



## RESEARCH ARTICLE

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## Seasonality and Life History Complexity Determine Vulnerability of Dungeness Crab to Multiple Climate Stressors

## Key Points:

- Dungeness crab vulnerability to future hypoxia is most severe overall due to increased exposure of the critical adult stage during upwelling
- The severity of vulnerability depends on the underlying spatiotemporal dynamics of ocean conditions and the crab's complex life cycle
- Our stage-based and season-sensitive approach is adaptable for many marine species with complex life histories that inhabit seasonal seas

## Supporting Information:

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

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**Abstract** Scaling climate change impacts from individual responses to population-level vulnerability is a pressing challenge for scientists and society. We assessed vulnerability of the most valuable fished species in the Northwest U.S.—Dungeness crab—to climate stressors using a novel combination of ocean, population, and larval transport models with stage-specific consequences of ocean acidification, hypoxia, and warming. Integration across pelagic and benthic life stages revealed increased population-level vulnerability to each stressor by 2100 under RCP 8.5. Under future conditions, chronic vulnerability to low pH emerged year-round for all life stages, whereas vulnerability to low oxygen continued to be acute, developing seasonally and impacting adults, which are critical to population growth. Our results demonstrate how ontogenetic habitat shifts and seasonal ocean conditions interactively impact population-level vulnerability. Because most valuable U.S. fisheries rely on species with complex life cycles in seasonal seas, chronic and acute perspectives are necessary to assess population-level vulnerability to climate change.

**Plain Language Summary** The release of carbon dioxide (CO<sub>2</sub>) into the atmosphere by human activities is altering ocean conditions including pH, oxygen, and temperature. One way to understand how these changing conditions will affect ecologically, economically, and culturally important marine species is to scale individual responses from laboratory experiments to population-level impacts. In this study, we assessed the vulnerability of Dungeness crab, one of the most valuable fisheries in the NW USA, to stressful conditions based on the predicted habitat exposure and response of each life stage (eggs, larvae, juveniles, and adults). The degree of vulnerability was determined by the seasonality of the ocean conditions in combination with the crab's complex life cycle. This approach revealed that Dungeness crab life stages and populations will be more vulnerable to low pH, low oxygen, and high temperature in the future (year 2100) under an aggressive CO<sub>2</sub> emissions scenario. Based on these results, we recommend that fishery managers incorporate changing conditions into their decision-making to protect vulnerable life stages in areas prone to stressful conditions (e.g., adult crabs in hypoxic areas). Our approach can be adapted for many other economically and ecologically important marine species in order to inform conservation and management strategies.

## 1. Introduction

The ocean's physical, chemical, and biological processes are undergoing measurable and predictable changes due to human activities. Anthropogenic emission of carbon dioxide into the atmosphere is the major driver of global ocean acidification (OA), deoxygenation, and warming (Gruber, 2011). These climate driven environmental changes are considered stressors because they (and their interactions) pose increasing threats to marine ecosystems (Gattuso et al., 2018) and serve as additional challenges for sustainable fisheries management (Hobday et al., 2018). To help inform management in a changing climate, especially for data-poor species (Pacifi et al., 2015), qualitative and semi-quantitative methods have been developed

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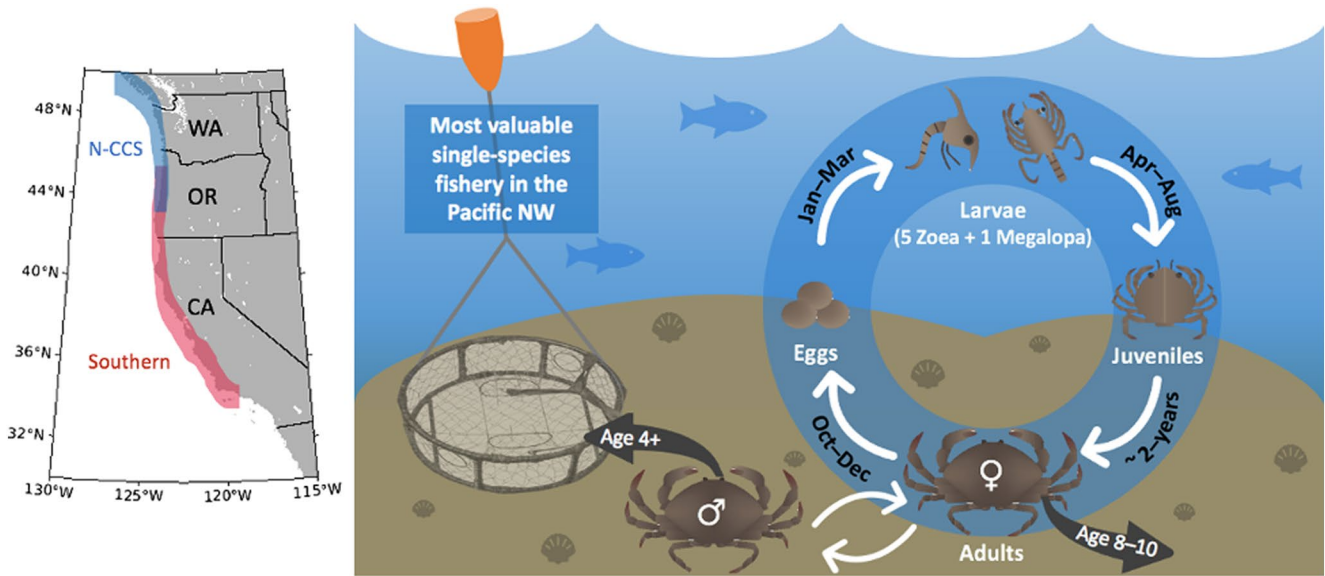
to assess the vulnerability of systems and species to stressful conditions (Hodgson et al., 2016; Stortini et al., 2015). In this context, vulnerability is defined as “the degree to which a system is susceptible to, or unable to cope with, adverse effects” (McCarthy et al., 2001) and is often characterized or ranked according to factors of consequence (or sensitivity), exposure, and adaptive capacity (Adger, 2006).

Vulnerability assessment is a powerful tool for predicting the response of ecologically and economically important species to environmental stressors before significant impacts occur, by integrating quantitative and qualitative information (Adger, 2006; Hare et al., 2016; Spencer et al., 2019). These assessments can help guide management through the identification of disproportionately vulnerable life stages, stressor hotspots, and refuge areas that should be monitored for population conservation (Hare et al., 2016). While results from vulnerability assessments cannot prescribe specific management actions, they can be used to improve the rationality, effectiveness, and efficiency of decision-making (Halpern et al., 2009), especially when used alongside other techniques to support Ecosystem-Based Management and climate change adaptation strategies (Hare et al., 2016; Stortini et al., 2015). Species-specific vulnerability assessments can also be used to help design multi-stressor experiments through the identification of key life stages and stressor targets (Hare et al., 2016). Although risk and vulnerability assessments have been criticized for only producing relative rankings that lack spatial granularity and are difficult to validate (Allyn et al., 2020), recent work has improved the quantitative, spatial, and uncertainty aspects of these methods (Hodgson et al., 2016; Stortini et al., 2015).

Recent population-level vulnerability assessments (Hodgson et al., 2016; Stortini et al., 2015) have also highlighted the importance of evaluating stressor consequence and exposure for individual life stages before generating a weighted sum of vulnerability for the population. Marine organisms often have complex life cycles that involve drastic morphological changes and occupancy of diverse habitats. Each life stage may, therefore, experience stage-specific exposure to a given stressor and/or display a unique response (consequence; Hodgson et al., 2016). Larval stages are often reportedly more susceptible to environmental stressors than adults (i.e., a higher consequence from exposure; J. J. Miller et al., 2016; Waldbusser et al., 2015). Yet, the relative brevity and high baseline mortality of these life stages (Rasmuson, 2013) may lessen their relative contribution to overall population vulnerability once adult longevity and fecundity are factored into models of population growth. Thus, estimation of population-level vulnerability needs to account for both stage-specific vulnerability and the relative contribution of each stage to population growth (Hodgson et al., 2016).

Dungeness crab (*Metacarcinus magister*) inhabit the California Current System (CCS) from Vancouver Island, British Columbia, to Santa Barbara, California (Rasmuson, 2013), and are an economically and culturally important species for this region, with fishery landings valued up to \$250 million per year (PSMFC, 2019). While there is no formal stock assessment for the fishery, it is currently considered to be sustainably managed because the harvest is restricted to seasonal catches of male crabs over a certain size (3-S management: season, sex, size) and yields have not decreased over time (Richerson et al., 2020). Interannual variability in yields has been linked to the abundance of the final larval stage (megalopae) 4 years prior (Shanks & Roegner, 2007; Shanks et al., 2010; Shanks, 2013). The abundance and distribution of megalopae is influenced by ocean conditions (Norton et al., 2020), including temperature (Sulkin et al., 1996; Wild, 1980), salinity (Brown & Terwilliger, 1999), carbonate chemistry (Bedaršek et al., 2020; Descoteaux, 2014; J.J. Miller et al., 2016), and food availability (Casper, 2013; Sulkin et al., 1998). Furthermore, megalopae abundance has been correlated with large-scale oceanographic features, such as the phase of the Pacific Decadal Oscillation (Shanks, 2013) and the timing of the spring transition (Shanks & Roegner, 2007), which marks the onset of seasonal upwelling. Thus, the stability of the Dungeness fishery may be compromised by changing ocean conditions, and management may need to consider these conditions in future decision-making.

Previous work using ocean projections for the year 2050 (under the previous IPCC A2 emissions scenario) found that Dungeness crab in Oregon through central California (referred to hereafter as the southern population; Figure 1) had a moderately low vulnerability to low pH (Hodgson et al., 2016). Here, we expand that previous semi-quantitative, life stage-specific framework (Hodgson et al., 2016) to assess the vulnerability of Dungeness crab to changing ocean conditions along the outer coasts of Vancouver Island, Washington, and Oregon (referred to hereafter as the N-CCS; Figure 1), specifically to low pH, low dissolved oxygen



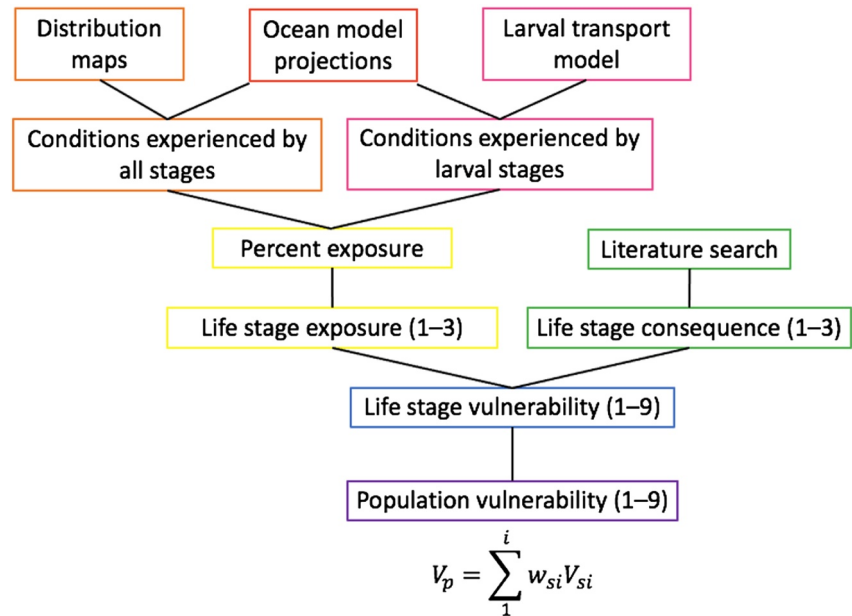
**Figure 1.** Left: A map showing the geographical ranges of the N-California Current System population examined in this study and the “southern” population examined in Hodgson et al. (2016). Right: The Dungeness crab life cycle with life history timings for the outer coasts of Washington and Oregon (Rasmuson, 2013). Adult males ( $\delta$ ) and females ( $\text{♀}$ ) mate between March and June. Adult females extrude  $\sim 2$  million eggs each between October and December and carry them within their abdomen until hatching between January and March. The larvae hatch as zoeae, which are transported offshore and undergo five molts before metamorphosing into megalopae. The megalopae are transported back onto the shelf and then settle and metamorphose into juveniles between April and August. Juveniles reach sexual maturity after  $\sim 2$  years, and the cycle begins again. Adult females have an average life span of 8–10 years, whereas adult males reach legal catch size around 4 years old and are captured by state and tribal-managed commercial and recreational fisheries.

(DO), and high temperature using updated ocean projections (IPCC RCP 8.5 emissions scenario for year 2100). We further expand this framework by using physical transport models to estimate exposure for pelagic larvae in addition to the previously used distribution maps.

As an eastern boundary upwelling system, the N-CCS experiences wide seasonal fluctuations in ocean conditions and is a hotspot for climate change stressors (Feely et al., 2018; Gruber, 2011; Reum et al., 2016). Spring and summer upwelling brings cold, nutrient-rich water onto the shelf that is low in DO, high in carbon dioxide ( $\text{pCO}_2$ ), and low in pH (Feely et al., 2018). Upwelling stimulates phytoplankton blooms (Hickey & Banas, 2008) and subsequently leads to the development of hypoxia (Hales et al., 2006) and associated low pH waters (Feely et al., 2018; Siedlecki et al., 2015, 2016). While the region already experiences effects from hypoxia and OA during the upwelling season, conditions are projected to worsen under climate change (Feely et al., 2018; Siedlecki et al., 2021). Conversely, the fall and winter downwelling season is characterized by shoreward advection of relatively warm, nutrient-depleted oceanic water that is relatively higher in DO, lower in  $\text{pCO}_2$ , and higher in pH (Reum et al., 2016).

Due to the seasonally dynamic ocean conditions in this region (Sutton et al., 2019) and the distinct phenology of Dungeness crab life stages (Figure 1), exposure to stressful conditions likely varies across life stages. Benthic life stages that are present year-round (juvenile and adult) are unable to avoid the low pH and low DO conditions associated with the upwelling season. Eggs carried by adult females during the downwelling season (Rasmuson, 2013) may escape low pH and DO conditions, while likely experiencing higher temperatures. Pelagic larvae disperse throughout the water column and experience a range of conditions, but megalopae are more likely to experience low pH and low DO than zoea because they return to the nearshore environment during the upwelling season to prepare for settlement (Rasmuson, 2013). Based on anticipated seasonal patterns (among other factors), we expect our estimates of exposure for life stages in the N-CCS to differ from those reported for the southern population (Hodgson et al., 2016), which experiences year-round upwelling (Jacox et al., 2018).

Here, we estimated life stage-specific vulnerabilities (consequence  $\times$  exposure) of Dungeness crab to present and future ocean conditions (pH, DO, and temperature) using regional projections for N-CCS waters



**Figure 2.** Schematic of vulnerability assessment methods (adapted from Hodgson et al., 2016). The numbers in parentheses represent the range of exposure, consequence, and vulnerability scores (low–high). Life stage vulnerability ( $V_{si}$ ) is the product of life stage exposure and consequence (Equation 1), while population vulnerability ( $V_p$ ) is the weighted mean of the life stage vulnerabilities, with weights ( $w$ ) derived from a population matrix model (Equation 2).

and a literature review (Figure 2). The literature review allowed us to identify stress thresholds and attribute consequence scores to each stressor and life stage combination. We then determined each life stage's seasonally and annually-averaged exposure to conditions exceeding stress thresholds as a percent of the time using two methods involving a regional model of ocean conditions in combination with: (a) spatiotemporal distribution maps and (b) larval transport models. These two methods to determine exposure allow quantification of the role that pelagic life stage exposure history to ocean conditions plays in vulnerability. The exposure percentages from both methods were linearly converted to an exposure score that could then be multiplied by the consequence score to estimate seasonal and annual life stage vulnerability. We calculated population vulnerabilities as the weighted mean of stage-specific vulnerabilities using weights from a population matrix model (Hodgson et al., 2016). Our assessment revealed increased vulnerability to all three stressors in the future and illustrated the importance of life stage and seasonality considerations. Based on our findings, the adult life stage is critical to Dungeness crab vulnerability. Although susceptible larval stages could act as a bottleneck to population growth, our transport models predicted low exposure of these stages to stressful conditions.

## 2. Methods

### 2.1. Life Stage Consequence

We estimated consequences to low pH, low oxygen, and high temperature for each Dungeness crab life stage (zoea, megalopa, juvenile 1, juvenile 2, adult) based on responses reported in the literature (Figure 2). Since younger juveniles may experience different responses to stressors than older juveniles, we broke the juvenile life stage into 1 and 2, representing the first and second year classes, respectively, as was also done by Hodgson et al. (2016). Here, the consequence is defined as the degree to which a life stage demonstrated negative responses to a stressor (Hodgson et al., 2016). Following Hodgson et al. (2016), we have used 'consequence' instead of the commonly used term 'sensitivity' because we are focusing on the negative impacts of the stressors and 'sensitivity' has numerous definitions. In our paper, 'sensitivity' is only used when describing how the results were influenced by our input assumptions.

We used Google Scholar to identify papers ( $n = 23$ ) that investigated the responses of Dungeness crab (or related species) life stages to low pH, low oxygen, or high temperature using laboratory experiments or field observations and citations therein. Preliminary search terms included Dungeness crab, *Metacarcinus magister*, or *Cancer magister* in combination with ocean acidification, pH, hypoxia, oxygen, warming, or temperature. Because studies used a range of experimental conditions and response measurements, the purpose of the literature review was to broadly categorize the effects of exposure. We scored consequence from low (1) to high (3), where a score of 1 indicated that exposure had no effects on development or survival, a score of 2 indicated sublethal effects, and a score of 3 indicated strongly adverse, lethal effects (Table S1). We updated consequence scores for low pH from a previous assessment for the southern Dungeness crab population (Hodgson et al., 2016) and assigned new scores for low DO and high temperature using the same methodology.

The literature review was also used to define stress thresholds for exposure estimates. Threshold values ( $\text{pH} < 7.65$ ;  $\text{DO} < 1.4 \text{ mL/L} = 2.0 \text{ mg/L} = 62.2 \mu\text{mol/kg}$ ;  $T > 15^\circ\text{C}$ ) were selected to represent conditions at which negative consequences are expected to occur for most life stages based on published stress exposure experiments (Table S2). Additionally, 7.65 pH was the mid-point threshold used in the southern population assessment (Hodgson et al., 2016), and 1.4 mL/L DO is the conventional hypoxic threshold (Vaquer-Sunyer & Duarte, 2008). We evaluated the sensitivity of our exposure estimates to several alternative threshold values ( $\text{pH} 7.1, 7.5, 7.75$ ;  $\text{DO} 0.7, 2.1 \text{ mL/L}$ ;  $T 17.5, 20^\circ\text{C}$ ) to encompass the range of values evaluated in the experimental studies used to establish consequence scores (details in Text S1).

## 2.2. Life Stage Exposure

We defined distinct spatiotemporal distributions of each life stage (Figure 2) using monthly presence/absence maps (Hodgson et al., 2016). Benthic life stages (egg, juvenile 1, juvenile 2, adult) were mapped along the seafloor between 30 and 90 m depth, where they are predominantly found (Figure S1; Rasmuson, 2013). To represent the temporal distribution of the benthic life stages, eggs were mapped between the months of October and March, while juveniles and adults were mapped for every month of the year. To calculate maximum potential exposure to either low pH and DO or high temperature, pelagic larval stages (zoea and megalopa) were mapped at either the maximum depth of their vertical migration (70 m; Hobbs & Botsford, 1992; Rasmuson, 2013) or the surface, respectively, because pH, DO, and temperature decline with depth. Zoeae were mapped as starting nearshore in January and progressively moving offshore before metamorphosing into megalopae between April and August (Figure S1). Unlike the southern population assessment (Hodgson et al., 2016), which applied an ocean model with a minimum limit of 30 m depth, the ocean model used in our study (described below) has been evaluated for the nearshore environment 15 m and deeper (Davis et al., 2014; Giddings et al., 2014; Siedlecki et al., 2015, 2016, 2021) allowing us to extend the distributions of the megalopae and juveniles. Geographic life stage distributions were assumed to remain the same between now and 2100. This assumption is supported by species distribution model projections for the Dungeness crab in 2100 under RCP 8.5, which predict similar distributions in the N-CCS despite decreased abundance (Morley et al., 2018).

Spatiotemporal fields of baseline present and future (year 2100) ocean conditions were derived from simulations (Figure 2) using the Regional Ocean Model System (ROMS) for the “Cascadia” domain (Davis et al., 2014; Giddings et al., 2014; Siedlecki et al., 2015, 2016, 2021), which encompasses the outer coasts of Vancouver Island, Washington, and Oregon. The three-dimensional model is forced with realistic atmospheric, freshwater, and tidal boundary conditions including physics and biogeochemistry to simulate mean modern conditions and project future conditions. The model has a high horizontal resolution ranging from 1.5 km at the coast to 4.5 km far offshore, allowing it to resolve coastal processes, such as upwelling, that are not well-resolved in global-scale models. Hindcast model fields have been validated against observations for the variables of interest and exhibit skill on all regions of the shelf (Davis et al., 2014; Giddings et al., 2014; Siedlecki et al., 2015, 2016, 2021). Model versus observation comparisons for 2007 revealed a significant cold temperature bias in the upper ocean introduced by atmospheric forcing (Siedlecki et al., 2021). We corrected this bias by adding the Root Mean Square Error (RMSE) for the upper 200 m ( $2.79^\circ\text{C}$ ; Figure S2) to present and future modeled temperatures in that depth range. Future downscaled projections are forced by anomalies from modern conditions using an ensemble mean of five global CMIP5 simulations under the

RCP 8.5 carbon emissions scenario (Howard et al., 2020; Siedlecki et al., 2021), which predicts 936 ppm of atmospheric CO<sub>2</sub> in 2100 (Bopp et al., 2013). The downscaled, high resolution CMIP5 projections are consistent with the direction of the future change projected by the global simulations, but the magnitude and spatial patterns of the future changes are modified by the inclusion of coastal processes—particularly for the carbon variables (Siedlecki et al., 2021).

We averaged modeled pH, DO, and temperature over three independent years at daily resolution under both present and future forcings to account for interannual variability. We calculated pH (on the total scale) from modeled dissolved inorganic carbon, alkalinity, temperature, salinity, and pressure using CO2SYS (Norton et al., 2020; Pelletier et al., 2007).

We overlaid life stage distribution maps (Figure S1) with monthly averaged baseline and future model projections (Figure 2), producing a pH, DO, and temperature value for each 2.25 km<sup>2</sup> grid cell within each stage's depth-specific distributional range for each month the life stage is present (see Figure 1). Using a threshold approach, we then calculated percent exposure to stressful conditions for a given life stage as the proportion of grid cells within its distribution that exceeded the stress thresholds (pH < 7.65, DO < 1.4 mL/L,  $T > 15^{\circ}\text{C}$ ) during each of four seasons (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec) and throughout the year. We converted percent exposure values into scores between 1 and 3: values greater than 75% were considered high exposure (score = 3) and values from 0% to 75% were linearly converted to values between 1 and 3 (Figure S3). This method of translation between percent exposure and exposure score is a simplified assumption that has been used in prior studies (Williams et al., 2011) including the southern population assessment (Hodgson et al., 2016). High exposure was defined as >75%, as opposed to 50% in other studies (Williams et al., 2011) because species in the CCS are already experiencing conditions exceeding the defined stress thresholds (Hickey & Banas, 2008). Hence, species in the CCS likely have adapted to local conditions allowing them to tolerate stressful conditions for longer periods than species in less stressful habitats. We chose to use the same method in order to compare our results to those of the southern population assessment (Hodgson et al., 2016) but also explored this choice and an alternative method for the pH exposures in the Supporting Information S1 (Text S1).

We also quantified stressor exposure of larval life stages using Lagrangian particle simulations (Figure 2) to provide a more robust estimate of conditions experienced by the pelagic life stages. We adapted the Larval TRANSport Lagrangian model (LTRANS.v2b; North et al., 2011; Schlag & North, 2012) to simulate Dungeness crab zoeae and megalopae (Norton et al., 2020) advected through present and future (year 2100) daily averaged ROMS-projected conditions. The offline particle tracking model simulates larval advection according to external ROMS physical forcing files, random displacement, and prescribed larval behaviors. We released particles ( $n = 3,640$ ) from the seafloor between 30 and 90 m depth throughout the domain (Figure S1) to simulate hatching from adult female spawning stock on the first days of January, February, March, and April for a total of 14,560 particles per model run. After release, each particle was tracked for 122 days, the average larval duration for this region (Hodgson et al., 2016; Rasmuson, 2013), with simulated dispersal trajectories updated every minute and particle locations/ambient conditions recorded every hour.

Because larval behavior can influence particle trajectories and exposure history (Norton et al., 2020), we performed model runs for each of three behaviors based on field and laboratory observations (Fernandez et al., 1994; Hobbs & Botsford, 1992; Rasmuson, 2013). These behaviors included passive transport, diel vertical migration (DVM), and an intermediate behavior with particles switching from passive transport to DVM after 92 days, which typically marks the end of the zoeal phase. DVM behavior followed prior Dungeness megalopae transport modeling (Norton et al., 2020), but with a maximum daytime depth of 70 m (Hobbs & Botsford, 1992; Rasmuson, 2013). While DVM behavior is most commonly reported for megalopae, zoeae exhibit limited swimming abilities (maximum swimming speeds of 2.6–4.2 cm s<sup>-1</sup> compared to 10 cm s<sup>-1</sup> for megalopae; Jacoby, 1982), which may be more accurately represented through passive particle transport (Norton et al., 2020), particularly in our study area where currents can move up to 20–50 cm s<sup>-1</sup> (Barth et al., 2005; Bi et al., 2011; Hickey et al., 2006). However, we also considered DVM for zoeae given the uncertainty in their behavior.

We quantified the exposure history of each particle for pH, DO, and temperature. We calculated zoeal and megalopal exposure scores using exposure histories for the first 92 days and the last 30 days of each particle

track, respectively, to represent their life history progression (Hodgson et al., 2016; Rasmuson, 2013). We averaged the percent exposure to low pH (<7.56), low DO (<1.4 mL/L), and high temperature (>15°C) across all zoeal and megalopal particles for each behavior under present and future conditions. We also calculated averages of the subset of particles that ended up inside the shelf break (200 m isobath) to represent particles that could settle (Rasmuson, 2013), since exposure histories of larvae lost from the region (61.4% of particles on average) do not affect local population-level vulnerability. Particles that had exited the model boundaries (17.9% of exposure history records), including those that had entered the Columbia River or the Salish Sea, were not included in averages because these regions act as a boundary condition to the outer coast (Giddings et al., 2014) and do not simulate biogeochemical cycles (Siedlecki et al., 2021). Additionally, particle exposure data that had unrealistic negative values due to extrapolation errors that occurred when a particle was located at the surface or seafloor were removed before averaging (3.3% of exposure history records). Finally, we used the percent exposure averages to calculate annual and seasonal exposure scores for the zoea and megalopa stages as described above (Figure S3).

### 2.3. Vulnerability

We calculated the vulnerability of each life stage ( $V_s$ ) as the product of exposure ( $E_s$ ) and consequence ( $C_s$ ) scores (Figure 2):  $V_s = E_s \times C_s$  (Equation 1; Hodgson et al., 2016). We did not account for adaptive capacity due to challenges associated with its scoring (Adger, 2006; Hodgson et al., 2016). One aspect of adaptive capacity is genetic variability, which has been reported as low among CCS populations (Jackson et al., 2018) and may constrain this species' ability to respond to climate change.

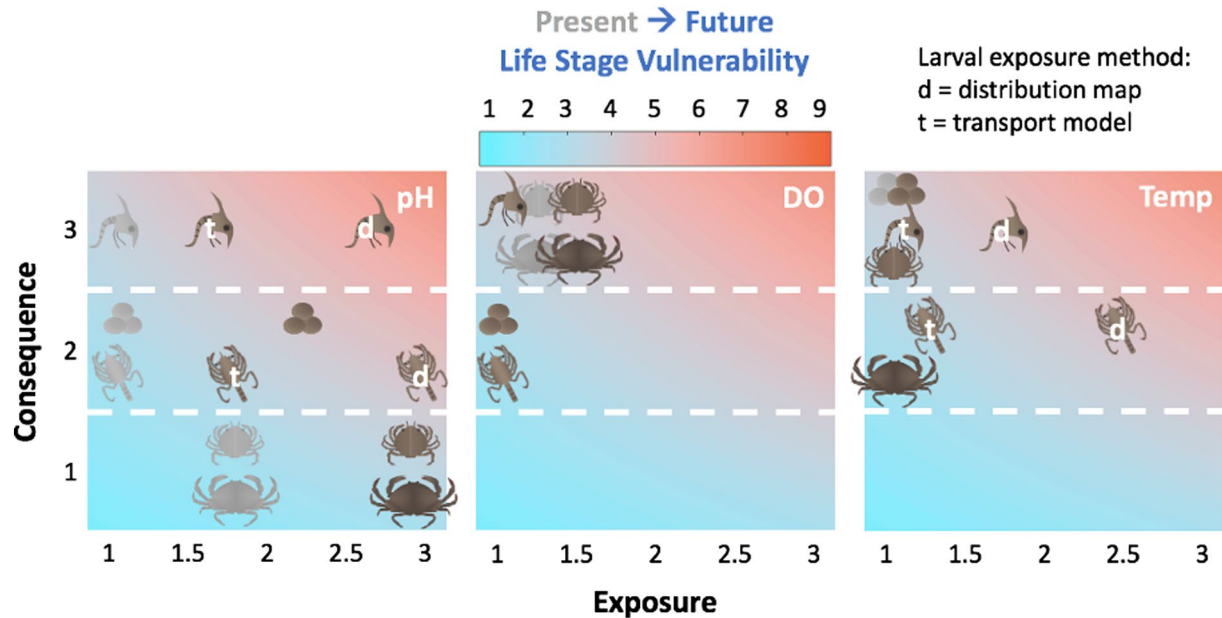
Life stage vulnerability was calculated for each of the three stressors (low pH, low DO, and high temperature) under present and future exposure. Since values of  $E$  and  $C$  both range from 1 to 3, life stage vulnerability ranges from 1 to 9, with 9 being the most vulnerable. We calculated stage vulnerabilities on both seasonal (acute) and annual (chronic) timescales.

We calculated population-level vulnerabilities ( $V_p$ ) for each stressor under present and future exposure as weighted means of annual life stage vulnerability estimates (Figure 2), with relative weights ( $w_s$ ) for each life stage,  $i$ :

$$V_p = \sum_1^i w_{si} V_{si} \quad (1)$$

As with life stage vulnerability scores, population vulnerability ranges from 1 to 9, with 9 being the most vulnerable. We also calculated an upper bound to population vulnerability from the maximum seasonal vulnerabilities for each life stage.

Relative life stage weights were derived from summed elasticity values from a stage-structured population matrix model developed for Dungeness crab (Hodgson et al., 2016), which has five life history stages (egg, larval, juvenile 1, juvenile 2, adult) with males and females grouped. Elasticities indicate how any proportional change in stage-specific survival, transition, or offspring production affects the population growth rate (Stevens, 2009). Therefore, elasticities provide a basis for identifying stages at which changes in demographic rates are likely to have the greatest population-level effect and provide insight into which stage may be most important for overall population growth. The elasticities were estimated from the field and laboratory-based survival rates, stage duration times, and fecundity values assuming the population growth rate  $\lambda = 1$  because the analysis was intended to estimate the relative contribution of each stage to population growth, not the 'true' population growth rate (Hodgson et al., 2016). Life stage weights were assumed to remain the same between present and future. The zoea and megalopa stages had the lowest relative life stage weights (0.01) and adults had the highest (0.44; Table S3). This same pattern emerged when testing the sensitivity of the population model to each of the matrix elements (Figure S4). Therefore, population-level vulnerability estimates for each stressor in the present and future were driven largely by adult stage vulnerabilities.



**Figure 3.** Consequence, exposure, and vulnerability scores for each life stage to low pH (<7.65), low dissolved oxygen (<1.4 mL/L), and high temperature (>15°C) in the present and future. Life stage vulnerability is the product of the consequence and exposure scores and is colored from blue (1) to red (9). In cases where the exposure score changed between present and future, the gray life stage icon represents the present score. In cases where larval exposure score differed depending on the estimation method used, ‘d’ represents the score calculated from the distribution map method and ‘t’ represents the score calculated from the larval transport model method with intermediate behavior.

#### 2.4. Uncertainty

We scored uncertainty for exposure and consequence scores of each life stage and combined scores to estimate overall population uncertainty for each stressor (low pH, low DO, high temperature). Similar to consequence scores, we scored uncertainties from low (1) to high (3) based on criteria defined in Table S4. Criteria from the southern population assessment (Hodgson et al., 2016) were updated to include uncertainty in exposure for the larval transport models. We calculated population-level uncertainty for each stressor as the geometric mean of uncertainty in consequence ( $U_c$ ) and exposure ( $U_e$ ) for each stage summed using the relative weights ( $w_i$ ) for each life stage ( $i$ ; Hodgson et al., 2016):

$$U_p = \sum_i \sqrt{U_c U_e} w_{si} \quad (2)$$

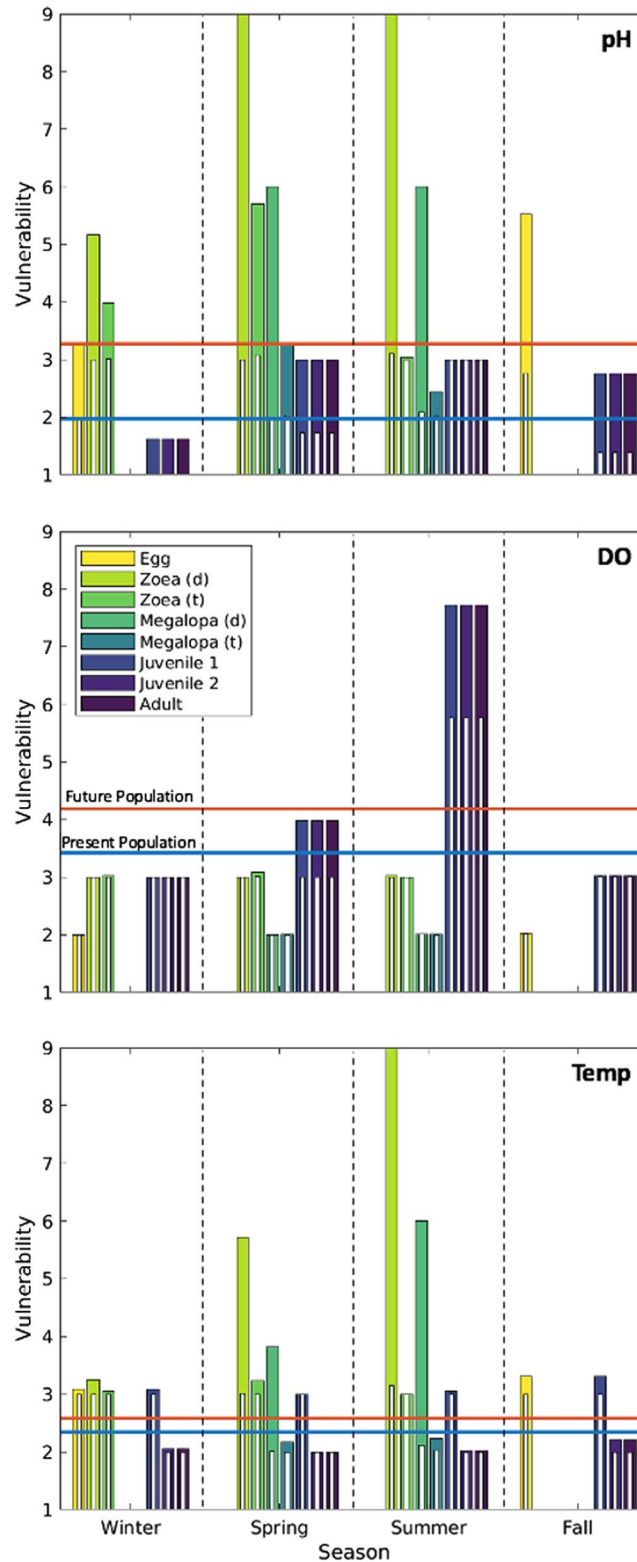
#### 2.5. Multi-Stressor Hotspots

We plotted the spatiotemporal overlap of stressors within benthic and pelagic life stage distributions to visualize multi-stressor hotspots in the present and future of each season. Seasonal averages of ocean model projections were used to visualize areas exceeding stress thresholds (pH < 7.65, DO < 1.4 mL/L,  $T > 15^\circ\text{C}$ ). Stressful areas were mapped along the seafloor for the benthic life stages, whereas low pH and DO were mapped at 70 m depth (Hobbs & Botsford, 1992; Rasmuson, 2013) and high temperatures were mapped at the surface for the pelagic stages.

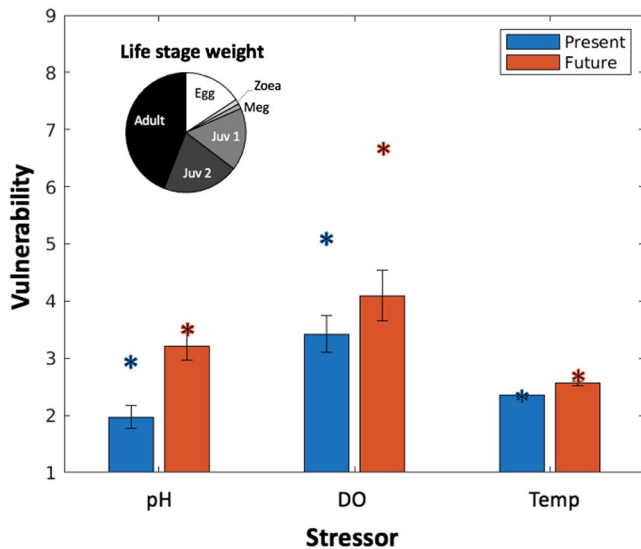
### 3. Results

Spatiotemporal variability in ocean conditions and life stage distributions caused exposure and resulting vulnerability scores to vary between present and future and across stressors, life stages, and seasons (Figures 3 and 4, Table S3). Consequence and exposure scores within a life stage often offset one another when annual averages were the focus and seasonality was not considered (Figure 3), leading to moderately low vulnerability estimates (i.e., life stages with high consequence were not highly exposed and vice versa). Estimates of life stage- and population-level vulnerability to each stressor and projected increases for 2100 depended on how each stage experienced vulnerability across the four seasons (Figures 4 and 5). Below





**Figure 4.** Acute seasonal vulnerabilities to low pH (<7.65), low dissolved oxygen (<1.4 mL/L), and high temperature (>15°C) for each life stage. White bars indicate present vulnerability and colored bars indicate future vulnerability. The horizontal blue and orange lines indicate present and future chronic annual population-level vulnerabilities (Figure 5), respectively. Seasons are Winter (Jan–Mar), Spring (Apr–Jun), Summer (Jul–Sep), and Fall (Oct–Dec). For zoea and megalopa stages, estimates from the map distribution method (d) and larval transport model with intermediate behavior (t) are shown. Bars are omitted in seasons when a particular life stage is absent.



**Figure 5.** Mean ( $\pm 95\%$  confidence interval) annual population-level vulnerability to low pH ( $<7.65$ ), low dissolved oxygen ( $<1.4$  mL/L), and high temperature ( $>15^\circ\text{C}$ ) under present (blue) and future (orange) conditions. Population vulnerability scores were calculated as the weighted mean of the stage vulnerability scores, using life stage weights (visualized in the pie chart; Table S3) from a population matrix model (Hodgson et al., 2016). Asterisks (\*) above bars represent the upper bound to population vulnerability calculated from the maximum seasonal vulnerability scores for each life stage (from Figure 4).

we describe consequence scores and individual stressor vulnerability estimates, compare annual and seasonal estimates of exposure, and identify spatio-temporal multi-stressor hotspots.

### 3.1. Consequence Scores

The consequence of exposure to low pH was low (1, no effect) for the juvenile and adult stages, medium (2, sublethal effect) for the egg and megalopa, and high (3, lethal effect) for the zoea (see Table S1 for consequence scoring criteria and Table S2 for consequence score justifications). The score for the egg stage was raised by 1 and that for the megalopa lowered by 1, compared to consequence scores reported by Hodgson et al. (2016), based on the findings of more recent studies (Bednaršek et al., 2020; J.J. Miller et al., 2016; P. McElhany, personal communication, August 21, 2019). Uncertainties for the consequence scores were lowest for the zoea and adult stages and highest for the juvenile 2 stage (see Table S4 for uncertainty scoring criteria and Table S5 for uncertainty score justifications). Compared to the uncertainty scores for consequence reported by Hodgson et al. (2016), the egg, zoea, megalopa, and juvenile 1 stage scores were lowered by 1 to reflect increased support from recent studies (Bednaršek et al., 2020; J.J. Miller et al., 2016; P. McElhany, personal communication, August 21, 2019).

The consequence of exposure to low DO was determined to be medium (2) for the egg and megalopa stages and high (3) for the zoea, juvenile, and adult stages (see Table S2 for score justifications). Responses of Dungeness crab eggs and zoeae to low DO have not yet been studied, so the consequence scores for these stages were based on studies with

related species. The response of the juvenile 2 stage also has not been studied, so the consequence score was assumed to be the same as the juvenile 1 and adult stages. The egg, zoea, and juvenile 2 stages received high uncertainty scores, while the remaining stages received medium (megalopa and juvenile 1) or low uncertainty scores (adult; see Table S4 for uncertainty scoring criteria and Table S5 for uncertainty score justifications).

The consequence of exposure to high temperature was scored as medium (2) for the megalopa, juvenile 2, and adult stages and high (3) for the zoea and juvenile 1 stages (see Table S2 for score justifications). Uncertainty in consequence was scored low for the zoea and juvenile 1 stages and medium for the remaining stages (see Table S4 for uncertainty scoring criteria and Table S5 for uncertainty score justifications).

### 3.2. Individual Stressor Vulnerability

Population-level vulnerability increased between present and future for all three stressors (Figure 5). While vulnerability to low DO was the most severe overall, the increase between present and future was greatest for low pH (63% compared to 20% and 9% for low DO and high temperature, respectively). These increases were largely driven by increases in the exposure and resulting vulnerability of the adult life stage, which had the highest life stage weight (Figure 5, Table S3) and thus contributed the most to integrated population vulnerability estimates.

Population vulnerability estimates were not affected by exposure estimation methods for larvae or juveniles, though life stage-level vulnerability was in some cases. Estimates of exposure for megalopae and juveniles were similar regardless of whether or not the nearshore environment (15–30 m depth) was included in the distribution maps for those stages (Table S3). While distribution map exposure estimates for the zoea and megalopa stages were greater than those estimated by the larval transport models for low pH and high temperature under future conditions (Figure 3, Tables S3 & S6, Movies S1–3), these differences did not affect population-level vulnerability because these have low relative life stage weights (Figure 5, Table S3). However, these differences impacted vulnerability estimates at the life stage-level with the highest vulner-

**Table 1**  
*Percent of Particles ( $\pm 95\%$  Confidence Interval) Ending up Inside of the Shelf Break (200 m Isobath) for Each Behavior in the Present and Future (Averaged Across the Four Monthly Initializations)*

Behavior	Present (% of particles)	Future (% of particles)
Passive	25.3 ( $\pm 0.2$ )	39.8 ( $\pm 0.4$ )
DVM	46.1 ( $\pm 0.4$ )	52.8 ( $\pm 0.7$ )
Intermediate	27.5 ( $\pm 0.2$ )	39.9 ( $\pm 0.4$ )

ability under future pH conditions. Larval exposure estimates also varied across transport model behaviors: particles exhibiting DVM behavior had greater exposure to low pH than those exhibiting passive or intermediate behavior when averaged across all particles or the subset that reached the shelf (Table S6). Under DVM behavior, the proportion of particles returning to the shelf was also greatest (Table 1).

Uncertainty scores for exposure were lowest for the egg, juvenile, and adult distribution maps (Table S3) and the larval transport models with passive behavior for the zoea and DVM behavior for the megalopae (Table S6). The zoea and megalopa distribution maps had high uncertainty because spatio-temporal distributions for these pelagic life stages are not

well-defined (Tables S4–5). In combination with stressor-specific uncertainty scores for consequence, these uncertainty scores for exposure translated into low overall population-level uncertainties for all three stressors (Table S7).

Sensitivity tests (detailed in Text S1) revealed that our results were not greatly affected by changes in stressor thresholds or perturbations to the population matrix model. While population vulnerability estimates for low pH and low DO were sensitive to the threshold used, vulnerability to low DO remained more severe under both present and future conditions when comparing across the thresholds. Vulnerability to high temperature was consistently low across thresholds. Likewise, the relative life stage weights were sensitive to changes in life stage survival rates or durations, but in all cases, the adult life stage maintained the greatest weight.

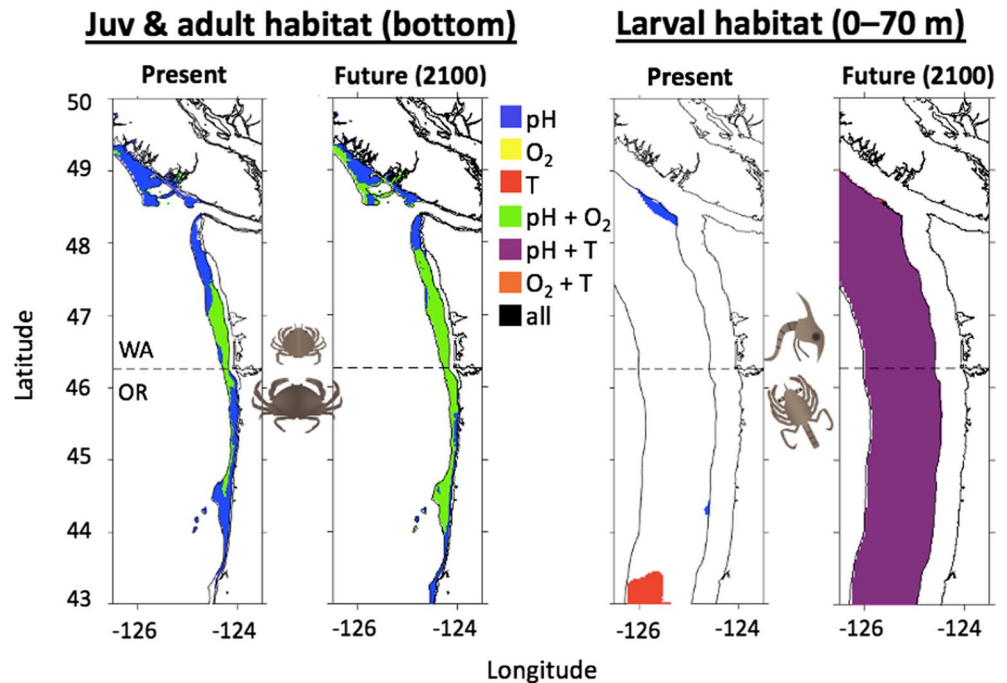
### 3.3. Annual Versus Seasonal Exposure

Changes in oceanographic conditions through the year resulted in shifting vulnerability levels at both life stage- and population-levels when exposure was estimated seasonally. For the benthic life stages (eggs, juveniles, and adults), vulnerabilities to low pH and low DO were highest during the summer upwelling season (Figure 4). Under future conditions, vulnerabilities of these stages to low DO only increased during spring and summer, while vulnerabilities to low pH increased in all seasons. The pelagic life stages (zoea and megalopae) experienced increased vulnerability to low pH and high temperature under future conditions in the spring and summer but were less severe when estimated from larval transport model exposure histories.

Integrating across maximum seasonal life stage vulnerability estimates resulted in upper bounds to population vulnerability estimates that were greatest overall for low DO (Figure 5). Furthermore, the upper bound estimates demonstrated a greater increase in population vulnerability from present to future for low DO (31%) and a lesser increase for low pH (19%) compared to annual estimates (20% and 63%, respectively). Upper bounds for low DO were also more sensitive to exposure thresholds (see Figure S5).

### 3.4. Multi-Stressor Hotspots

The spatial overlap of conditions exceeding thresholds for all three stressors was prevalent in the summer (Jul–Sep) under future conditions (Figure 6) compared to the other seasons (Figure S6). During summer, the entire juvenile and adult habitat experienced increased exposure to both low pH and low DO under future conditions, whereas the entire larval habitat experienced increased exposure to both low pH at 70 m and high temperature at the surface. The larval habitat also experienced exposure to all stressors at a hotspot along the northeast edge of their distribution near the outskirts of the Juan de Fuca eddy ( $\sim 48.5^\circ\text{N}$ ) in the summer under future conditions. In all other seasons, low pH emerged as a consistent stressor under future conditions. However, low pH alone is of low consequence for the juvenile and adult stages (Table S3). Under future conditions, novel hotspots of both low pH and high temperature emerge in the benthic habitat in fall and in the larval habitat in winter and spring. Low pH and high temperature conditions in the larval habitat during winter are driven by future ocean acidification and warming under RCP 8.5 (Siedlecki et al., 2021). However, the spatial coverage of stressful conditions was minimal in the winter overall.



**Figure 6.** Multi-stressor hotspots for the juvenile and adult habitat and larval habitat in the summer (Jul-Sep) according to stressor exposure in the present and future estimated using the distribution map method. For the larval habitat, low pH and low dissolved oxygen are mapped at 70 m, while the high temperature is mapped at the surface (see Methods for explanation). The only area where all three stressors overlap (black) is along the northeast edge of the larval habitat near the outskirts of the Juan de Fuca eddy ( $\sim 48.5^{\circ}\text{N}$ ) under future conditions. See Figure S6 for the remaining seasons.

## 4. Discussion

Our results demonstrate that the vulnerability of Dungeness crab populations to low pH, low DO, and high temperature is projected to increase by 63%, 20%, and 9% respectively under future climate change conditions (year 2100, RCP 8.5) in the N-CCS. Overall, population-level vulnerability to low DO was most severe (Figure 5) despite current and projected seasonal relief of hypoxic stress (Siedlecki et al., 2021). Changes in vulnerability to each stressor over the next century depend on the ways that seasonality of ocean conditions and life-stage specific vulnerabilities are incorporated into estimates of population-level vulnerability. For example, increased vulnerability to low pH resulted from chronic elevated exposure of all life stages year-round, while increased vulnerability to low DO was due to a combination of acute elevated exposure during the summer upwelling season (Figure 4) and its consequence for juvenile and adult life stages (Figure 3), which contribute strongly to population growth (Figure 5). As a result, the projected increase for population-level vulnerability to low DO (31%) was even more severe when calculated from the maximum seasonal vulnerability scores for each life stage as opposed to scores determined on an annual basis (20%; Figure 5). Our results thus illustrate the value of considering population-level vulnerability that includes life stage-specific habitat from both seasonal (acute) and annual (chronic) perspectives for species with complex life cycles in seasonal environments.

### 4.1. Importance of Life Stage Considerations

Our results highlight the importance of including the entire life cycle and stage-specific vulnerabilities in estimates of population-level vulnerability for two main reasons. First, they demonstrate the importance of each life stage's relative contribution to population growth in determining its impact on population vulnerability. In our assessment, adults had the highest relative life stage weight and therefore could contribute the most to population-level vulnerability. For example, while adults had the highest exposure to low pH, the low consequence of this stressor for adults translated to low overall population vulnerability. In

comparison, adult exposure to low DO was relatively low, but when paired with the high consequence, the overall population vulnerability increased. Although the adult life stage often determines species distribution and population health, early life stages often determine recruitment success and can act as a bottleneck to population growth (Stortini et al., 2015). Low to moderate population-level vulnerabilities, therefore, require careful attention when early life stage vulnerabilities are high.

Second, the inclusion of the entire life cycle allows for consideration of each stage's dynamic habitat use, which is necessary for species with complex life cycles like Dungeness crab. Given that different life stages occupy different regions of the pelagic and benthic realms, exposure estimation methodology influenced our results. Unlike benthic life stages, for which distribution map methods represent experienced conditions, particle dispersal trajectories provided a much more realistic estimate of stressor exposure for pelagic larvae. For example, transport model estimates of larval exposure to low pH and high temperature under future conditions were much lower than those estimated from distribution maps (Figure 3, Table S3). This result was expected because the depths of the larval distribution maps (70 m for pH and DO, surface for temperature) were chosen to represent maximum potential exposure. However, dispersing larvae do not spend their entire stage duration at any single depth, so particle dispersal trajectories, especially those that model larval behavior, offer a more realistic view of exposure history. Indeed, the type of larval behavior simulated in our models affected exposure and potential settlement success (Bednaršek et al., 2020; Norton et al., 2020). For instance, diel vertical migration (DVM) throughout the entire larval phase (zoea and megalopa) yielded the greatest return of particles to the shelf (Table 1) but also the greatest exposure to low pH (Table S6) compared to passive (no DVM) or intermediate (megalopa DVM only) behaviors. Intermediate behavior may therefore balance a tradeoff between settlement rates and exposure to low pH.

Across all modeled behaviors, 6.7%–14.5% more particles reached the shelf under future conditions (Table 1) but experienced greater exposure to low pH (Table S6), which could negatively impact settlement rates given the high and medium consequences for zoeae and megalopae, respectively. Future conditions may also impact larval dispersal and settlement by altering the timing and/or duration of the pelagic life stages, influencing larval swimming behavior (Christmas, 2013), or compressing the vertical extent of DVM (Wishner et al., 2020). Compressed DVM would decrease larval exposure to stressful conditions but could also make the larvae more susceptible to predation or food limitation. Future work could explore larval transport and behavior using dynamic thresholds to set the timing and duration of the simulated larval stages or the bottom limit of DVM (e.g., hypoxic depth), which would likely alter the dispersal patterns of the larvae with potential impacts on recruitment.

#### 4.2. Importance of Seasonality

Dungeness crab life stages are currently and will continue to be most vulnerable to low pH and DO during spring and summer (Figure 4) because of the seasonality in upwelling in the N-CCS. Seasonal upwelling is a central characteristic of the N-CCS and other eastern boundary currents. It confers high productivity to the region and its fisheries, but also high vulnerability to low pH and DO (Checkley & Barth, 2009). The incorporation of seasonality should, therefore, improve vulnerability assessments for species in seasonal seas (Jones et al., 2018; Spencer et al., 2019). The regional model used to project the ocean conditions continues to experience seasonality in the projected ocean conditions in the future (2100), but despite an increase in the projected winds in the CMIP5 projections, the future upwelling intensity does not change much due to compensation from increased stratification (Howard et al., 2020; Siedlecki et al., 2021). The timing and duration of the upwelling season in the N-CCS also remain the same in the future model projections (Siedlecki et al., 2021).

Our assessment is the first of its kind to consider seasonal variation in stressor exposure and vulnerability. While the prior vulnerability assessment for the southern Dungeness crab population (Hodgson et al., 2016) did not consider seasonality, seasonal averages would have likely been similar to annual averages in this region because upwelling conditions occur year-round in this region of the CCS (Jacox et al., 2018).

The seasonality identified by our results would not have emerged if we had only estimated vulnerability on an annual basis. For example, the annually averaged vulnerability to low DO under future conditions for the juvenile and adult stages was 4.53, while the seasonally averaged vulnerability during summer (Jul–Sep)

was 7.72 (Figure 4). Thus, acute seasonal vulnerability to hypoxic events may be a greater concern than chronic annual vulnerability to long-term deoxygenation. However, neither of these averages took stressor intensity into account. Because DO can reach lower values than our threshold (1.4 mL/L) during summer (Hales et al., 2006; Siedlecki et al., 2015), our estimates of vulnerability were conservative (see also our sensitivity analysis for DO thresholds in the Supporting Information S1).

Other species that occupy both the northern and southern regions of the CCS could benefit from further assessment of their seasonal vulnerability in this region. This is especially true for species with larval durations that coincide with seasonal exposure to climate stressors like the Dungeness crab, such as pink shrimp (*Pandalus jordani*). Seasonality and life stage are directly linked for stages that are not present year-round (e.g., larvae). Should these stages produce a population bottleneck, annual vulnerability estimates may fail to capture true population-level vulnerability. Hence, seasonality and exposure estimates are important to consider in vulnerability assessments for species that live in seasonally dynamic habitats and have complex life cycles, especially when multiple stressors may interact.

### 4.3. Comparison to Prior Assessments

Our results for vulnerability to low pH were generally consistent with findings of previous work from other regions within the CCS. Our stage- and population-level vulnerabilities for low pH in the N-CCS in 2100 were similar or higher than those reported for the southern population in 2050 (Hodgson et al., 2016). However, we cannot draw any direct conclusions from this comparison because the two studies used different ROMS simulations and future forcings. Furthermore, the southern population study (Hodgson et al., 2016) did not evaluate present-day, seasonal, or other climate stressor (e.g., low DO or high temperature) vulnerabilities. Nevertheless, both assessments found that future population-level vulnerability to low pH was far lower than the maximum life stage vulnerability for zoeae using the distribution map method (Figure S7). However, our larval transport model results suggest that the future vulnerability of zoeae and megalopae to low pH is actually less than that of eggs on both annual and seasonal timescales (Figure S7). While the juveniles and adults had a low vulnerability to low pH in both assessments, our inclusion of other climate stressors revealed that these life stages are most vulnerable to low DO, causing population vulnerability to be most severe for this stressor, especially when calculated seasonally (Figure S7).

Other methodologies (e.g., ecosystem and economic modeling) have also been used to investigate the effects of future pH and OA on Dungeness crab in the CCS and have predicted negative impacts on survival, biomass, landings, and revenue (Busch & McElhany, 2016; Hodgson et al., 2018; Marshall et al., 2017). These studies factored in potential indirect effects of lower pH environments, including changes in prey resources, and all suggest that Dungeness crab populations will be negatively affected by future OA.

A model study in Hood Canal (Froehlich et al., 2017) predicted that local harvest will increase under future hypoxia due to shoaling of adult habitat (Dungeness crab adults avoid hypoxic areas; Froehlich et al., 2014). However, hypoxia-related mortality or changes in growth or reproduction were not considered in their model. In our study, we did not consider changes in the habitat distribution of the outer coast population, as we relied on species distribution model projections (Morley et al., 2018), but stressful future conditions may result in distributional shifts, as projected in Hood Canal.

Compared to effects of pH and DO, projected temperature increases for year 2100 caused only a small increase in vulnerability of the N-CCS Dungeness crab population (Figure 5). However, the regional ocean model projections used in this assessment were designed to represent mean modern and future conditions and did not consider anomalous warming events (marine heatwaves) that are expected to become more common in the future (Frölicher et al., 2018). These events could drive regional temperatures above our threshold level of 15°C, as evidenced by recent marine heatwaves (Di Lorenzo & Mantua, 2016; Gentemann et al., 2017; Jacox et al., 2016) and projections of these events in the future (Frölicher et al., 2018). Future studies are needed to address the impacts of these events on Dungeness crab populations.

Assessments of Dungeness crab elsewhere in the CCS reveal both positive and negative effects of projected temperature increases (Magel et al., 2020; Toft et al., 2014). For example, small temperature increases in Hood Canal may increase local harvest by increasing the survival of juvenile crabs in the estuary (Toft et al., 2014), whereas increased temperatures are predicted to decrease catch per unit effort (CPUE) across

the entire CCS (Magel et al., 2020). It is important to note that our work focused on the outer coast N-CCS crab populations, which experience unique oceanographic conditions due to strong seasonal upwelling compared to California and Hood Canal. Although Dungeness life stages are indeed responsive to warming temperatures (Table S2), our regional ocean projections indicated low exposure to stressful temperatures  $>15^{\circ}\text{C}$  (Figure 3). However, coastal embayments and estuaries, where this temperature threshold may be exceeded, were not simulated in the regional ocean model used here and should be considered in future research.

Taken together, results from our study and prior assessments advocate that managers should incorporate changing ocean conditions and vulnerabilities into their decision-making. The current 3-S management strategy, which has yielded high and sustainable harvests in the past (Richerson et al., 2020), may not be adequate in the future, especially in areas where future conditions generate multi-stressor hotspots (Figure 6). Specifically, managers may find a need to apply more precautionary versions of 3-S management, or additional measures (Burns et al., 2020; Froehlich et al., 2017), particularly in areas prone to stressful conditions. This recommendation stems from our consideration for life stages and their respective habitats in our analysis.

#### 4.4. Integrating Across Multiple Stressors

The classic multi-stressor framework predicts that two or more stressors can have additive, synergistic, or antagonistic effects on an organism (Griffen et al., 2016) and generally assumes that these stressors are experienced at the same time. Our approach considers the ways in which multiple climate stressors co-occur in the N-CCS, but also how different life stages experience these stressors distinctly in space and time. In doing so, our assessment revealed a variety of ways in which the multi-stressor effects of climate change could impact Dungeness crab vulnerability; however, we do not go as far as to estimate interactive effects of these stressors on vulnerability because the required experiments have not yet been conducted.

We found that both pelagic and benthic life stages are expected to become more vulnerable to co-occurring stressors (Figures 4 and 6). During future summers under RCP 8.5, pelagic larvae will experience increased exposure to low pH at 70 m depth and high temperature at the surface, while juveniles and adults will experience increased exposure to both low pH and low DO on the bottom (Figure 6). The vertical locations of these stressors in the water column highlight the importance of ontogenetic habitat shifts but also the role of larval behaviors such as DVM in determining exposure to multiple stressors (Table S6, Movies S1–3). Current literature suggests that juvenile and adult Dungeness crabs are more susceptible to low DO (Bancroft, 2015; Barth et al., 2018; Grantham et al., 2004) than to low pH (Pane & Barry, 2007). Interactions between these two stressors have only been tested with Dungeness megalopae (Gossner, 2018), which do not exhibit a synergistic multi-stressor response. However, pH and DO have been shown to have negative synergistic effects on the larval and adult stages of other crab species, such as blue crabs (Tanner et al., 2006; Tomasetti et al., 2018).

Even if concurrent stressors do not have interactive effects on a given life stage, multi-stressor effects could emerge across ontogeny (Donelan et al., 2020). Such carryover effects have not been tested in Dungeness crabs but could be a fruitful avenue of research. Ultimately, population-level vulnerability to multiple stressors will depend on how each life stage responds to multiple stressors and how multi-stressor effects integrate across ontogeny. Vulnerability assessments like ours can help identify the combinations of life stages and stressors that are most likely to coincide in nature and inform the multi-stressor experiments necessary to understand the biological impacts of changing ocean conditions.

## 5. Conclusions

To take appropriate action, it is critical that decision-makers can anticipate which, when, and where multiple climate stressors may be most impactful. Like Dungeness crab, most species targeted by the top 10 commercial fisheries in the U.S. have complex life cycles and/or strong seasonal and ontogenetic migrations among distinct habitats (lobsters, crabs, salmon, scallops, shrimp, pollock, oysters, clams, flatfish, menhaden; ranked by value of landing; NMFS, 2020). Our work, therefore, can inform how we assess the

population-level vulnerabilities of the many economically and ecologically important species facing future change in seasonally dynamic habitats to guide management decisions.

## Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

## Data Availability Statement

Archived model fields are available online from the Zenodo library (<https://10.5281/zenodo.4627961>). Analysis code will be made public upon acceptance of the paper.

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