hood Canal, recreational crabbing in the model was allowed to occur through the season(s), while commercial crabbing was restricted to 5 weeks per season. We used a single hypoxia intrusion scenario (2010) for all equilibrium comparisons (Fig. 2a). Equilibrium values were determined by running the model for 50 years and using the end point. Sensitivity tests were conducted using high ($h = 0.8$) and low ($h = 0.5$) steepness levels.

## Stochastic model scenarios

Harvest control and stochasticity (recruitment and hypoxia) were added to the model to explore the performance of the harvest strategy under dynamic conditions. We modelled the total annual catch limit as the 3 year running average of catches to match the procedure used to set limits in Puget Sound. Additionally, the management system always allows summer fishing but prevents winter season crabbing if the catch limit is met or surpassed during summer. Again, seasonal commercial tribal and state recreational crabbing was modelled to occur over a 20 week period. Recruit stochasticity was incorporated by assuming log-normal recruitment variability. We assumed log-scaled standard deviation ($\sigma = 0.7$) based on reports of similar stock–recruit crustacean parameter estimates (Zheng et al. 1995). Catchability variation was induced by randomly selecting one of eight possible annual hypoxia intrusions for each year for every model run (500 runs per scenario).

We compared the expected catch time-series projections over 50 years under the base-case management when there is no illegal crabbing, incidental mortality, or reproduction limitation. Using baseline (low) crabbing effort (maximum = 7000 pots·week$^{-1}$) determined by the co-managers, we compared the effects of incorporating each individual stressor into the model, with and without hypoxia-driven seasonal changes in catchability. We separately explored the results over a range of illegal harvest and incidental mortality parameter values (0–0.8), while inclusion of the effective reproductive ratio was a function of mature male abundance and thus could only be explored in a binary fashion (on or off). Sensitivity of the model to the same stressors was also explored at high effort (20 000 pots·week$^{-1}$).

Four metrics were used to compare management performance. We specifically assessed changes in the level of population variability ($CV_N$), catch variability ($CV_C$), the frequency of sharp interannual catch declines of more than 70 000 crabs from the previous year ($\Delta C_t > 70k$), and absolute minimum catch. Currently, there are no formal, estimated metrics used to monitor the Puget Sound Dungeness crab fishery, so these metrics were developed based on the actual catch data patterns and input from co-managers. As an additional measure to confer and bound our model to comparable realistic outputs, the simulated catch CV and absolute minimum

**Fig. 3.** 50 year equilibrium catch (number of legal male crabs) versus effort (number of pots per week) relationships under the (*a*) base-case scenario when no additional pressures are considered ($\Omega$, $\delta$, or $\Phi = 0$), (*b*) constant illegal retention of sublegal males ($\Omega_{constant} = 0.8$), (*c*) functional illegal retention of sublegal males ($\Omega_{function} = 0.8$), (*d*) incidental morality of sublegal males ($\delta_{male} = 0.8$), (*e*) incidental morality of females ($\delta_{female} = 0.8$), or (*f*) an effective reproductive ratio ($\Phi = 1$). Each panel depicts catch versus effort with (black) and without (gray) minimum hypoxic depth changing catchability of the crabbing season (20 weeks). Crabbing effort goes from low (0 pots·week$^{-1}$) to high (20 000 pots·week$^{-1}$). Although only the extreme levels are depicted, values of the probability of additional mortality ranging from 0 to 0.8 were explored. Similarly, multiple steepness (*h*) values were evaluated, but only the high compensation level (0.8) results are depicted. See supporting information for sensitivity to low steepness.
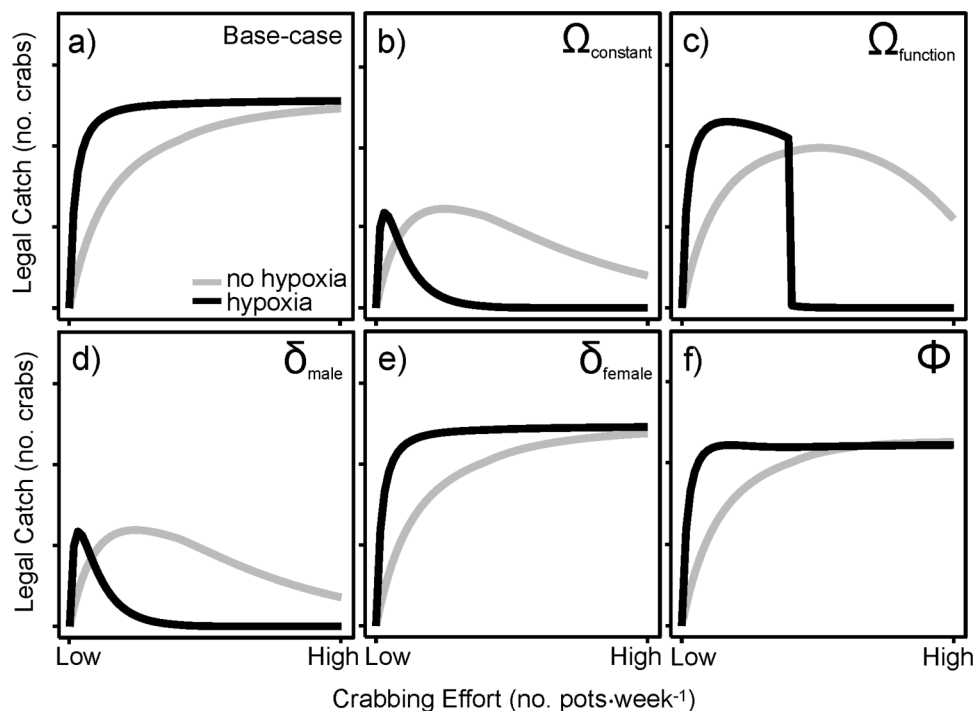


catch values were compared with the actual metrics from the Hood Canal catch data. Again, sensitivity was assessed under high effort (20 000 pots·week$^{-1}$).

## Results

### Equilibrium catch versus effort relationships

We first explore the equilibrium catch versus effort relationship to reveal the broad sensitivities of the fishery to hypoxia under scenarios of incidental capture mortality, illegal retention, and impaired reproduction. In particular, we identify the contexts under which overfishing — a decline in catch with increasing effort — is possible and the extent of decline in catches that result. Under the base-case model that lacks any of these features, catch is an asymptotic function of effort (i.e., depletion of large males alone cannot lead to overfishing). If we include hypoxia-induced increases in catchability (2010 hypoxia profile) (Fig. 2), then the effect is only to shift the relationship to the left — the expected response to higher catchability (Fig. 3*a*).

All scenarios with sublegal take and incidental mortality reduce the population to levels where catch is also reduced (Figs. 3*b*–3*f*). Incorporation of a functional (instead of constant) response for illegal catch — driven by legal catch rate — buffered the effect of illegal retention at lower effort levels, but still results in a decline of catch at higher effort (Figs. 3*b* and 3*c*). Hypoxia magnified these effects, such that overfishing began at lower effort levels, and fishing could drive the legal catch towards zero. Incorporation of incidental mortality (without illegal retention) of sublegal males had near identical catch patterns as constant illegal crabbing with

and without hypoxia (Fig. 3*d*). Notably, the addition of female illegal take (Fig. S1[1]) or incidental mortality (Fig. 3*e*) produced smaller effects on maximum yield. Similar patterns were observed when steepness was lower (*h* = 0.5), although in that scenario, the joint effect of hypoxia and illegal female take was somewhat larger (Figs. S1 and S2*e*).

The model was generally insensitive to whether reproduction could be limited by male abundance (Fig. 3*f*). In other words, the biological assumption that females require older, larger males for successful reproduction did diminish equilibrium catch levels at equivalent crabbing effort, but did not result in a downward trend of yield. However, we found stronger effects of male limitation under the low population steepness scenario (*h* = 0.5) (Fig. S2*f*).

### Stochastic modeling and harvest strategy evaluation

Hypoxia amplified the sensitivity of the harvest strategy to illegal and incidental mortality. Mean crab abundance and catch declined with increasing illegal retention probability (Figs. 4*a* and 4*d*), but these effects were greater in the presence of hypoxia. Hypoxia had even greater effects in governing the sensitivity of abundance and catch to incidental mortality (Figs. 4*b* and 4*e*). The system was also more sensitive under higher levels of effort (20 000 pots·week$^{-1}$), with greater reductions in average population and catch under equivalent probabilities of illegal and incidental mortality (Fig. S3).

Hypoxia governed the consequences of reproductive impairment through male limitation. Population density was reduced sharply with the inclusion of an effective reproductive ratio in the presence of hypoxia, but was only modestly reduced in the ab-

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**Fig. 4.** 50 year mean simulated Dungeness crab (a–c) population abundance and (d–f) legal (male) catch given the probability of illegal female and sublegal male retention ($\Omega_{s,a,t}$) (Figs. 4a and 4d), incidental mortality ($\delta_a$) (Figs. 4b and 4e), and an effective reproductive ratio ($\Phi_{a,t}$) (Figs. 4c and 4f). Values are depicted for four harvest and hypoxia scenarios of low effort (7000 pots·week$^{-1}$), with (black) and without (gray) hypoxia. All results are based on 500 simulation runs ($h = 0.8$, $\sigma = 0.7$). See supporting information for sensitivity to high effort (20 000 pots·week$^{-1}$).
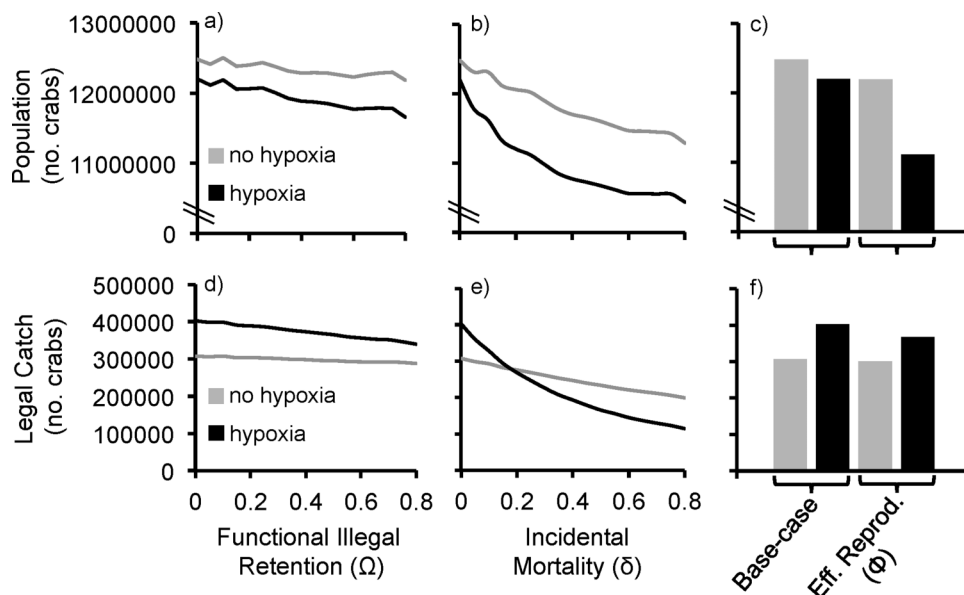


sence of hypoxia (Fig. 4c). However, male limitation did not result in catch reductions — instead, catch was enhanced with the inclusion of an effective reproductive ratio, and this enhancement was not affected by hypoxia (Fig. 4e). Under the same scenarios with higher effort, management was more sensitive — particularly to hypoxia — with greater average reductions in population numbers, while mean catch levels only increased (without hypoxia) or remained relatively unchanged (with hypoxia) (Figs. S3c and S3f).

Evaluation of the four performance metrics revealed stronger hypoxia effects on catch than on the population. In fact, for all scenarios, hypoxia had little effect on population variability (Fig. 5a). In contrast, hypoxia caused greater variability in catch, likely due to interannual variation in catchability (Fig. 5b). The probability of greater catch extremes (>70 000) was also larger for all hypoxia scenarios. Noticeably, the hypoxia $\Delta C_t > 70\,000$ scenarios became more similar, but the probability of extremes under hypoxia scenarios was still higher (Fig. 5c). The lowest legal minimum catch values also occurred under every hypoxia scenario (Fig. 5d). Overall, the fishery was more susceptible to undesirable catch outcomes in the presence of hypoxia-induced catchability variation, particularly when there was illegal take and incidental mortality. The directly comparable actual catch-to-model output metrics (catch CV and absolute minimum catch) were also similar — particularly the simulations with hypoxia (Figs. 5b and 5d). Again, high effort levels resulted in similar but amplified patterns, with hypoxia effects on catchability causing the largest variation with the lowest catch returns (Fig. S4).

Overall, we saw hypoxia cause more variable legal catch (high CV and lower catch minimums) for two very different reasons. With hypoxia and sublegal male retention, the population does not decline or vary as greatly (Figs. 4 and 5) because smaller females ($a < 4$) and males ($a < 3$) are not illegally captured ($q = 0$; escape rings and fisher preference), and thus, the population is supported by the younger age classes. However, catch declines markedly because the age distribution is skewed right towards the younger, smaller ages, resulting in too few legal-male crabs, catch limits systematically declining over time, and causing illegal retention to intensify because of the functional response of the fishers (Figs. 4 and 5). For incidental mortality, the opposite occurs. Older females ($a > 2$) make up the majority of the popula-

tion, while the younger males and females expire — ultimately providing no opportunity for the male population to replenish and thus legal catch declines (Figs. 4 and 5).

## Discussion

Although direct mortality caused by environmental stressors is important in marine ecosystems, our MSE of Hood Canal Dungeness crab identifies the possible indirect risk that hypoxia poses to the management system and the benefits that people receive from the fishery. We found the 3-S management strategy most sensitive to the influence of hypoxia only when other sources of fishing pressure are considered. Expressly, illegal crab retention and (or) incidental mortalities from crabbing could reduce long-term catch levels and population abundance and increase variability, outcomes magnified by time-varying hypoxia dynamics. Accounting for an effective reproductive ratio limiting the contribution of older females dramatically impacted the total population, but not the legal catch, making the population more sensitive to other factors (e.g., reduced population resilience). While our study is a specific exploration of the possible Dungeness crab population and harvest repercussions from hypoxia, a simulation approach such as this can be applied to numerous fisheries to highlight areas of concern, determine gaps in understanding and data — in terms of both ecology and management — and explore uncertainties around fishing and environmental perturbations.

We found that accounting for hypoxia increases the sensitivity of management to other pressures, such as illegal retention of nonpermitted catch and incidental catch mortality. In general, illegal fishing is a major concern regarding the overexploitation of harvested species and sustainability of fisheries (Agnew et al. 2009; Pauly and Zeller 2016). However, the interaction of illegal take relative to environmental change is not typically considered or well understood. For many fish and crab fisheries, the pervasiveness of illegal retention is unclear — particularly for recreational or small-scale fisheries (Cox et al. 2002; Cooke and Cowx 2004, 2006; Purcell and Pomeroy 2015). Similar to illegal retention, hypoxia magnified the effects of incidental capture mortality, reducing yield and population abundance and increasing variability. Incidental mortality, also referred to as discard or bycatch mortality,

**Fig. 5.** Dungeness crab metric results, including (*a*) population coefficient of variation (CV), (*b*) catch CV, (*c*) probability of catch declines greater than 70 000 crabs·year⁻¹ ($P(\Delta C_t) > 70\,000$), and (*d*) absolute minimum catch ($|C_{min,t}|$). Metrics are depicted with (black) and without (gray) hypoxia (i.e., nonconstant catchability). Assuming low effort (7000 pots·week⁻¹) results are depicted for the base-case (no additional pressures outside of legal crabbing), addition of functional illegal retention ($\Omega_{s,a,t}$), and incidental mortality ($\delta_a$), an effective reproductive ratio ($\Phi_{a,t}$). Values selected for the additional mortality parameters reasonably reflect catch percent outcomes provided by co-managers and primary literature when assuming that low effort is the current fishery state. When applicable, horizontal broken lines show the metrics calculated from actual catch records. All results are based on 500 simulation runs ($h = 0.8$, $\sigma = 0.7$). See supporting information for sensitivity to high effort (20 000 pots·week⁻¹).
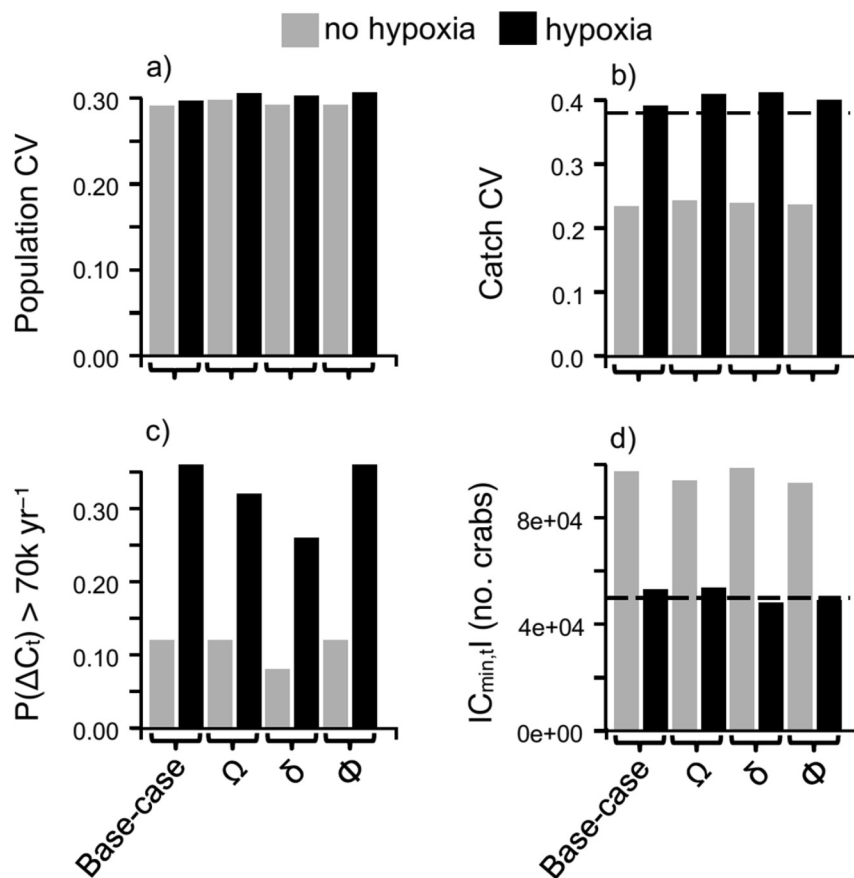


generally encompasses any mortality — immediate or delayed — due to harvest practices (Murphy and Kruse 1995; Davis 2002; Barber and Cobb 2007, 2009; Yochum et al. 2017). The contributions of various forms of incidental death are typically unknown and likely differ between recreational and commercial practices (Cooke and Cowx 2006; Yochum et al. 2017) as well as the extent and severity of the environmental stressor. When robust data and assessments are lacking, which is the case for the majority of stocks (Geromont and Butterworth 2015), and fishing areas are prone to increased environmental perturbation(s), like hypoxia, managers may want to consider a more precautionary approach to management, such as reducing catch limits and (or) removing open-access to the fishery.

Inclusion of biologically meaningful reproductive attributes of a population also has important implications for the sustainability of fisheries when other threats to the fishery are considered. Alone, the incorporation of an effective reproductive ratio in our model did not greatly impact catch, but did reduce the total population abundance. As a result, the reproductive restriction exacerbated the influence of weaker recruitment events, additional sources of mortality, and hypoxia. Such information is important for sex-selective fisheries (e.g., snow crab, red king crab), especially those without formal population estimates, like Dungeness crab (Armstrong et al. 2010; Rasmuson 2013).

Our model results provide at least one possible explanation for the observed high levels of catch variability in Hood Canal that caused concern among fishers and managers (Sonntag 2010). We found that hypoxia influencing catchability can create greater extremes in catch from year to year, similar to variability reported in the actual catch records. However, other aspects of the population and fishery could also contribute to such variability, including unique pulse recruitment events and (or) variable crabbing effort unrelated to hypoxia (Armstrong et al. 2010; Rasmuson 2013). Although our simplified operating model may not represent the absolute "true" system-state, the MSE, even in the absence of long-term data, is an effective approach to deal with uncertainty and aid in identifying vulnerabilities of a fishery to various stressors. This is particularly important when considering the array of environment stressors expected to increase due to climate change (Roessig et al. 2005; Brander 2010; Hollowed et al. 2013; Koenigstein et al. 2016).

Our findings may extend to other environmental conditions that change the overlap between population and fishery distributions. Temperature-induced shifts are documented for numerous species (Perry et al. 2005; Roessig et al. 2005; Cheung et al. 2016), the most similar to hypoxia, in terms of spatiotemporal response, resulting from ENSO events (Jordan 1991). Other stressors, such as salinity, may also be applicable in a behavioral context, particu-

larly in dynamic coastal and estuarine systems that experience high levels of freshwater input (e.g., Chesapeake Bay) (Buchheister et al. 2013). Overall, using behavioral movement data to explore increases in catchability and the interactive effects of other demographic impacts is something that certainly could be explored further for other fisheries (Allen and Singh 2016).

We made assumptions regarding parameter values and model structure to explore the relationship of hypoxia and Dungeness crab harvest in Hood Canal. One key parameter that dictates the relative influence of the other parameters in the model is catchability, $q_{s,a,t.}$ We selected a range for $q$ that corresponded to catch levels reported in the primary literature and management reports (Table 1). However, a more precise and robust estimate requires direct, formal investigation. In addition, we assumed that natural mortality, which encompasses predation, did not vary with hypoxia. Our model also lacked a spatial context. Indeed, the northern region of Hood Canal is less susceptible to severe hypoxia intrusion and could reduce the impact of the indirect hypoxia effects investigated in this simulation study (Froehlich et al. 2014, 2015). In addition, we assumed that the Hood Canal Dungeness crab population is closed. While adult crabs appear to exhibit restricted movement (Froehlich et al. 2014) and the population may rely on self-recruitment (Dinnel et al. 1993), genetic information is needed to determine the extent of population connectivity. We also did not account for any other sublethal hypoxia-related impacts on growth or reproduction due, in part, to Dungeness crab species' apparent tolerance to low DO and active foraging behavior in hypoxic conditions (Bernatis et al. 2007). Aspects such as these could be explored in more detail, but the intent of this study was to demonstrate overall harvest patterns and identify key gaps in the understanding of a data-limited fishery.

Critical to the development of the operating model and scenarios of interest was the collaboration with Washington State and tribal co-managers. Indeed, cooperative and statistically robust approaches that utilize expert opinion and ecological knowledge are becoming more common in fisheries management (Dambacher et al. 2015; Edwards and Dankel 2016). In the present example, managers' expertise was essential in the identification and parameterization of model components that helped us to explore multiple aspects of the fishery relative to hypoxia influence, including illegal crab fishing, incidental mortality, and limitation affecting reproduction. While adding other sources of mortality and reducing the reproductive input reduced catch, increased variability, and made the population more susceptible to overfishing — as is the case for many fisheries — including the hypoxia-induced changes in catchability exacerbated these negative consequences. Thus, nonlethal impacts of environmental forcing may make the population more sensitive to an expanding recreational fishery and other perturbations. While the 3-S management strategy appears effective presently, models such as ours highlight the uncertainty and heightened threats to harvested organisms under stressed environmental conditions.

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