Towards a conceptual model for the management and conservation of Dungeness crab in the South Puget Sound

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Abstract

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Despite continued fishery closures as of 2018, significant declines in the abundance of Dungeness crab have been documented within the South Basin of Puget Sound, prompting an urgent need to understand the vulnerability of Dungeness crab to climate change and anthropogenic effects within the inland waters of the Salish Sea. An expert focus group and regional literature review were used to identify direct and indirect stressors on the Dungeness crab population in South Puget Sound. In this severely data-limited system, expert knowledge is used to provide the best available science to address critical resource management decisions. The goal of this project was the co-production of a conceptual model of the drivers of Dungeness crab abundance in South Puget Sound to inform research and management priorities, identify local knowledge gaps, and support future qualitative modeling efforts. Based on the results of the

literature review and expert focus group discussions, the main drivers of Dungeness crab abundance appear to be the overlapping effects of climate change and eutrophication on dissolved oxygen, water temperature, and ocean acidification.

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1. Introduction

Dungeness crab (*Metacarcinus magister*) is culturally, ecologically, and economically important to the Pacific Northwest, and is one of the highest valued and most heavily exploited fisheries along the West Coast. In Washington alone, the coastal Dungeness crab fishery had a total catch of over 21 million pounds during the 2023-2024 season with a total ex-vessel value of state landings of over $66.8 million (WDFW 2025). However, while the biology and ecology in coastal populations of Dungeness crab are relatively well-understood, questions remain regarding how inland populations interact with complex, local estuarine ecosystems. As such, there are significant knowledge gaps regarding the status of Dungeness crab populations and the sustainability of harvest in the inland waters of Puget Sound.

Dungeness crab harvest in Puget Sound is managed by the Washington Department of Fish and Wildlife in ten crab management regions. Dramatic changes in Region 7 have prompted urgent action across management regions to address knowledge gaps. Region 7, which contains Marine Area 13 (MA 13), also known as South Puget Sound or South Basin, encompasses all waters south of the Tacoma Narrows Bridge (Washington Department of Fish & Wildlife 2021). Dungeness crab harvest from both state and tribal fisheries peaked at 289,500 pounds in 2012 and declined to 9,500 pounds (approximately 97%) in 2017 (Dufault and Bosley 2024). As a result of this drastic decline and continued low abundance determined by test fisheries, Region 7 has remained closed since 2018. In addition to Region 7, in recent years Regions 4, 5 and 6 have all seen declines in recreational harvest prompting the closure of fisheries (Dufault et al. 2021). Uncertainty around how vulnerable Dungeness crabs are to climate change and the declining harvests has led to increased research and collaboration to address the immediate need to fill data gaps and better inform management and conservation of this species.

A major factor contributing to the gaps in knowledge is the reliance fishery dependent data (Winnacott et al. 2024). There is no formal stock assessment of Dungeness crab populations in Washington state. Fishery management actions are determined by pre- and post-season test fisheries conducted by WDFW which collect data on catch per pot (legal, sub-legal, female), bycatch, carapace width, and sex/stage composition. As such there is no accurate estimate of absolute population abundance. Additionally, there is a lack of information on “the spatial and temporal distribution of larvae and juvenile settlement, adult migration patterns, genetic population structure, and environmental influences on vulnerable life history stages” (Buckner et al. 2022).

The Pacific Northwest Crab Research Group (PCRG) was formed in 2018 to address critical research gaps regarding Dungeness crab in the inland waters of Washington state. Pending PCRG research projects include a qualitative network model (QNM), which examines the effects of perturbations on a system, making them useful for predicting the outcomes of management interventions (Levins 1998; Harvey et al. 2016). Most importantly, QNMs are useful in supporting decision making when data, time, and funding are limited and restrict the use of quantitative methods (Reum et al. 2020). The basis of the QNM is a conceptual model, which offers a systematic and transparent vehicle for synthesizing existing knowledge, evaluating the risks and uncertainties of climate impacts, and exploring management strategies (Addison et al. 2013).

The goal of this project is the co-production of a conceptual model of the Dungeness Crab fishery in South Puget Sound to inform research and management priorities, identify knowledge gaps, and support future qualitative modeling efforts for this data-poor system. This model was developed in collaboration with PCRG utilizing the collective expert knowledge of the group from August 2022 to February 2025. I additionally conducted a keyword focused literature review to identify existing literature that supports the relationships identified in the conceptual model. When lacking in quantitative, experimental, or observational data, the expert knowledge synthesized in this effort is key to model complex ecosystem processes with the added benefit of engaging stakeholders and increasing transparency (Hollarsmith et al. 2022). This is crucial for the future development of a QNM designed to forecast population trends in response to environmental influences, as stakeholders and decision makers are less likely to incorporate a model into the decision making process if it departs from their own mental models of the system (Addison et al. 2013).

2. Methods

2.1 Co-creation of Conceptual Model

We used the DPSIR (Drivers–Pressures–State–Impact–Response) framework as the basis of our conceptual model. This framework can be effective in conceptualizing coastal social-ecological systems, supporting transdisciplinary knowledge, allowing stakeholders to articulate and structure challenges, as well as supporting policy and management outcomes (Lewison et al. 2016). The components of this framework are defined as follows: 1) Drivers – human activities which impact the environment (indirect stressors); 2) Pressures – direct effects of Drivers on the environment (direct stressors); 3) State – an environmental condition; 4) Impact – the effect of Pressures as measured by the change in State; and 5) Response – policies, interventions, or priorities adopted to improve undesired changes in State (Kristensen 2004; Hollarsmith et al. 2022). The conceptual model co-produced with PCRG focused only on the Drivers, Pressures, and States components, as analysis of Impacts and Responses would be handled by the future development of a QNM. Intermediate states were introduced to provide specificity and describe a particular causal pathway of identified drivers.

A focus group of experts on Dungeness crab within the PCRG network was invited to a workshop in August 2022 at the University of Washington, Tacoma to develop conceptual models of direct and indirect pressures on Dungeness crab in South Puget Sound. This group consisted of 25 researchers, resource managers, and academics from Washington Department of Fish and Wildlife (WDFW), Washington Department of Natural Resources, Puget Sound Restoration Fund, Pacific Shellfish Institute, University of Washington and UW Tacoma, and the Swinomish, Nisqually, Suquamish, Squaxin Island, and Puyallup Tribes.

After presentations of historical data and observations by WDFW and the Nisqually, Squaxin, and Puyallup tribes, participants were divided into three breakout groups led by a facilitator who moderated the discussion. Facilitators asked a series of questions to identify the states of interest, in this case which of the Dungeness crab life stages to include, as well as the direct and indirect stressors Dungeness crab faced in South Puget Sound. Specifically, breakout groups were asked the following four questions:

1. What life stage(s) are we considering as a management target (i.e. the relevant ‘State(s)’)?
2. What are the direct stressors (human or natural) that drive change in Dungeness crab populations in south Puget Sound (i.e. ‘Pressures’)?
3. What are the indirect stressors (human or natural) that drive change in Dungeness crab populations in south Puget Sound (i.e. Drivers of the pressures)?
4. What are the interactions/connections between these direct and indirect stressors with Dungeness crab populations? Are there any feedback loops?

PSM, EB, and Dr. Bonnie Becker facilitated breakout groups by: posing questions; listing the drivers, pressures, and states; and sketching out a conceptual diagram on a white board or easel pad. A member from each group volunteered to keep notes on the individual group discussions in real time. Facilitators used a consensus-based approach to determine the life stages and demographics of the Dungeness crab population as the focus of this exercise and to determine which direct and indirect stressors were most important. All group members were invited to respond to the questions until no additional stressors were identified by the group. There was often consensus among experts. Emerging disagreements or refinements were discussed until all participants were satisfied. The three groups reconvened to share results from the breakout group modeling exercise and identify similarities and differences. The conceptual diagrams and notes from each group were used to develop a consensus conceptual model showing the interactions between direct and indirect stressors on Dungeness crab in the South Puget Sound (Figure 1).

The consensus conceptual model was presented at the PCRG Annual Winter Meeting in February 2023, where attendees were asked to make revisions and offer feedback for the model. This meeting was open to all PCRG members, with nearly 50 people present during the revision workshop. Many of those from the first expert focus group were also in attendance. Attendees were split into six groups and given a large copy of the consensus conceptual model, which they were instructed to modify and annotate while considering the following questions:

1. What indirect stressors (human or natural) that drive change in crab populations (i.e., Drivers of the pressures) are not adequately represented in the model?
2. What direct stressors (human or natural) that drive change in crab populations (i.e., Pressures on crab) are not adequately represented in the model?

3. What states of Dungeness crab are not adequately represented in the model?
4. Are there interactions/connections between these direct and indirect stressors with crab populations that are not adequately represented in the model? Please indicate
5. What human interventions (positive/negative) might be enacted in the future that could affect the population of Dungeness crab in South Sound?

Groups from the February meeting submitted discussion notes and individuals submitted their answers to the questions above on a voluntary basis using a worksheet provided during the exercise. All worksheets, notes, and modified models were used in constructing a final conceptual model.

2.2 Literature Review

I performed a keyword-focused literature review following the methods described in Hollarsmith et al. (Hollarsmith et al. 2022) in order to identify published research that supported the interactions in the expert-based conceptual model. I searched Web of Science (https://www.webofscience.com/) for driver-pressure and pressure-state interactions depicted in the conceptual model, limiting the geographic scope to studies done within the Salish Sea. Search strings were based on the descriptions of the main drivers and pressures used in the focus group. For instance, a driver like *shoreline development* included shoreline armoring, construction, and otherwise modifying the natural shoreline. Intermediate states, such as Aquaculture, Native Crab Competitors, and Fishery, were used to generate search strings in place of the associated driver (in this case, "Human impacts on trophic structure"). Life stages were not specified in the literature search, and interactions between life stages were not included in the search strings. The list of search strings used in this review are documented in Appendix A. Reviews and meta-analyses were excluded from the search to prevent double-counting articles.

Known foundational papers were also included due to the age of the paper, as Web of Science coverage of papers published prior to the 1990s is incomplete. Some relevant studies that were not previously known to the authors may have been missed if they are not included in Web of Science.

The findings of reviewed publications were summarized, and relevant driver-pressure and pressure-state interactions were recorded. The directionality of the interactions was categorized as positive, negative, neutral (no relationship), or other (e.g., synergistic, antagonistic, threshold effect). Research methods of studies included observational, experimental, and modeling. Whether a study's experiment was done *in situ* or under laboratory conditions was also noted. Studies may have examined more than one interaction from the conceptual model and thus were counted once for each interaction, resulting in a total study count that exceeds the final number of publications reviewed.

3. Results

The expert knowledge-based conceptual model identified four primary Drivers (indirect anthropogenic stressors) and ten primary Pressures (direct physical and ecological stressors on the various Dungeness crab life stages) with four intermediate states, which resulted in a total of 78 interactions between Drivers, Pressures, and States represented by the arrows in the conceptual model: 24 Driver-Pressure interactions, including interactions through intermediate states; 44 Pressure-State interactions, including Pressure-Pressure interactions; and 10 State-State interactions, reflecting the relationships between Dungeness crab life stages. I reviewed 41 publications and identified a total of 73 studies that tested the interactions from the conceptual model. Of the total interactions identified in the conceptual model, 57 were tested, leaving 21 interactions unrepresented in published literature (Figure 2).

3.1 Indirect human stressors (Driver-Pressure)

Drivers within the model each have four to six pathways connected to Pressures (or States). The Driver with the most pathways originating from it is “Human impacts on trophic structure” which passes through three Intermediate States- Aquaculture, Native Crab Competitors, and Fisheries- resulting in six pathways to Pressures or directly to States. The two Pressures influenced by the greatest number of Drivers are Dissolved Oxygen and Water Temperature, each of which are influenced by Eutrophication, Shoreline Development, and Climate Change. Of the 17 Driver to Pressure pathways, five are not represented in the reviewed literature.

3.1.1 Eutrophication

Estuaries such as the Salish Sea are defined by seasonally variable freshwater inputs which influence a network of biogeochemical processes (Cai et al. 2021). Freshwater draining from coastal watersheds can deliver large amounts of organic and inorganic nutrients into estuaries, which can lead to eutrophication. Accompanied with vertical stratification driven by freshwater inputs, estuaries may have large vertical and horizontal gradients in pH and dissolved oxygen (Cai et al. 2021). Several studies have sought to model biogeochemical processes in the Salish Sea to assess the extent of eutrophication trends, as the increasing influx of nutrients lead to increased ocean acidification and hypoxia (Khangaonkar et al. 2012; Pelletier et al. 2018; Santana and Shull 2023). These models explore various factors differing between the many basins of the Salish Sea which influence the complex biogeochemical processes, including vertical mixing, residence times, and buffer capacity.

The literature review did not identify studies which tested the influence of eutrophication on water temperature or habitat used by Dungeness crab. Eutrophication may have an indirect effect on water temperature due to increased stratification. Effects of eutrophication on available Dungeness crab habitat may be mediate through its influence on dissolved oxygen and pH.

3.1.2 Shoreline Development

The intertidal zone is important foraging habitat for Dungeness crab in order to support populations living within estuaries (Holsman et al. 2003). Adult and subadult crabs tend to migrate into the intertidal environment during nights at high tide to avoid predators while foraging (Holsman et al. 2006). Intertidal shell habitat has also been identified as an important refuge from predators for early settlement juvenile crabs (Fernandez et al. 1993). Expert knowledge linked shoreline development to impacts on dissolved oxygen, water temperature, habitat, and water movement. According to the Shoreline Management Act, shoreline development in Washington state constitutes any alterations of the natural condition of the shoreline. Shoreline armoring, artificial methods of stabilizing banks and bluffs to prevent erosion and protect infrastructure, was the most common form of shoreline development discussed in the reviewed literature.

Alterations in shoreline characteristics can directly impact nearshore habitats, including those important to Dungeness crab. The adverse effects of shoreline armoring include reductions in beach width, vegetation, and beach wrack and associated invertebrates (Sobocinski et al. 2010; Dethnir et al. 2016). Shoreline armoring can also negatively impact eelgrass beds, another habitat important to juveniles, by reducing sediment supply (Rehr et al. 2014). The creation of engineered beaches within the armored shorelines of Elliot Bay can mitigate the negative habitat effects of shoreline armoring and support fish and crab communities generally not associated with armored areas (Munsch et al. 2015).

Much of the literature focused on habitat, with only a couple of studies testing the other identified linkages. While a study found shoreline armoring increases substrate temperature, there was no apparent impact on water temperature (Morley et al. 2012). Modeling suggests that large floating structures, such as a floating bridge, have the potential to reduce tidally averaged mean outflow and impact water circulation (Khangaonkar and Wang 2013). None of the reviewed literature tested the effects of shoreline development on dissolved oxygen.

3.1.3 Climate Change

Due to the high degree of agreement on the environmental effects of climate change, these linkages were not included in the literature search. However, two of the studies included in the review discuss the effects of climate change on dissolved oxygen, ocean acidification, and water temperature. Alin et al. (2024) characterized the seasonal ocean acidification, hypoxia, and warming conditions within the southern Salish Sea (Puget Sound and its boundary waters), while Khangaonkar et al. (2019) simulated a 95-year projection of change on select water quality parameters within the Salish Sea. The results of Khangaonkar et al. (2019) indicate changes in average Salish Sea temperature (+1.51°C), dissolved oxygen (−0.77 mg/L), and pH (−0.18) in the year 2095 compared to historical year 2000 values. Additionally, hypoxia is projected to expand from less than 1% to nearly 16% of total area.

The subsurface waters of the Northeast Pacific Ocean naturally have low oxygen and high dissolved inorganic carbon, making ecosystems vulnerable to marine heatwaves, hypoxia, and ocean acidification (Alin et al. 2024). Estuarine systems like the Salish Sea tend to exhibit lower buffering capacity and high levels of CO_2 due to natural local processes, further increasing vulnerability. Using a seasonally resolved cruise time series (2014-2018) in the southern Salish Sea, Alin et al. (2024) qualitatively analyzed environmental anomalies and how they affected seasonal patterns and interannual variability. In response to the Pacific marine heatwave event in 2014, the time series revealed the largest temperature increases in Puget Sound during the 2015-2016 timeframe. The fall of 2017 saw a carbonate system anomaly with unprecedentedly low aragonite saturation state (Ω_{arag}) and high carbon dioxide fugacity ($f CO_2$) occurring in areas of Puget Sound not usually as acidified. The authors discuss the importance of understanding changing conditions in the Salish Sea, including the effects of hypoxia, ocean acidification, and warming water temperatures on Dungeness crab, which will be explored further in later sections.

3.1.4 Water movement

The role of ocean currents in the dispersal of larval Dungeness crab in the open ocean is well understood, however less is known about the effects of estuarine circulation on the dispersal of larvae within enclosed waters such as the Salish Sea (reviewed by Rasmuson 2013). Studies have shown that larval abundance can project future Dungeness crab harvests (Shanks and Roegner 2007; Shanks et al. 2010). The ability to predict spatial patterns of larval distribution is therefore important to inform and evaluate conservation and management of Dungeness crab. Only one reviewed study discussed the role of larval transport in the horizontal distribution of Dungeness crab larvae as an alternative hypothesis to variation in larval distribution due to salinity, temperature, and dissolved oxygen (Sorochan and Quijón 2014). Recent efforts have been made to better understand the influences of estuarine circulation on hydrological characteristics like temperature and salinity (e.g. Yang and Khangaonkar (2010)).

3.1.5 Aquaculture

Bivalve aquaculture has the potential to alter intertidal habitat, the effects of which are not yet well studied. Expert knowledge suggests bivalve aquaculture may impact important habitat for early settlement juveniles as well as prey availability. In monitoring nine locations across the 3 basins of Puget Sound during the summers of 2017-2018, Ferriss et al. (2021) characterized the affiliations of fish and crabs with bivalve aquaculture by species groups, culture type, and regional environmental and habitat conditions. The study found regionally distinct differences in associations between fish and crab species, including Dungeness crab, and shellfish aquaculture-associated habitats. Large crabs partially followed their association with sediment habitats and were observed under suspended flipbags when present in aquaculture habitat. Another study analyzed the use of bivalve aquaculture and eelgrass habitat for foraging by multiple species using stable isotopes. The mean precent of diet by source for Dungeness crab was 63.3% eelgrass habitat, 13.1% bivalve farm habitat and 23.7% pelagic (Veggerby et al. 2024).

3.1.6 Local native crabs

Expert knowledge suggests that Dungeness crab may have varied relationships with other local crabs such as Red rock (*Cancer productus*), Graceful (*Metacarcinus gracilis*), and shore crabs (*Hemigrapsus nudus* and *H. oregonensis*). While I did not identify any literature in my review on the topic within the Salish Sea, a few studies exist from coastal Washington estuaries on the negative relationship between densities of *H. oregonensis* and juvenile Dungeness crab (Banks and Dinnel 2000; Visser et al. 2004).

3.1.7 Fisheries

While there are not currently Dungeness crab fisheries in the South Puget Sound region, the impacts of fisheries were included with the intention of supporting future sustainable fisheries. There are several questions regarding the impacts of fisheries on Dungeness crab populations which experts identified, such as whether a skewed gender ratio caused by the heavy harvest of adult male crabs has consequences for reproduction rates, and the mortality rate of female and sublegal crabs caught and released.

There are several studies which discuss the consequences of derelict fishing gear on crab populations. It is estimated that nearly 12,000 crab traps are lost annually in the Salish Sea waters of Washington, translating to a loss of approximately 179,000 legal size male crab, or 4.5% the value of recent harvests (Antonelis et al. 2011). Antonelis et al. (2023) tested the effectiveness of Dungeness crab escapement based on trap design to reduce crab mortality through influencing resource management and gear manufacturing. Another study conducted a cost/benefits analysis of derelict net removal and determined that the removal of one derelict gillnet (with a removal cost of $1358) would prevent the entanglement of 4368 Dungeness crabs (worth $19,656) (Gilardi et al. 2010).

Other studies looked at the variable short and long term effects of management strategies. Zhang et al. (2004) models long-term yields in British Columbia, Canada, under an intensive fishery coupled with handling mortality, determining that crabs had a 70.1% chance to survive one-month post-molt. The authors developed a method to calculate a threshold of discarded or retained crabs beyond which would reduce harvests long-term. Froehlich et al. (2017) examined how management strategies performed during periods of seasonal hypoxic zones in Hood Canal, Washington, highlighting the need to take hypoxia-induced catchability changes into consideration. The final two studies highlight how fishery closures can mitigate the effects of fisheries on Dungeness crab. Research in British Columbia supports that fisheries decrease both the abundance and size of Dungeness crab, but that fishery closures may reduce those effects by providing temporary refuge (Frid et al. 2016; Burns et al. 2020).

3.2 Direct physical and ecological stressors (Pressure-State)

Out of the ten pressures, experts identified ocean acidification influencing all life stages of Dungeness crab. Water temperature and prey availability were each identified as affecting all life stages other than eggs. In total, thirteen interactions between Pressures and States were not represented in the literature, mostly involving the relationship between biotic factors and life stages other than adult crabs. As show in Figure 2, out of the 52 studies which tested Pressure-State linkages, water temperature (23%), ocean acidification (19%), and dissolved oxygen (17%) were the most frequently tested pressures, and the adult life stage (44%) was most frequently the subject of the study, followed by zoea (21%) and juveniles (19%).

3.2.1 Dissolved Oxygen

According to surveys between 2014-2018, the open waters of South Puget Sound are consistently well-oxygenated both at the surface and at depth, although oxygen steadily declines from spring to fall (Alin et al. 2024). While Dungeness crab have been characterized as being tolerant to low levels of dissolved oxygen (Froehlich et al. 2015), studies have investigated various behavioral and physiological impacts of hypoxic conditions. While there may not be large-scale migration from hypoxic regions, Dungeness crab are observed to move towards shallower water and have heightened levels of activity which may increase their vulnerability to crabbing and indirect ecological consequences (Froehlich et al. 2014). A laboratory study revealed that crabs stopped feeding below 3.2 kPA O_2 and unfed crabs are less likely to enter hypoxic waters to forage. When crabs obtained and fed in hypoxic water, they returned to areas of higher oxygen to digest (Bernatis et al. 2007). The same study also observed behavioral responses of fed and unfed crabs released into the field. The crabs tended to prefer slightly hypoxic water, with unfed crabs showing elevated activity while the fed crabs settled and did not move far from the release site, suggesting that crabs cannot balance the simultaneous energy requirements of activity and digestion (Bernatis et al. 2007). Low dissolved oxygen has also been linked to reduced immune and respiratory ability in Dungeness crab (Scholnick and Haynes 2012).

3.2.2 Water temperature

There have been several studies which have assessed the effects of variable water temperature on larval development and early juvenile mortality. Different zoeal stages have a variable response to temperature, with duration and survival values being largely independent from stage to stage. In laboratory studies, all zoeal instars show high mortality as water temperature approaches 20°C , but especially as terminal fifth stage zoea metamorphose into megalopae with 50% of larvae dying at 15°C and 100% at 20°C (Sulkin and McKeen 1989). Temperature also influences duration of zoeal stages. A study revealed that a temperature treatment simulating the colder waters of Puget Sound increased zoeal duration by 44% and megalopae exhibited a significantly lower rate of mortality compared to oceanic waters off the central coast of California (Sulkin and McKeen 1996). Another study on megalopae and juveniles found that survival of megalopae was not directly affected by temperature, but that time to metamorphosis and growth differed among treatments (14, 18, and 22°C). Juvenile survival differed among temperature treatments, with only 2% of crabs surviving to crab IV stage at 22°C, compared to 84 and 90% survival at 14°C and 18°C (Sulkin et al. 1996).

While it is understood that the coastal outer populations of Dungeness crab recruit from a single cohort supplied by the California current (Rasmuson 2013), there is evidence of populations in Puget Sound recruiting from local waters with supplementation from the outer coast (Dinnel et al. 1993). When the two cohorts are reared in similar laboratory conditions, cohort-of-origin had greater effect on growth than variable temperature treatments. The cohort originating from Puget Sound molted more frequently at smaller increments (Cook et al. 2024).

3.2.3 Salinity

Studies have tested the effects of salinity on larval and juvenile development on coastal Dungeness crab (Reed 1969; Moloney et al. 1994; Holsman et al. 2006), however the results of these studies may not be representative of populations from inland waters. According to Reed (1969), waters with salinities less than 25 PSU may cause negative physiological effects in larval Dungeness crab. A study of larval abundance in the Strait of Georgia from 2009-2010 found a negative correlation between salinity and larval abundance (Sorochan and Quijón 2014).

3.2.4 Ocean acidification

The acidification of estuary waters poses several risks to Dungeness crab across life stages. Lower pH does not appear to affect the hatching probability of eggs, but was shown to delay hatching when eggers were exposed to a treatment of pH 7.1 prior to hatching (Miller et al. 2016). At the larval stage, lower pH and carbonate mineral saturations states associated with ocean acidification results in observed carapace dissolution at the zoea stage (Bednarsek, Pelletier, et al. 2020; Bednarsek, Feely, et al. 2020), as well as decreased larval width (Bednarsek, Feely, et al. 2020; Saenger et al. 2023). It is suggested that the zoea stage is more sensitive to elevated levels of CO_2, as megalopae and early juveniles reared in high CO_2 conditions exhibited a higher survival rate than those at ambient levels, albeit with a higher resting metabolic rate and smaller overall size (McElhany et al. 2022). Elevated CO_2 levels additionally impact foraging behavior through impairment of olfactory pathways (Durant et al. 2023).

3.2.5 Habitat

As discussed previously, late stage megalopae and early juveniles rely on suitable habitat which provides refuge from predation. Studies conducted in estuaries along the Washington coast found that intertidal shell habitats enhance survival during early stages of benthic life (Fernandez et al. 1993; Iribarne et al. 1995; Banks and Dinnel 2000) and provide important foraging habitat (Holsman et al. 2003). However, there was a lack of studies in the reviewed literature which characterize habitat use by life stage in the Salish Sea.

3.2.6 Disease & Parasites

There is very little research on the impacts of various diseases and parasites on Dungeness crab in the Salish Sea. One study on the distribution of a microsporidian parasite, *Nadelspora canceri*, found that the parasite was prevalent in coastal populations from California to southern Washington, but was absent in Puget Sound (Childers et al. 1996). Another study described molt mortalities related to infection by the ciliate, *Mesanophrys pugettensis* (Morado et al. 1999). In British Columbia, another microsporidian parasite, *Ameson meticarcini*, was found to infect the skeletal musculature of Dungeness crab and has been observed since 1998 (Small et al. 2014), however little is known about the distribution and transmission of *A. metacarcini* or crab mortality related to infection.

3.2.7 Competition

As previously discussed, little research exists on interspecies competition between Dungeness crab and other local crab species within the Salish Sea. Expert knowledge suggests Dungeness crab may experience competition with other species, such as red rock, graceful, and shore crab, depending on life stage.

3.2.8 Predation

There were no studies found on the risks of predation specific to Dungeness crab in the Salish Sea region. Juvenile crabs are common food items for several predators such as starry flounder (Platichthys stellatus), English sole (Parophrys vetulus) and Staghorn sculpin (Leptocottus armatus), while adult crabs have relatively few predators due to their size (Rasmuson 2013).

3.2.9 Prey Availability

I found no existing studies on the prey availability of Dungeness crab in the Salish Sea. Only one experimental study was identified, which found that larval growth schedules of distinct cohorts originating from coastal or inland populations were not maintained regardless of temperature and food availability (Cook et al. 2024).

4. Discussion

Eliciting expert knowledge and advice is commonly used in order to provide the best available science to address critical resource management decisions in relation to how marine species may respond to a changing climate (Donlan et al. 2010; Ryder et al. 2010; Martin et al. 2012). In this study, motivated by the sudden and dramatic decline in Dungeness crab harvest in South Puget Sound and a lack of local empirical data, we invited fishery managers and researchers to co-develop a conceptual model of the direct and indirect stressors across Dungeness crab life stages to inform research and management priorities. Although specific to South Puget Sound, this conceptual model is the first to identify and describe stressors on Dungeness Crab populations within the Puget Sound and synthesizes expert knowledge and literature relevant to the greater Salish Sea region. Validating this model, and quantifying the direction and strength of relationships, is the first step towards developing predictive models of Dungeness crab abundance in response to natural and anthropogenic impacts.

Based on discussions during the initial expert workshop and subsequent PCRG meetings, and substantiated by the literature review, the main drivers of Dungeness crab abundance in South Puget Sound appear to be the overlapping impacts of climate change and eutrophication on dissolved oxygen, water temperature, and ocean acidification. Additionally, climate change can intensify eutrophication in estuarine and coastal waters through increased temperatures and changes in precipitation (Rabalais et al. 2009; Nazari-Sharabian et al. 2018). The larval stages of Dungeness crab appear the most vulnerable to the effects of increasing temperature and ocean acidification. Studies have found that South Puget Sound has lower buffer capacity and higher levels of eutrophication than the main basin of Puget Sound, and larval Dungeness crab may be exposed to less-than-optimal levels of pH which can result in reduced survival and lethality (Cai et al. 2021). Low Dungeness crab abundance may be a result of larva migrating out of South Puget Sound or suffering lower survival rates at the zoeal stage. The decline in Dungeness crab harvest between 2012 and 2017 coincides with anomalously high temperatures observed due to the NE Pacific marine heat wave. Subsurface water temperatures peaked on the coast during 2014 and proliferated into Puget Sound throughout 2014-2016 (Alin et al. 2024). As previously discussed, increased water temperature has several negative effects on larval and juvenile

Dungeness crab and can also decrease dissolved oxygen in the water. Although adult Dungeness crabs do not exhibit mass migration away from hypoxic regions, noted behavioral changes due to hypoxia enhanced by elevated temperatures may have increased catchability between 2014-2016.

The Driver-Pressure-State interactions identified in our conceptual model co-developed with the expert-based focus group was overall well supported by the greater body of literature on Dungeness crab, which primarily focuses on the coastally distributed populations spanning from California to Alaska. It is repeatedly noted in the literature that there is a lack of studies on populations residing in inland waters like the Salish Sea (as reviewed by Rasmuson 2013), and that studies on Dungeness crab originating from the California Current may not be representative of those residing in inland waters. Therefore, the literature review conducted for this paper focused on identifying published literature regionally focused on the Salish Sea and identifying where gaps exist. Of the 78 interactions identified in the conceptual model, 73% of the interactions had at minimum a single published study on the topic. The lack of regional data to support these interactions may limit the application of the conceptual model to conservation and management decisions within the Salish Sea. However, the strong consensus among experts may indicate the results are a reasonable approximation of the processes taking place in South Puget Sound.

Several trends emerged in reviewing available literature on Dungeness crab in the Salish Sea. Studies which assessed Driver-Pressure interactions made up 24.3% of all the studies reviewed compared to studies testing Pressure-State interactions (75.7%). This reflects a general lack of research on the impacts of increasing temperatures and acidification within estuaries, as compared to open coastal waters and the ocean (as reviewed by Cai et al. 2021). Climate change and shoreline development were the most common Drivers discussed. When considering

Pressure-State interactions, the most studied Pressures are water temperature (23%), ocean acidification (19%), and dissolved oxygen (17%). The Pressures with existing literature are primarily abiotic factors, while biotic factors are largely unrepresented. There was also a noticeable trend in studied life stages (States). The adult stage was the focus of 44% of Pressure-State studies, followed by zoea (21%) and juveniles (19%). This is likely due to the ease of studying each life stage by laboratory experiments or field data. It is far easier to collect data on adult crabs in the field due to their size, and because of the Dungeness crab fishery there is infrastructure already in place to facilitate these studies. Zoea and Juveniles both go through several molts and can be hatched and reared in a lab, however the intervening megalopae stage is very brief in comparison. Overall, more attention is paid to the adult stage than any of the younger life stages. A significant limitation of the model is that it does not include sex in determining the States. Female Dungeness crab go through a different life history than male crabs, and evidence suggests ovigerous females differ in habitat utilization (Rasmuson 2013). Very few studies in the reviewed literature included the South Puget Sound region, and those that did were larger studies analyzing environmental differences across Puget Sound.

Puget Sound is a diverse and complex system, amplifying the complexities of anthropogenic stressors in an estuarine ecosystem. The task of managing a culturally and economically important fishery as large as Dungeness crab requires a great deal of time and resources, both of which are in short supply in South Puget Sound. By gathering a focus group of local experts on Dungeness crab, this project was able to quickly model the direct and indirect stressors that are likely to contribute to Dungeness crab abundance to inform a keyword focused literature review which identified knowledge gaps in local data. The results inform the direction of future research and provide resource managers with a framework which can be used in the absence of quantitative data. This comes just in time for the Pacific Northwest Crab Research Group, whose members participated in the focus group and revisions, as they re-evaluate research goals and priorities for the next five years through the development of a new research guide.

Appendix A: Search Strings
All searches completed by April 2025

Driver-Pressure

Eutrophication and dissolved oxygen
- (ALL=(eutrophication) AND ALL=(dissolved oxygen) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia") NOT ALL=("lake" OR "river"))

Eutrophication and water temperature
- (ALL=("eutrophication") AND ALL=("water temperature") AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia") NOT ALL=("lake" OR "river"))

Eutrophication and ocean acidification
- (ALL=("eutrophication") AND ALL=("ocean acidification") AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia") NOT ALL=("lake" OR "river"))

Eutrophication and habitat
- (ALL=("eutrophication") AND ALL=("benthic" OR "intertidal" OR "eel grass") AND ALL=("habitat") AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia") NOT ALL=("lake" OR "river"))

Shoreline development and dissolved oxygen
- ALL=("shoreline armoring" AND "dissolved oxygen")
- ALL=("shoreline development" AND "dissolved oxygen")

Shoreline development and water temperature
- ALL=("shoreline armoring" AND "water temperature")
- ALL=("shoreline development" AND "water temperature")

Shoreline development and habitat
- ALL=("shoreline armoring" AND "habitat") AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")
- ALL=("shoreline development" AND "habitat") AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Shoreline development and water movement
- ALL=(shoreline development) AND ALL=("estuarine circulation")
- ALL=(shoreline development) AND ALL=(circulation) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

- ALL=(shoreline development) AND ALL=(hydrodynamic) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")
- ALL=(shoreline armoring) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Due to the high degree of agreement on the environmental effects of climate change, these linkages were not included in the search.

Aquaculture and habitat

- ALL=(aquaculture) AND ALL=("Dungeness crab") AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Aquaculture and prey availability

- ALL=(aquaculture) AND ALL=("Dungeness crab") AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Native crab competitors interactions part of Pressures searches

Fishery and native crab competitors

- (ALL=("red rock" AND crab)) AND ALL=(fisher*) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Fishery and Dungeness crab

- ALL=("Dungeness crab" AND fisher*) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Pressure-Pressure

Water temperature and dissolved oxygen.

- Due to the high degree of agreement on the environmental effects of climate change, these linkages were not included in the search.

Salinity and Disease & Parasites

- ALL=("Dungeness crab") AND ALL=(salinity) AND ALL=(diseas*)
- ALL=("Dungeness crab") AND ALL=(salinity) AND ALL=(parasit*)

Ocean Acidification and Disease & Parasites

- ALL=("Dungeness crab") AND ALL=(ocean acidification) AND ALL=(parasit*)
- ALL=("Dungeness crab") AND ALL=(ocean acidification) AND ALL=(disease*)

Competition and Habitat. Part of Pressure-State search.

Pressures-State

Dissolved oxygen

- ALL=("Dungeness crab") AND ALL=(dissolved oxygen) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Water temperature

- ALL=("Dungeness crab") AND ALL=(temperature) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Salinity

- ALL=("Dungeness crab") AND ALL=(salinity) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Ocean Acidification

- ALL=("Dungeness crab") AND ALL=(acidification) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Habitat

- ALL=("Dungeness crab") AND ALL=(habitat) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Population connectivity

- ALL=("Dungeness crab") AND ALL=(population connectivity) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Disease and parasites

- ALL=("Dungeness crab") AND ALL=(disease) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")
- ALL=("Dungeness crab") AND ALL=(parasit*) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Prey availability

- ALL=("Dungeness crab") AND ALL=(prey availability) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

- ALL=("Dungeness crab") AND ALL=(prey) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Competition

- ALL=("Dungeness crab" AND compet*) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

Predation

- ALL=("Dungeness crab") AND ALL=(predation) AND ALL=("Salish Sea" OR "Puget Sound" OR "Strait of Georgia" OR "San Juan Islands" OR "Gulf Islands" OR "Vancouver Island" OR "Washington" OR "British Columbia")

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Figures

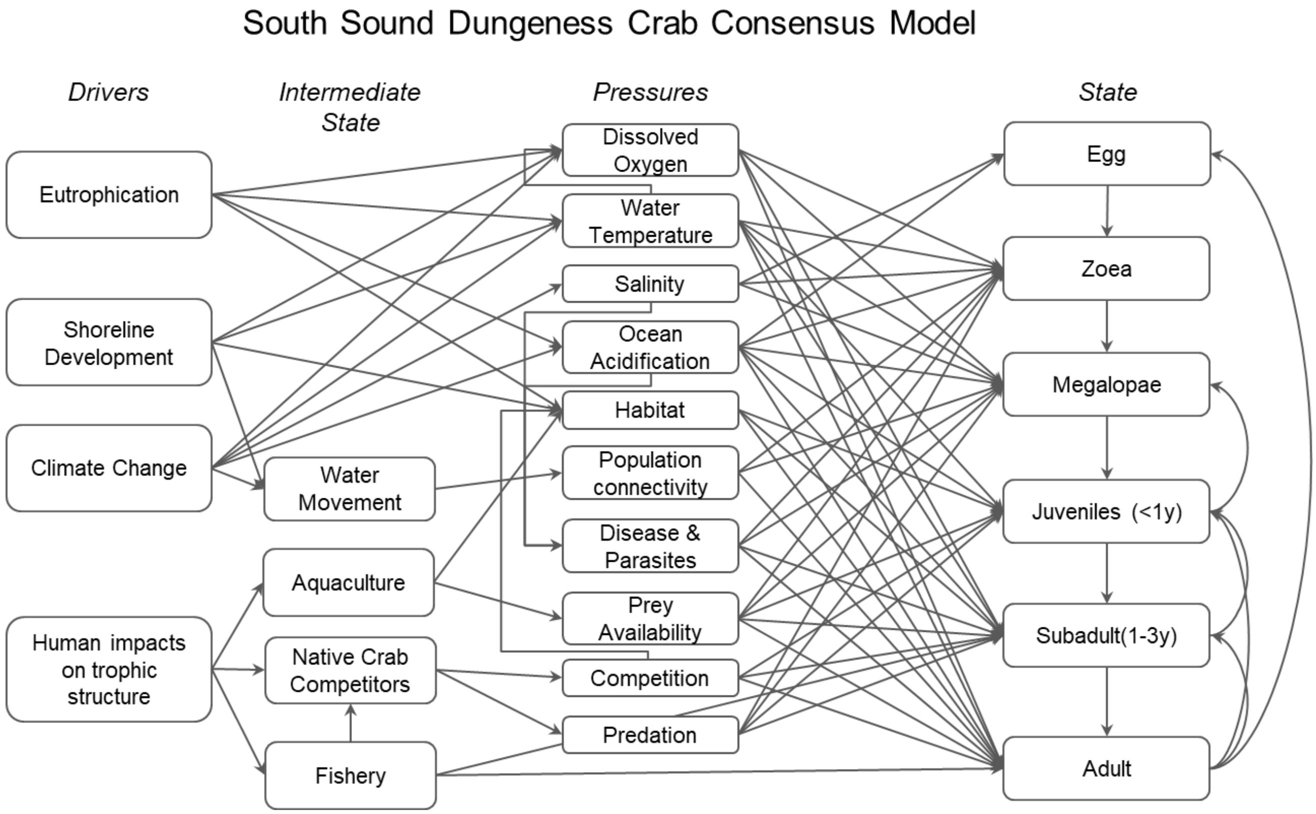

Figure 1. The final conceptual model authors co-developed with PCRG members using expert elicitation. The model identifies indirect human influences (Drivers) on direct environmental stressors (Pressures) on the various life stages of Dungeness crab (States). Four additional environmental conditions (Intermediate States) are included to clarify interaction pathways and may be targeted by management interventions.

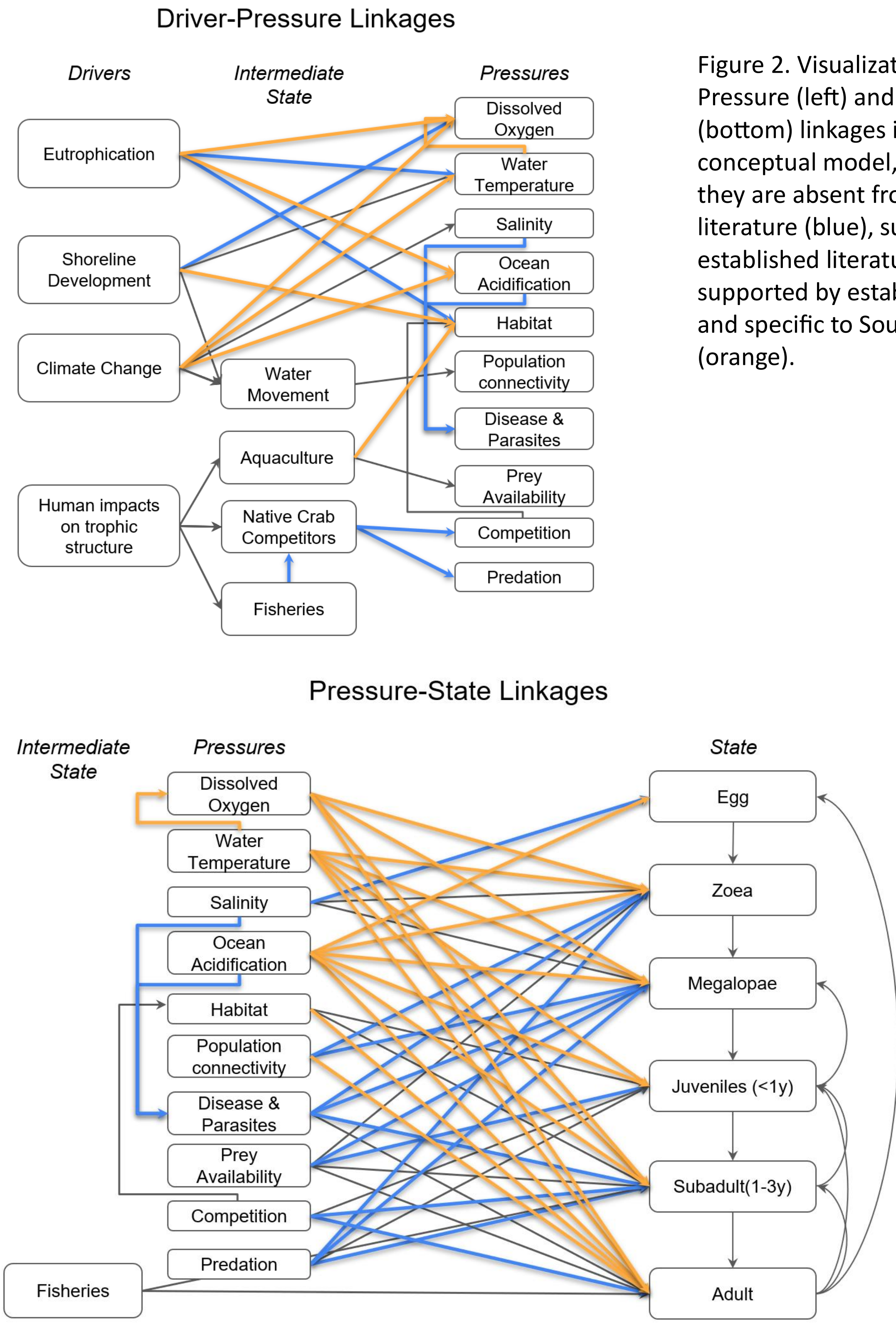

Figure 2. Visualization of Driver-Pressure (left) and Pressure-State (bottom) linkages identified by the conceptual model, and whether they are absent from established literature (blue), supported by established literature (gray), or supported by established literature and specific to South Puget Sound (orange).