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Technical Memorandum

Quantifying species-specific changes in aerobic habitat associated with seasonal dissolved oxygen depression in Puget Sound and the Straits

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Table of Contents

EXECUTIVE SUMMARY ... 5
1 INTRODUCTION AND BACKGROUND ... 7
1.1 Measured and modeled seasonal oxygen dynamics in Puget Sound ... 7
1.2 Species-specific habitat and exposure ... 8
1.3 Applying physiologically derived oxygen thresholds ... 9
2 METHODS ... 11
2.1 Metabolic index inputs and calculation ... 11
2.2 Study area and regional boundaries ... 19
3 RESULTS AND DISCUSSION ... 21
3.1 Dungeness crab aerobic habitat ... 21
3.2 English sole aerobic habitat ... 32
3.3 Chinook salmon aerobic habitat ... 38
4 CONCLUSIONS ... 44
5 FUTURE RESEARCH AND APPLICATION BUILDING ON THE CURRENT STUDY 48
6 REFERENCES ... 50
7 APPENDICES ... 54

List of Figures

Figure 1.3.1. Measured critical oxygen pressure (p_{crit}; kPa) observations as a function of temperature and body size. Each point represents a reported p_{crit} value from a published source, with points colored by phylum. The y-axis is plotted on a logarithmic scale. Reproduced from Figure 2 of Essington et al. (2026).. 9
Figure 1.3.2 Plot of p_{crit} vs. temperature for salmon (purple line) and crab (orange line) calculated from the values for each in the current database from Essington et al. (2026). The p_{crit} estimated for each species is shown for each temperature value, compared to the corresponding pO2 for each temperature (black line), calculated where dissolved oxygen is equal to 2 mg/L. 10
Figure 2.1.1. Frequency histogram of estimated critical oxygen pressure p_{crit} values for 148 species, based on Essington et al. (2026); p_{crit} values are estimates standardized at a reference temperature and body size. Red arrows identify the imputed reference p_{crit} values calculated for the three Puget Sound focal taxa used in this study: ES = English sole, DC = Dungeness crab, and CS = Chinook salmon. 14
Figure 2.1.2. Potential aerobic habitat — the physical space a species could occupy without limitations from oxygen and temperature — is defined differently for each of three species: seafloor area shallower than 80 m for Dungeness crab, seafloor area at all depths for English sole, and water volume in the top 100 m of the water column for Chinook salmon. This UW analysis only considers depth to define potential aerobic habitat. Other factors (e.g., substrate, food availability, etc.) may also limit a species' available habitat. Graphic: Emily Eng for PSI. 18
Figure 2.2.1. Spatial delineation of six regions based on Salish Sea Model cell groupings covering Puget Sound and extending to United States waters in the Strait of Juan de Fuca (SJF) and Strait of Georgia (SOG) (after Ahmed et al., 2021).. 19
Figure 3.1.1. Daily time series of routine metabolic index (Φ) for Dungeness crab in bottom waters during 2014: Penn Cove, Whidbey Basin (Cell 8841, top panel) and southern Hood Canal (Cell 13789, bottom panel). Y-axis is on a natural log scale. The dashed line indicates Φ = 1, below which oxygen supply is insufficient to meet routine metabolic demand. 21
Figure 3.1.2. Spatial extent and number of days during 2014 when routine Φ < 1 for Dungeness crab in bottom waters <80 m. 26
Figure 3.1.3. Daily time series of bottom water area <80 m during 2014 when routine Φ < 1 for Dungeness crab, by region, for existing and reference conditions. 27
Figure 3.1.4. Spatial extent during 2014 when routine Φ < 1 for Dungeness crab in bottom waters <80 m, showing cells where the threshold was exceeded on at least one day, for the reference scenario (grey) overlaying the larger existing scenario extent with 2014 nitrogen loads (orange). The top panel shows Whidbey and the bottom panel shows Hood Canal and parts of South and Central Sound regions. See Appendix 4 for all locations. 29
Figure 3.1.5. Change in number of days when routine Φ < 1 for Dungeness crab in bottom waters <80 m between existing and reference conditions during 2014. Positive values indicate additional days below the threshold, showing habitat loss attributable to nitrogen from human activities in Washington State. 31
Figure 3.2.1. Spatial extent and number of days during 2014 when routine Φ < 1 for English sole in bottom waters.. 33

Figure 3.2.2. Daily time series of bottom water area during 2014 when routine Φ < 1 for English sole, by region, for existing and reference conditions. 34
Figure 3.2.3. Change in the number of days when routine Φ < 1 for English sole in bottom waters between existing and reference conditions during 2014. Positive values indicate additional days below the threshold, showing habitat loss attributable to nitrogen from human activities in Washington State. 37
Figure 3.3.1. Spatial extent and number of days during 2014 when routine Φ < 1 for Chinook salmon in bottom waters that fall within the 100m habitat range (left panel) and surface waters (right panel). Bottom waters contain almost all calculated habitat compressed (discussed in the accompanying text), and additional plots and analysis of parts of the water column are presented in Appendix 6... 39
Figure 3.3.2. Daily time series of water column volume during 2014 when routine Φ < 1 for Chinook salmon, by region, for existing and reference conditions. 41

List of Tables

Table 2.1.1. Species-specific model parameters from phylogenetic analysis. (logV) determines baseline oxygen requirements, (n) controls body size effects, (E_o) controls temperature effects. p_{crit} is the calculated species-specific oxygen threshold. Further details on species weights are provided in the accompanying text. 13
Table 3.1.1. Annualized daily average area and percent of habitat during 2014 when routine $\Phi < 1$ for Dungeness crab for existing and reference conditions, as well as the difference between the two........ 24
Table 3.1.2. Average area and percent of habitat during the period of compression in each region in 2014 when routine $\Phi < 1$ for Dungeness crab, for existing and reference conditions, as well as the difference between the two. 28
Table 3.1.3. The maximum extent of habitat in 2014 with routine $\Phi < 1$ for Dungeness crab, by region, for existing and reference conditions. 28
Table 3.2.1. Annualized daily average area and percent of habitat during 2014 when routine $\Phi < 1$ for English sole, for existing and reference conditions, as well as the difference between the two........ 32
Table 3.2.2. Average area and percent of habitat during the period of compression in each region in 2014 when routine $\Phi < 1$ for English sole, for existing and reference conditions, as well as the difference between the two. 35
Table 3.2.3. The maximum extent of habitat in 2014 with routine $\Phi < 1$ for English sole, by region, for existing and reference conditions. 35
Table 3.3.1. Annualized daily average volume and percent of habitat during 2014 when routine $\Phi < 1$ for Chinook salmon, for existing and reference conditions, as well as the difference between the two. 39
Table 3.3.2. Average volume and percent of habitat during the period of compression in each region in 2014 when routine $\Phi < 1$ for Chinook salmon, for existing and reference conditions, as well as the difference between the two. 42
Table 3.3.3. The maximum extent of habitat in 2014 with routine $\Phi < 1$ for Chinook salmon, by region, for existing and reference conditions. 42
Table 3.3.1. Summary of available aerobic habitat available to three Puget Sound species*. Habitat metrics (rows) of aerobic habitat compression ($\Phi < 1$) and mean refuge under 2014 existing and reference conditions are shown for each species (columns) for each of the two model scenarios, as well as the calculated loss due to nitrogen from human activities in Washington State (existing-reference scenario). The percent of habitat for each metric is based on the species-specific total habitat available (shown in grey on row 3). 47

EXECUTIVE SUMMARY

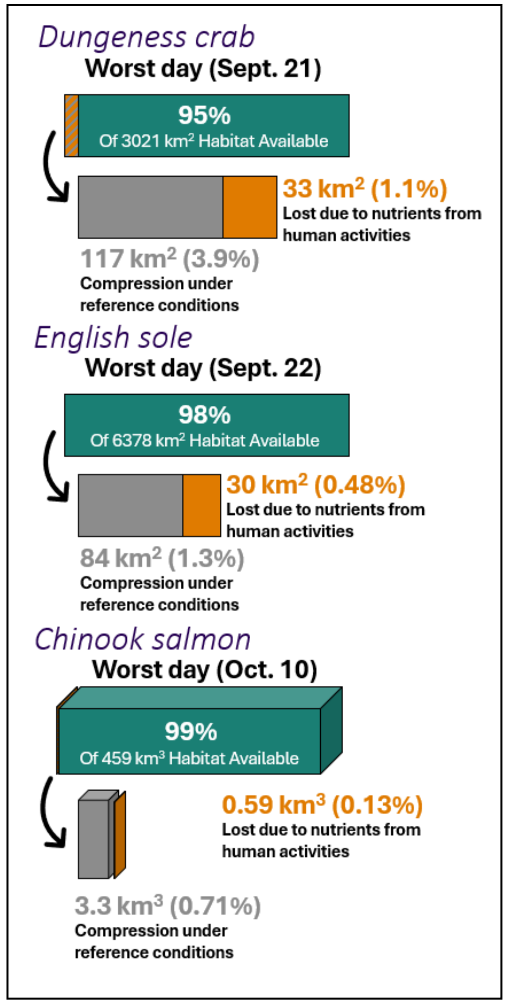
The waters of Puget Sound and the Straits naturally experience seasonally low dissolved oxygen concentrations. Nitrogen from human activities may further decrease dissolved oxygen levels in specific locations, especially in Hood Canal and some terminal inlets and embayments during certain times of the year. To inform strategic nitrogen management efforts, it is crucial to understand not only when and where human-driven nitrogen inputs intensify lower-oxygen conditions, but also where these changes are likely to translate into biologically meaningful risk for marine life. To address this, we developed an approach to assess the aerobic habitats of key species in Puget Sound that compares the species-specific oxygen requirements for routine metabolic activities determined using the metabolic index trait-imputation framework of Essington et al. (2026) to dissolved oxygen and temperature conditions determined using a biogeochemical model. The metabolic index approach applied in this research offers a more nuanced assessment framework to understand the impacts of lower dissolved oxygen concentrations on marine organisms, improving upon approaches that use a low dissolved oxygen concentration threshold alone (such as using <2 mg/L to indicate hypoxic conditions). This is because the approach explicitly includes differences in oxygen requirements among species, while at the same time accounting for the coincident influences of temperature. The metabolic index (Φ) is defined as the ratio of oxygen supply to demand, both of which depend on temperature and body size. The index incorporates laboratory-derived measurements of oxygen levels needed to support an organism's metabolic demands and how those thresholds vary with temperature and body size. When detailed laboratory data are unavailable for a species, statistical methods are used to estimate metabolic index parameters based on taxonomic relatedness to other species that have such data. By combining these with water quality model-derived projections of oxygen concentrations and temperature with and without human-derived nutrient inputs, we aim to provide improved estimates of the risks that such nutrient inputs pose to the habitats used by Puget Sound taxa.

We developed and applied an approach to assess impacts of reduced oxygen levels that draws on three core elements: (1) statistically estimating species-specific physiological oxygen thresholds from laboratory data; (2) using the Salish Sea model to estimate oxygen levels on a fine spatio-temporal scale for the year 2014, with and without nutrient inputs from human activities in Washington; and (3) combining the elements above to assess reductions in each species' aerobic habitat caused by nutrients from human activities. Throughout this work, when forced to make methodological decisions, we chose options that we identified as being most protective of species.

Key results derived from this approach

This analysis demonstrates that species-specific aerobic habitat assessment is achievable using existing biogeochemical model outputs and statistically derived, temperature-dependent, physiological thresholds for each species, providing a practical framework for incorporating biological thresholds into water quality management. Key findings on habitat compression are summarized below and in the adjacent box.

- The waters of Puget Sound and the Straits experience seasonal cycles of temperature and dissolved oxygen, with predictably higher temperatures and lower dissolved oxygen in summer and fall. These cycles are especially pronounced in inlets and parts of Hood Canal. Results from this study show that species-specific aerobic habitat varies seasonally and spatially, consistent with the documented patterns of circulation, stratification, and oxygen dynamics in the region. Seasonal temperature and dissolved oxygen cycles together compress species-specific aerobic habitat in bottom waters of terminal inlets during the warmer summer and fall months, with Hood Canal experiencing much greater and more persistent compression that also extends into the winter.
- Throughout the year, at least 95% of each species' potential habitat contains adequate dissolved oxygen levels to serve as a refuge even during the worst times of the year. For Chinook salmon, this also includes the overlying water column where oxygenated habitat remains accessible, directly above bottom waters with lower oxygen levels. Salmon and other pelagic species move through the water column, allowing them to potentially avoid unfavorable conditions in deeper waters.



- During the worst time of the year in late summer, when dissolved oxygen concentrations are lowest and temperatures are still relatively warm, at most 5% of the total available Dungeness crab habitat and <2% of English sole habitat are compressed throughout Puget Sound and the Straits. While less than 0.84% of Chinook habitat volume was compressed during the worst time of the year.
- The amount of seasonal habitat compression varies spatially. For example, on each region's worst day of the year, 1.2% of Dungeness crab habitat within the Straits of Juan de Fuca is compressed, compared to 35% of habitat within Hood Canal.
- Nitrogen from human activities in Washington State contributed a relatively small share of total habitat compression across Puget Sound and the Straits. For the three species examined here, ≤1.1% of habitat was predicted to be lost during the worst time of the year due to nitrogen from human activities in Washington State.

1 INTRODUCTION AND BACKGROUND

Nutrients in Puget Sound are both natural and essential — they fuel primary productivity and support the base of the marine food web. However, the addition of too much nitrogen from human activities can intensify natural processes to a point of detrimental stress and impact on marine ecosystems, including harmful algal blooms, shifts in food-web structure, reduced eelgrass habitat, changes in carbon chemistry, and lowered dissolved oxygen. Coastal waters influenced by upwelling shelf systems experience naturally low-dissolved-oxygen conditions because incoming ocean water is nutrient-rich and relatively oxygen-poor (Fennel and Testa, 2019). For Puget Sound, understanding the relative influence and impacts of nutrients from human activities on biological processes is essential for setting effective nutrient management targets within a system shaped by complex natural drivers and processes. Applying a framework to assess aerobic habitat change for Puget Sound species with modeled nutrient reduction targets is possible by building on existing research within this region on drivers and predictions of low dissolved oxygen, while understanding the methodologies and limitations of approaches applied elsewhere to assess risks to marine organisms (e.g., Frieder et al., 2024). This includes:

- Measured and modeled seasonal oxygen dynamics in Puget Sound
- Species-specific habitat compression and remaining refuge
- Applying physiologically derived oxygen thresholds

1.1 Measured and modeled seasonal oxygen dynamics in Puget Sound

Seasonal and inter-annual oxygen dynamics in Puget Sound have been examined through a combination of field observations, long-term monitoring programs, and the development of coupled hydrodynamic-biogeochemical models.

Low dissolved oxygen conditions have been observed across multiple basins of Puget Sound and the Salish Sea for decades, with substantial variability in severity, persistence, and seasonal timing among regions. Low dissolved oxygen and hypoxia have been documented in Puget Sound and the broader Salish Sea for decades, including early work by Barnes and Collias (1958), seasonal hypoxia studies in Hood Canal (Newton et al., 2007), and low dissolved oxygen levels identified in terminal inlets such as Penn Cove (PSAT, 2007). More recent analysis by Mascarenas et al. (2026, in review) of nearly 100 years of data showed that fall bottom waters in the deeper parts of Main Basin in Puget Sound have warmed and lost dissolved oxygen, with approximately 40–100% of this oxygen loss attributed to warming-driven reductions in oxygen surface saturation. The observed warming was correlated with regional atmospheric and offshore ocean warming trends.

Concern about nutrient effects on dissolved oxygen has led to the expansion of multiple hydrodynamic and biogeochemical modeling efforts in Puget Sound to better understand circulation, nutrient dynamics, and drivers of dissolved oxygen variability (e.g., MacCready et al., 2021; Khangaonkar et al., 2018). This includes applying the Salish Sea Model to evaluate dissolved oxygen conditions and the effectiveness of nutrient-reduction scenarios and targets (Ahmed et al., 2019; Ahmed et al., 2021; Figueroa-Kaminsky et al., 2025). Together, these observations and modeling studies have highlighted the importance of both natural physical processes and anthropogenic nutrient inputs in shaping seasonal oxygen conditions across Puget Sound basins.

Using the Salish Sea Model, Khangaonkar et al. (2018) quantified seasonal bottom-water hypoxia in the Salish Sea, estimating approximately 143 km^2 of hypoxic area (1% of the Salish Sea). The largest and most persistent hypoxic region was in Hood Canal, where the model reproduced a 30–40 km hypoxic region during peak conditions. The authors attributed hypoxia in Hood Canal primarily to its fjord-type, two-layer circulation, and a nearly stagnant deep layer occupying about 60% of the water column. Critically, because summer nitrogen in the euphotic zone was depleted to near-zero levels in parts of Puget Sound, the authors concluded that land-based nitrogen inputs may stimulate primary production and related oxygen-demand processes, including organic matter remineralization and sediment oxygen demand; thereby intensifying seasonal low dissolved oxygen. This is consistent with recent Puget Sound monitoring studies showing that higher sediment oxygen uptake is associated with higher primary production and greater sedimentation of organic matter, linking nutrient-stimulated production to increased bottom-water oxygen demand (Santana and Shull, 2023).

Some Salish Sea basins are particularly vulnerable to nutrient pollution in part because restricted circulation, shoreline complexity, islands, and sill-controlled bathymetry can produce long flushing and residence times (MacCready et al., 2021; Premathilake and Khangaonkar, 2022). Modeled flushing time for the Puget Sound region as a whole was estimated at approximately 115 days, while individual parts of the system were found to varied from approximately 2 days in Admiralty Inlet to more than 100 days in Hood Canal, with South Puget Sound and Whidbey Basin estimated at about 40 and 28 days, respectively (Premathilake and Khangaonkar, 2022). These longer transport times increase the opportunity for nutrients entering the euphotic zone to support primary production before being exported from a particular part of the system and out of Puget Sound.

1.2 Species-specific habitat and exposure

Despite substantial progress in characterizing dissolved oxygen conditions and nutrient-response processes in Puget Sound, a key gap remains in understanding how these patterns translate into species-specific aerobic habitat availability. Exposure to low dissolved oxygen thresholds within a species' habitat range is commonly used in estuarine and coastal systems to quantify habitat compression and potential biological impact. These approaches range from complex habitat suitability models (Frieder et al., 2024) for specific species to threshold-based summaries that apply a dissolved oxygen criterion to a defined habitat, season, and/or exposure duration, as was applied in the Chesapeake Bay (US EPA, 2003; US EPA, 2017). For threshold-based metrics to be protective across species, life stages, and seasons, criteria are often set using sensitive species or life stages to understand potential impacts relevant to all marine organisms. For example, US EPA (2000) recommends criteria protective of all but 5% of the most sensitive species. Because species differ in oxygen requirements, mobility, and vertical habitat use, quantifying potential aerobic habitat provides a relevant context for interpreting exposure and risk to marine organisms in Puget Sound.

1.3 Applying physiologically derived oxygen thresholds

Water temperature influences both the amount of dissolved oxygen available in the water and each species' metabolic demand. For this reason, temperature- and species-specific physiologically derived oxygen thresholds provide a stronger foundation for evaluating potential aerobic habitat than dissolved oxygen thresholds alone.

Among commonly used physiological thresholds, p_{crit} describes the oxygen level at which aerobic metabolism can no longer be maintained (e.g., Deutsch et al., 2015), whereas LC50 describes the oxygen level associated with 50% mortality over a defined exposure period (Vaquer-Sunyer and Duarte, 2011). Both p_{crit} and LC50 are temperature dependent, with lower LC50 and higher p_{crit} with increasing temperature (Vaquer-Sunyer and Duarte, 2011; Essington et al., 2026). Because p_{crit} reflects physiological limitation before mortality, and is less dependent on exposure duration than LC50, it can be considered better suited for evaluating aerobic habitat constraints. This can be seen in measured p_{crit} observations compiled by Essington et al. (2026), which span nearly two orders of magnitude with temperature, and generally increase with temperature and body size (Figure 1.3.1).

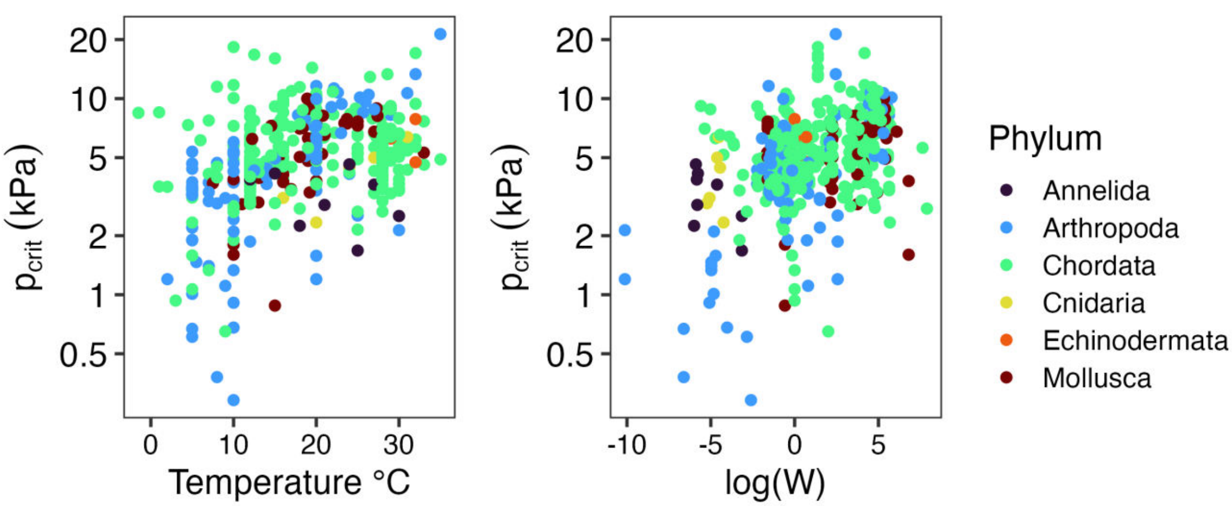


Figure 1.3.1. Measured critical oxygen pressure (p_{crit}; kPa) observations as a function of temperature and body size. Each point represents a reported p_{crit} value from a published source, with points colored by phylum. The y-axis is plotted on a logarithmic scale. Reproduced from Figure 2 of Essington et al. (2026).

Because of variation in species' oxygen demand and the role of temperature therein, fixed oxygen thresholds, such as 2 mg/L, cannot reliably predict oxygen levels needed to support organisms.

To illustrate this, we calculated the critical oxygen partial pressures (p_{crit}) for two key species present in Puget Sound across a range of temperatures experienced and compared those to the commonly used "hypoxia" threshold of 2 mg/L (Figure 1.3.2). For Chinook salmon, the species-specific threshold is consistently above the 2 mg/L line across the entire temperature range shown, meaning that waters technically above the hypoxia threshold may still be insufficient to support normal salmon activity at any temperature. While for Dungeness crab, the hypoxic threshold overestimates what crabs need at temperatures below 8-9°C and underestimates what crabs need at warmer temperatures. Chinook salmon also consistently need more oxygen than Dungeness crab.

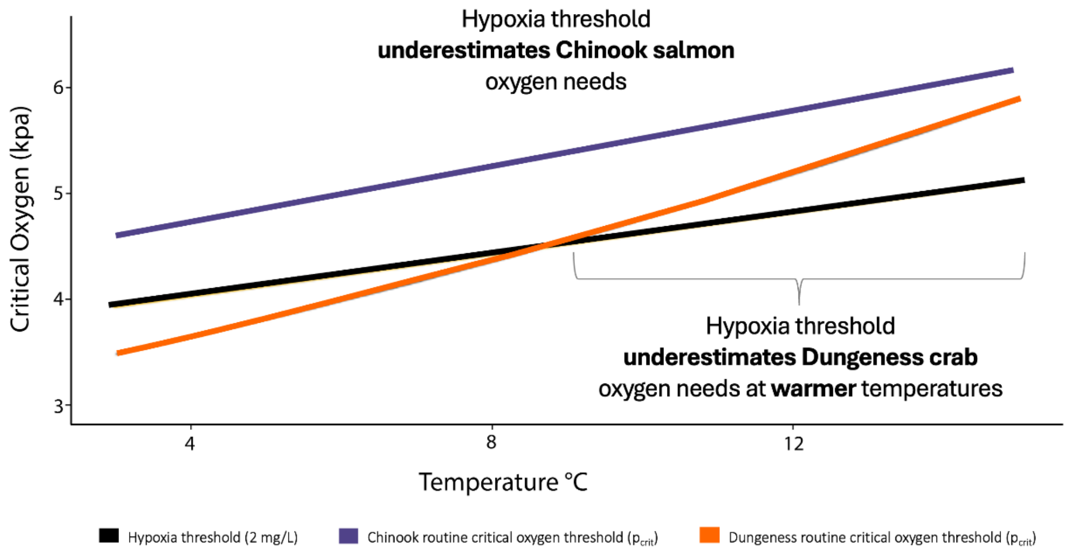


Figure 1.3.2 Plot of p_{crit} vs. temperature for salmon (purple line) and crab (orange line) calculated from the values for each in the current database from Essington et al. (2026). The p_{crit} estimated for each species is shown for each temperature value, compared to the corresponding pO2 for each temperature (black line), calculated where dissolved oxygen is equal to 2 mg/L.

Together, these comparisons demonstrate that taxa-specific p_{crit} provide a more nuanced and biologically meaningful oxygen threshold than a fixed dissolved oxygen concentration, particularly when evaluating risk across species and temperature gradients.

2 METHODS

The objectives and methods for this study can be summarized as follows:

1. To define the amount of aerobic habitat available (i.e., waters with sufficient dissolved oxygen to meet metabolic demand) to three Puget Sound species of regional environmental, economic, and social importance—Dungeness crab, English sole, and Chinook salmon.

    This is achieved by extending the phylogenetic trait imputation approach of Essington et al. (2026) to calculate the metabolic index for the three species. Temperature and dissolved oxygen outputs from the Salish Sea Model are used in the metabolic index calculation to define where and when the waters of Puget Sound and the Straits have sufficient dissolved oxygen concentrations to support the routine metabolic demand of each of the species.

2. To determine how the aerobic habitat of each of these species changes throughout the year under existing conditions, and across Puget Sound and the Straits, including identifying seasonal timing, extent, and spatial distribution of where habitat is compressed.

    This is achieved by using the metabolic index as a framework to integrate the spatially- and temporally-explicit temperature and dissolved oxygen outputs from the Salish Sea Model for the year 2014 with the empirically derived dissolved oxygen requirements of each species. Habitat compression (the reduction in available habitat due to a reduction in dissolved oxygen) is then quantified and mapped to characterize when and where habitat is seasonally reduced.

3. To quantify the contribution of nitrogen loadings from human activities in Washington State to seasonal aerobic habitat loss.

    This is achieved by evaluating the aerobic habitat available to each of the three species using modeled temperature and dissolved oxygen outputs from the Salish Sea Model runs with and without nitrogen loadings from human activities in Washington State.

The methods for defining and quantifying species-specific aerobic habitat are organized into two sections: physiological thresholds and metabolic index, and study area and regional boundaries.

2.1 Metabolic index inputs and calculation

Physiological thresholds for three Puget Sound taxa were investigated to understand the potential impacts of low dissolved oxygen events on marine organisms using numerical model outputs of spatial and temporal distribution of low dissolved oxygen and corresponding temperature. The three species examined were: Dungeness crab, English sole, and Chinook salmon.

We based physiological thresholds on extensive literature on metabolic theory that considers how temperature and body size govern the balance between oxygen supply and demand, using and extending the Essington et al. (2026) trait imputation methodology. The metabolic index (Φ)

is defined as the temperature- and body size-dependent ratio of oxygen supply to oxygen demand. The index calculated using the expression described by Penn and Deutsch (2022):

$$\phi = pO_2 \frac{1}{V} \left(\frac{W}{W_{ref}} \right)^n \exp\left(\frac{E_o}{k_b} \left(\frac{1}{T} - \frac{1}{T_{ref}} \right) \right)$$

Where W is body size (g), T is temperature (kelvin), k_b is Boltzmann's constant, and V, n, and E_o are species-specific parameters that describe the baseline vulnerability, allometric scaling, and temperature dependence of the metabolic index, respectively. T_{ref} and W_{ref} are reference temperatures and body sizes, which make the resulting parameter estimates more interpretable (i.e. V represents the critical oxygen pressure for an organism at the reference temperature and body size). Following Essington et al. (2026), these reference values were set at 15 C and 5 g, respectively.

Estimating critical oxygen thresholds of selected taxa

The metabolic index species-specific parameters can be calculated from experiments that measure the critical oxygen threshold, p_{crit}, and how it depends on temperature. Because conducting these experiments is time-consuming and sometimes logistically infeasible for many species, metabolic index parameter values are lacking for most aquatic animal species, including many of the species that inhabit Puget Sound. Recently, Essington et al. (2026) developed and applied a taxonomic trait imputation approach to estimate metabolic index parameters for species where data are lacking based on taxonomic relatedness. This allows us to predict the outcome of laboratory-based p_{crit} measurement for any species, at a given temperature and body size. For example, laboratory data are more limited for Dungeness crab and English sole, increasing reliance on trait-imputed parameter estimates. Readers are referred to Essington et al. (2026) for details of this methodology, including diagnostics and applications.

Briefly, the trait imputation method described in Essington et al. (2026) uses data on measured critical oxygen pressure, p_{crit}, for over 140 species of marine animals to estimate V, n, and E_o for any marine species in Phyla Annelida, Arthropoda, Cnidaria, Chordata, Echinodermata, and Mollusca. In this study, we augmented the dataset that informs these estimates to include as many p_{crit} estimates from species in the Salmonidae, Pleuronectidae, and Cancridae families as we could identify from the published literature. We then re-ran the taxonomic trait imputation model with the additional p_{crit} estimates to improve predictions for species specifically in these taxonomic groups (Table 2.1.1).

We use the imputed p_{crit} estimates as an index of oxygen conditions needed to support organism metabolism, but recognize that there are important limitations to this approach. p_{crit} measures the oxygen needed to support routine metabolism, but the levels needed to support active swimming, growth, and reproduction could be higher. Consequently, species may exhibit behavioral avoidance in habitats with oxygen greater than p_{crit}. On the other hand, laboratory-based measurements do not account for physiological acclimation, which can be substantial. Thus, the p_{crit} measured via an acute laboratory exposure may be higher than those experienced *in situ*. These opposing effects offset each other, but the net effect is uncertain.

Two critical p_{crit} endpoints were calculated:

- Basal metabolic index threshold (Φ_{basal}: calculated using parameters for the minimum energy required to maintain essential physiological functions (e.g., cellular function, circulation, respiration) while at rest.
- Routine metabolic index threshold ($\Phi_{routine}$: calculated using parameters for the energy required to support basal functions plus routine movement (e.g., non-directed swimming and other normal behavioral activities).

In this analysis using the Salish Sea Model outputs, we focus on applying the most conservative (protective) estimates of potential impact for each species examined to address inherent uncertainties. Therefore, we apply and report on the routine metabolic index where $\Phi < 1$ rather than using basal results. Predicted habitat compression using basal results is available in Appendices 4, 5, & 6. Results where $\Phi < 1$ are referred to throughout this report as aerobic habitat compression, showing when and where organisms may have a **high likelihood** of experiencing some level of impact on routine behavior; even if they survive the particular event, they may not thrive.

The three taxa investigated in this initial study (Dungeness crab, English sole, and Chinook salmon; Table 2.1.1) were selected as focal species based on their economic, ecological, and cultural importance in the region, their distribution across habitats potentially exposed to low dissolved oxygen conditions, and the availability of physiological input data needed to calculate the metabolic index. Although English sole is not as economically valuable as a fishery, it is one of the target species monitored for change by the Puget Sound Partnership's vital signs (Puget Sound Partnership, 2025) and is widely distributed throughout the Salish Sea.

Each taxon was analyzed using taxon-specific physiological parameters (V, E_o, and n) derived using trait imputation, along with best available estimates of representative body masses and depth distributions characteristic of each species' life history in Puget Sound. These standardized biological characteristics were applied consistently across all model scenarios to isolate the effects of changing environmental conditions on metabolic index values. Metabolic index results are based on the maximum likelihood predictions from the phylogenetic trait imputation (Essington et al., 2026), and upper and lower bounds of the 95% prediction interval for each were determined (Appendix 2). Thus, our calculations of the daily metabolic index capture the uncertainty resulting from parameter uncertainty.

Table 2.1.1. Species-specific model parameters from phylogenetic analysis. (logV) determines baseline oxygen requirements, (n) controls body size effects, (E_o) controls temperature effects. p_{crit} is the calculated species-specific oxygen threshold. Further details on species weights are provided in the accompanying text.

Species	log(V)	n	E_o	p_{crit} (kPa)	Weight (g)	Depth (m) range
Chinook salmon	1.58	-0.04	0.18	4.88	6400	Top 100 m of the water column
Dungeness crab	1.40	-0.07	0.30	4.04	1200	Bottom level at locations <80 m
English sole	1.22	-0.08	0.27	3.37	1000	Bottom level

To provide context for the thresholds applied for each species, Figure 2.1.1 shows the distribution of reference critical oxygen pressure p_{crit} values for 148 species represented in the Essington et al. (2026) dataset, with the three species-specific imputed values calculated and used in this study indicated in red. These red arrows correspond to the p_{crit} values in Table 2.1.1 for Dungeness crab, English sole, and Chinook salmon. These values fall within the broader range represented in the dataset, rather than at the extreme ends of the distribution. Among the focal taxa, Chinook salmon had the highest estimated reference p_{crit} and therefore the greatest oxygen sensitivity, English sole had the lowest, and Dungeness crab was intermediate.

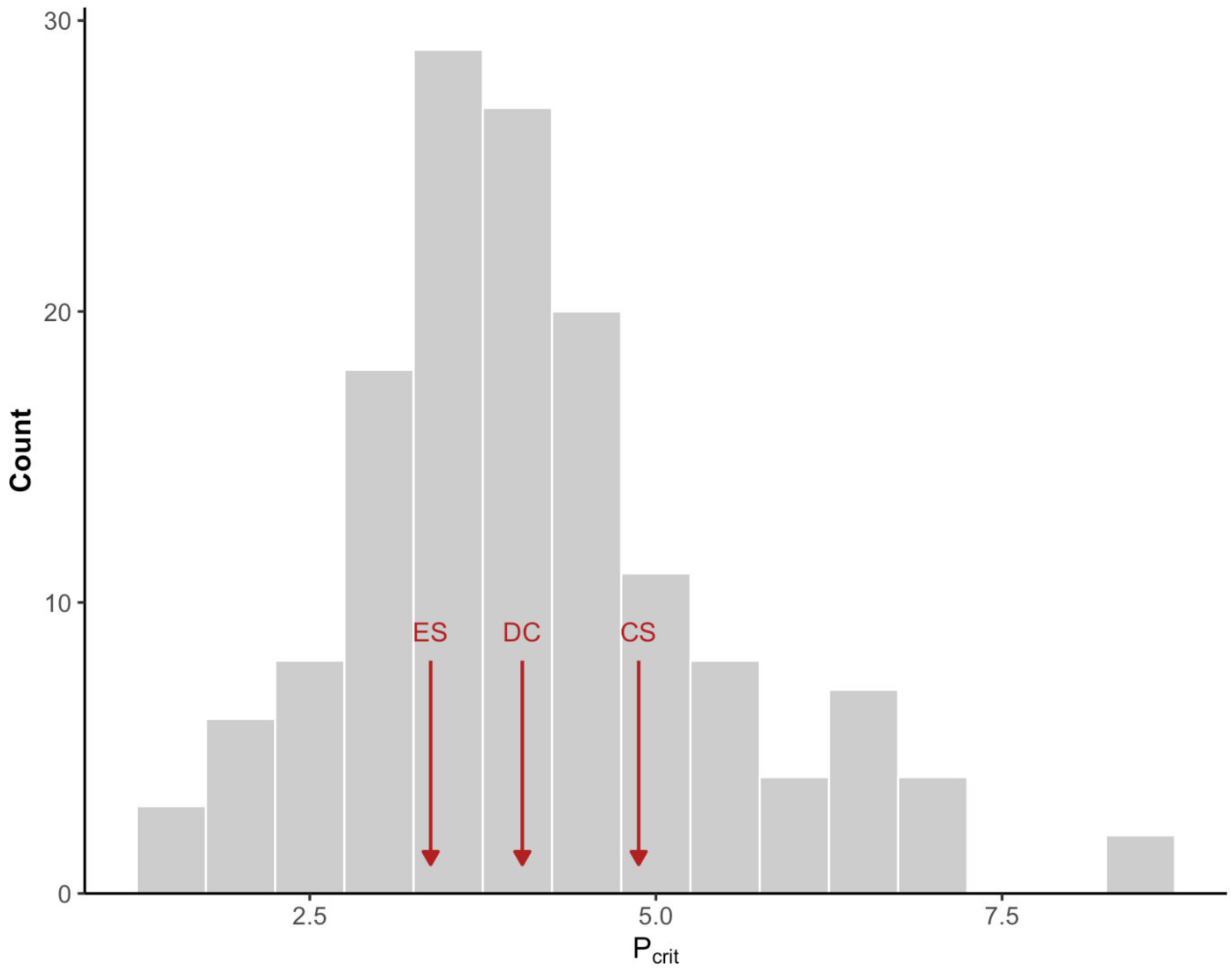


Figure 2.1.1. Frequency histogram of estimated critical oxygen pressure p_{crit} values for 148 species, based on Essington et al. (2026); p_{crit} values are estimates standardized at a reference temperature and body size. Red arrows identify the imputed reference p_{crit} values calculated for the three Puget Sound focal taxa used in this study: ES = English sole, DC = Dungeness crab, and CS = Chinook salmon.

The metabolic index also depends on body size. The following weights were used for each species.

Adult Dungeness crab: A representative adult Dungeness crab weight of 1,200 g was applied. 1,200 g corresponds to the upper weight range reported by Gamblewood et al. (2018), who sampled 446 legal-sized male Dungeness crabs from test fisheries in Crescent Harbor and Similk Bay between 2015 and 2017. Legal male crab weights ranged from approximately 600 to 1,200 g. The upper bound was selected as a conservative assumption to avoid underestimating metabolic demand, particularly given that female Dungeness crabs can attain larger sizes than males. For context, Gamblewood et al. (2018) reported a Puget Sound mean crab weight of 816.5 g that is used by the Washington Department of Fish and Wildlife for management purposes.

Adult English sole: Metabolic index calculations were performed using a weight of 1,000 g. A 1,000 g English sole is equivalent to an individual of approximately 45 cm total length, calculated using the FishBase length-weight relationship (Froese and Pauly, accessed April 3, 2026), and falling in the upper range of the Strait of Georgia dataset used in the equation's parameterization (length range 22–55 cm, n = 1,643; Fadeev, 2005). This weight represents a simplified assumption of size for large adult females, well above typical sizes at maturation, and as such is protective of the vast majority of the spawning population.

Adult Chinook salmon: A representative adult Chinook weight of 6400 g was applied. This weight is based on the estimated average adult mass in Puget Sound reported by Losee et al. (2019) for the year 2014, corresponding to the model year used in this study. The authors derived annual average weights from commercial purse seine landings by dividing the total landed weight by the number of fish caught each year. Across the period 1970–2015, adult Chinook mass ranged from approximately 5,500 to 10,000 g. For this study, the estimated mean of 6,400 g from the year 2014 was used.

Modeling environmental oxygen levels

To estimate the temperature-dependent environmental oxygen level an organism experiences, daily pO_2 levels were derived from Salish Sea Model predictions, which provided spatially and temporally resolved environmental conditions for each taxon examined. The Salish Sea Model is a finite element, three-dimensional hydrodynamic and biogeochemical model of the Salish Sea developed by the Pacific Northwest National Laboratory (Khangaonkar et al., 2018), in collaboration with the Department of Ecology. The daily Salish Sea Model biogeochemical outputs were derived from an existing conditions (2014) scenario at all 10 depth layers at each grid cell location within Puget Sound and the Straits. The existing conditions scenario represents an estimation of actual nitrogen loading and hydrodynamics for 2014, including estimates of river and point source wastewater treatment plant inputs from Washington State and Canadian watersheds to the receiving waters of the Salish Sea. The model outputs used here are virtually identical to those in the Washington State Department of Ecology's optimization scenarios report (Ahmed et al., 2021). The Salish Sea Model outputs used were temperature (T, in degrees Kelvin), salinity, depth, and dissolved oxygen concentrations. Dissolved oxygen concentrations were converted to partial pressure of oxygen (pO_2, in kPa) using the corresponding temperature, salinity, and depth pressure model outputs for each specific time and location.

The minimum and average daily metabolic index value for each grid location and depth layer were calculated for each taxon as follows:

1. The daily minimum partial pressure of oxygen (pO_2) was calculated at each depth layer and grid location from the minimum hourly dissolved oxygen, as well as average daily temperature and salinity for each of these depths and locations.
2. The minimum daily metabolic index for each depth layer at each grid location was calculated using the minimum daily pO_2, average daily temperature, and average daily salinity for that layer and grid location. This conservative approach both takes the minimum pO_2 and avoids unrealistic combinations of minimum pO_2 with minimum temperature that rarely co-occur.
3. An analogous process was conducted using the maximum pO_2 to generate the approximate maximum daily metabolic index for comparison.

The spatial and temporal distributions of low dissolved oxygen events and metabolic index results were analyzed using multiple metrics, with calculations described further below and scripts available on GitHub for each step of data processing (Appendix 1). We capture variation from environmental variability by repeating the calculations for all days of the year. Appendix 2 provides daily time series for three locations in Puget Sound where there is lower dissolved oxygen, showing uncertainties associated with the metabolic outputs.

Calculating habitat compression

Aerobic habitat compression — defined here as conditions where routine $\Phi < 1$, meaning oxygen supply is insufficient to meet a species' routine metabolic demand — was quantified spatially for each of the three study species. Compression was expressed as a percentage of each species' potential habitat, enabling comparison across regions of differing sizes. For the benthic species (Dungeness crab and English sole), compression was evaluated by area, reflecting their bottom-dwelling nature, while for the pelagic species (Chinook salmon), compression was evaluated by volume to reflect movement across both depth and horizontal space.

Potential habitat is defined from known species depth ranges within the unmasked sections of the Salish Sea Model domain. This approach means that a very broad estimate of potential habitat area and volume is assessed for each species, in the absence of available species occupancy or more granular habitat-specific data at each location. Resulting compressed habitat and refuge therefore depend not only on the depth ranges used to delineate potential habitat, but also on how well the Salish Sea Model represents the model domain and bathymetry.

Based on published field studies, the following depth ranges were used to define each species potential habitat in Puget Sound and the Straits; illustrated for all three species in a conceptual diagram of Figure 2.1.2.

Adult Dungeness crab: Metabolic index results were evaluated for bottom waters at locations shallower than 80 m. The depth constraint of 80 m in this study was based on observations summarized by Rasmuson (2013), who reported that non-ovigerous female Dungeness crabs in Puget Sound are typically found at depths of approximately 20–80 m, while males are generally observed at shallower depths (10–20 m), based on submersible surveys conducted by Armstrong et al. (1988).

Adult English sole: Bottom-layer model outputs were evaluated across all depths in the study region, rather than applying a maximum depth threshold, as was done with Dungeness crab. Evaluating all bottom-layer model outputs across all total water column depths in the study region is consistent with observations indicating a wide depth range for this species throughout Puget Sound (Blaine et al., 2024) and can be considered protective. From a review of available 2023 Puget Sound Bottom Trawl Survey data, Blaine et al. (2024) found that English sole was encountered across all sampled regions and depth strata.

Adult chinook salmon: Metabolic index results were evaluated within the upper 100 m of the water column. Field data from Puget Sound supports defining the adult marine Chinook salmon habitat as the upper 100 meters of the water column, specifically: acoustic telemetry data synthesized by Freshwater et al. (2024) and further catch data reviewed in Smith et al. (2015). Freshwater et al. (2024) included more than 3,600 depth-validated detections from 338 tagged Chinook collected between 2019 and 2021 across Puget Sound, the Strait of Juan de Fuca, the Strait of Georgia, and adjacent coastal waters. While detections across the full study area ranged from the surface to 352 m with an average of 28 m, all Puget Sound-specific observations occurred shallower than 100 m (see Figures S6 & S7 in Freshwater et al., 2024). It should be noted that deeper detections were observed off the coast; however, Smith et al. (2015) found ranges of <44 m for studies focused specifically on the deepest parts of Puget Sound. Smith et al. (2015) observed Chinook salmon in Puget Sound between 0 and 44 m, with typical depths of ~22–33 m during summer and fall, when low dissolved oxygen is most likely. Although the study was conducted throughout Puget Sound and the Straits, most of the 141,497 detections occurred in the Main Basin, which is generally deeper, with many areas exceeding 100 m. Taken together, these studies support the use of a 0–100 m depth range to represent adult Chinook salmon habitat in Puget Sound for the purpose of evaluating available aerobic habitat.

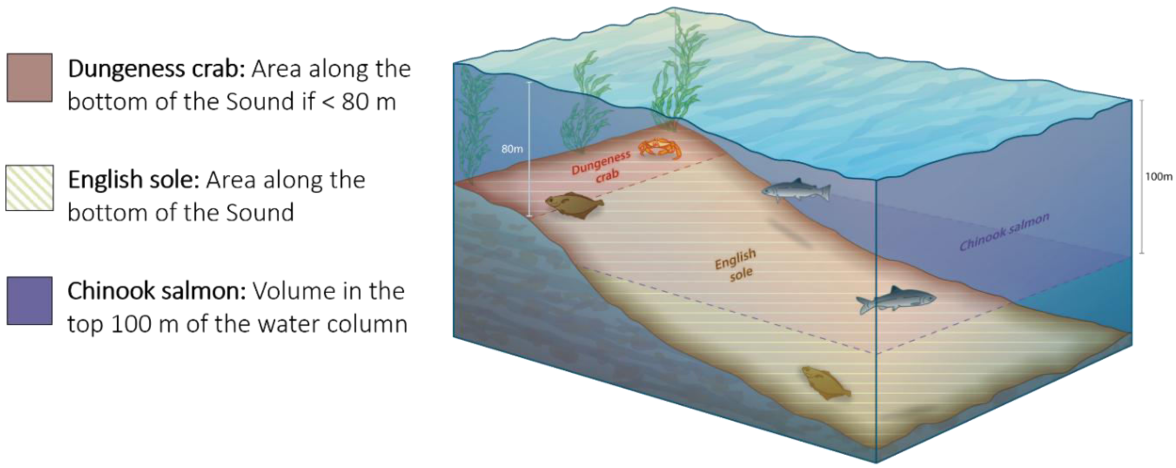


Figure 2.1.2. Potential aerobic habitat — the physical space a species could occupy without limitations from oxygen and temperature — is defined differently for each of three species: seafloor area shallower than 80 m for Dungeness crab, seafloor area at all depths for English sole, and water volume in the top 100 m of the water column for Chinook salmon. This UW analysis only considers depth to define potential aerobic habitat. Other factors (e.g., substrate, food availability, etc.) may also limit a species' available habitat. Graphic: Emily Eng for PSI.

To ensure results are interpreted at a level of precision consistent with the resolution of the Salish Sea Model, the following reporting conventions were applied throughout. Habitat areas and volumes were reported to the nearest km^2 or km^3, with resulting compressed habitat metrics reported to two significant figures (reflecting a typical spatial uncertainty of ±0.40 km^2 based on the median grid cell in the area of interest in Puget Sound and the Straits). Values below a minimum threshold (defined by the 10th percentile of grid cell size: 0.20 km^2 or 0.020 km^3) were reported as below this limit, maintaining a consistent threshold for meaningful comparison across regions. Accordingly, a conservative 0.1% limit was also applied across all subsequent calculations of the percentage of total species habitat area and volume. All calculations were performed using full-precision values before rounding to maintain statistical integrity.

2.2 Study area and regional boundaries

For this analysis, Puget Sound and the Straits were divided into six regions that cover marine waters of Washington State (Figure 2.2.1). Outside of Puget Sound itself, the study area extends to all United States portions of the Strait of Juan de Fuca (SJF) and the Strait of Georgia (SOG) but excludes all coastal waters outside of the straits. These regional boundaries of the study area follow those used in nitrogen reduction strategy assessments with the Salish Sea Model (Ahmed et al., 2021). Throughout this report, this combined area is referred to as Puget Sound and the Straits, which is the focus of this study; recognizing that four of the regions lie entirely within Puget Sound, while the SJF and SOG regions also extend into the adjacent straits, with the latter including the Northern Bays. An additional region, "SJF/SOG border region" (183 km^2 or 22.2 km^3), is not shown in Figure 2.2.1 but lies within Washington State waters, covering a limited number of cells adjacent to the Canadian border. This border region is included in all total regional calculations (6378 km^2 or 563.5 km^3). However, as no metabolic threshold exceedances for any species occurred in this region, the 0-value result was excluded from all tables and plots.

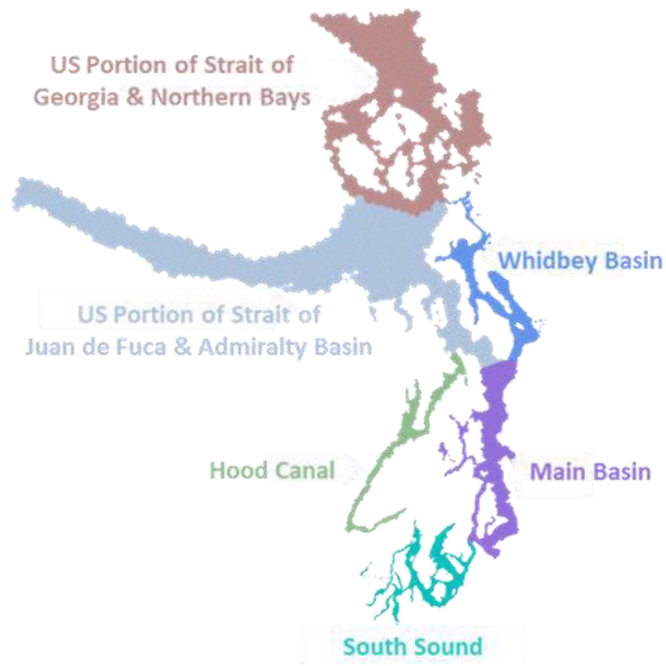


Figure 2.2.1. Spatial delineation of six regions based on Salish Sea Model cell groupings covering Puget Sound and extending to United States waters in the Strait of Juan de Fuca (SJF) and Strait of Georgia (SOG) (after Ahmed et al., 2021).

Nearshore and shallow water areas and associated Salish Sea Model outputs are masked in Ahmed et al. (2021), and the same exclusion was applied here. Ahmed et al. (2021) masked model cells exposed to tidal wetting and drying, as well as areas where confidence in model outputs was lower. In particular, river mouths, estuarine deltas, and other shallow masked areas may include ecologically important nearshore habitat for species assessed in this study. River mouths and deltas may be particularly important for consideration of future work specific to juvenile Chinook salmon, given the variation in "smoltification" timing and estuary residence strategies that may overlap with the habitat compression periods identified in this study.

The 2014 model year was selected pragmatically from the available Salish Sea Model scenario years. The 2014 model year is one of the most widely cited and used at the time of this analysis, published prior in Ahmed et al. (2021). The 2014 model run aligns with modeling that the Washington State Department of Ecology has used to inform nutrient management planning, including the development of nutrient reduction targets. Using consistent model runs ensures the aerobic habitat results presented here are directly comparable to the modeling framework informing regulatory decision-making in Puget Sound.

Conditions in 2014 included warmer-than-average temperatures in much of Puget Sound and basin-specific oxygen depression during late summer and autumn, but 2014 should not be interpreted as a clear system-wide worst-case year. The year 2014 has been identified as a warm transition year into the 2014–2016 Northeast Pacific marine heatwave period, influenced by the positive, warm phase of the Pacific Decadal Oscillation, while El Niño–Southern Oscillation remained neutral for most of the year and shifted only toward weak El Niño conditions late in the year (PSEMP Marine Waters Workgroup, 2015). The Northeast Pacific marine heatwave, commonly known as "the Blob," included offshore waters that were approximately 3°C warmer than normal in February 2014 and expanded to the U.S. Pacific Northwest continental shelf toward the end of 2014 (Bond, 2014). Stronger temperature effects in the Salish Sea were documented during 2015–2016, including depth-averaged temperature increases up to 1.5°C at Washington State Department of Ecology monthly monitoring stations relative to 2013 (Khangaonkar et al., 2021). Within Puget Sound, water temperatures began colder than normal following cold late-2013 and very cold February 2014 conditions, but warmed through the year, with unusually warm conditions in much of Puget Sound later in 2014 (PSEMP Marine Waters Workgroup, 2015). Critical to this study, these warmer conditions overlapped the summer–fall period when low dissolved oxygen and temperature-dependent aerobic habitat availability are most relevant. In fall, lower Hood Canal shifted to hypoxic conditions that persisted through the end of the year — a condition not seen in the 10-year record — and fall hypoxia was also documented elsewhere, including Quartermaster Harbor (PSEMP Marine Waters Workgroup, 2015).

3 RESULTS AND DISCUSSION

3.1 Dungeness crab aerobic habitat

Comparison of temporal patterns at two different locations

Comparison of daily metabolic index time series for Dungeness crab in bottom waters shows how predicted aerobic habitat availability changed through the year at two contrasting locations in Puget Sound (Figure 3.1.1). Two locations were selected based on proximity to continuous dissolved oxygen monitoring sites that are part of ongoing Puget Sound observational programs, and within areas of concern identified in prior modeling studies where reduced dissolved oxygen conditions occur for at least part of the year (Ahmed et al., 2021). The sites span contrasting oceanographic and morphological settings within Puget Sound, from the Whidbey to Hood Canal regions.

The Penn Cove location (top panel, Figure 3.1.1) on the seaward side of the cove in the Whidbey region, maintained a metabolic index above one throughout most of the year, indicating crabs at this location likely have sufficient dissolved oxygen to maintain routine metabolic capacity year-round except a few days in late summer/earlier autumn. The metabolic index

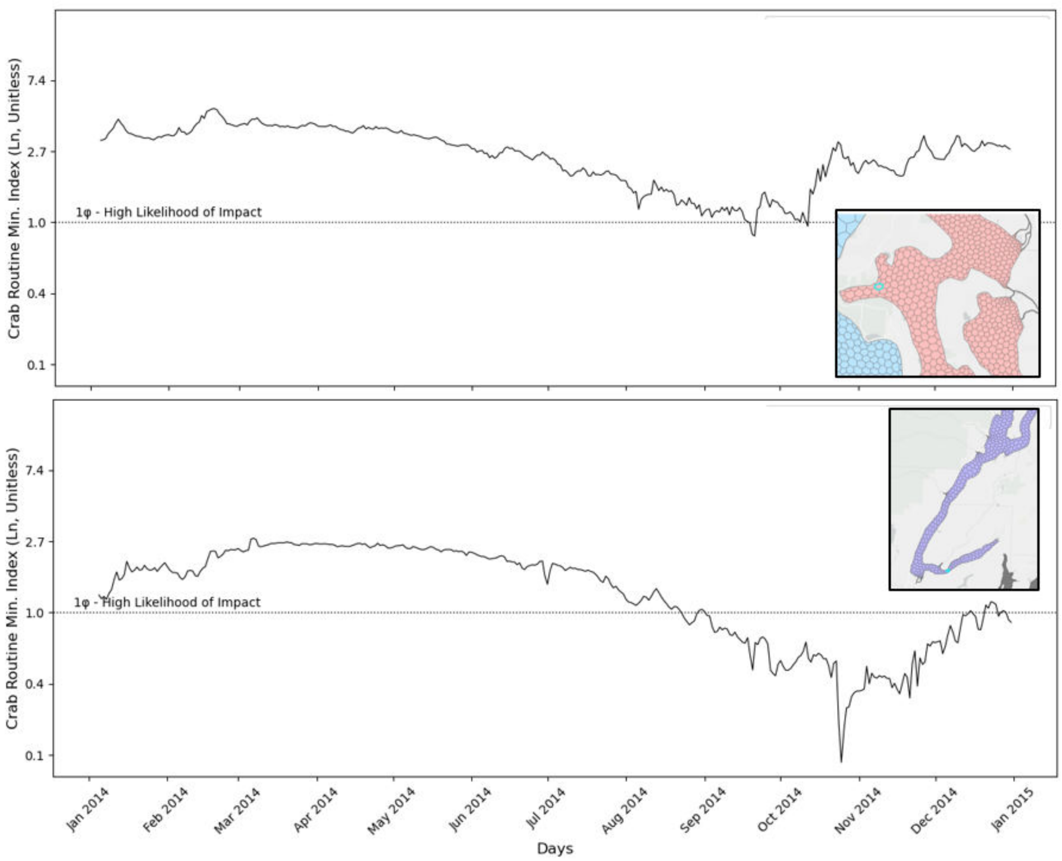


Figure 3.1.1. Daily time series of routine metabolic index (Φ) for Dungeness crab in bottom waters during 2014: Penn Cove, Whidbey Basin (Cell 8841, top panel) and southern Hood Canal (Cell 13789, bottom panel). Y-axis is on a natural log scale. The dashed line indicates Φ = 1, below which oxygen supply is insufficient to meet routine metabolic demand.

decreased during summer and autumn, then recovered to winter baseline levels of around 2.7 (well above 1). For comparison, the Twanoh location in southern Hood Canal (bottom panel, Figure 3.1.1), is within an area known to experience seasonal hypoxia (PSEMP Marine Waters Workgroup, 2025). This site also exhibited a similar modeled winter baseline to the Penn Cove site for part of that period. However, it showed a steeper decline and lower index through summer and autumn, crossing below $\Phi = 1$ from late August to late December, which coincided with modeled seasonal hypoxia (dissolved oxygen < 2 mg/L). If crabs occupying this location could not move to another more oxygenated area, they are likely to experience impacts on their routine activities during the sustained $\Phi < 1$ event period.

The following sections use complementary metrics to describe the various temporal and spatial patterns of Dungeness crab aerobic habitat compression and remaining aerobic refuge. The callout box below explains how to interpret these metrics together for each species assessed in this report.

Interpreting aerobic habitat compression and remaining refuge metrics

No single metric fully captures the spatial and temporal dynamics of aerobic habitat compression or its potential consequences for marine life — the complementary metrics presented below are designed to be interpreted together, each showing a different dimension of when, where, and how extensively habitat is compressed for each species.

1. Worst day metrics identify the largest, or maximum, spatial footprint a species may experience in aerobic habitat compression during the modeled year. Worst day metrics indicate when compression is most spatially extensive. However, it does not quantify how long this, or other events, persist or the relation to refuge areas and times. Therefore, the worst day outputs should be interpreted with the complementary metrics following.

2. Average during the period of compression summarizes what habitat compression is like for a region on a typical day when compression occurs. The period of compression is defined by the first and last days when compression is detected anywhere within the region in a given year, and the average is calculated across all days within that window. This approach better captures the average of the seasonal compression rather than just isolating the largest worst day/maximum event in that period, making it particularly useful for comparing typical conditions across regions during affected periods.

3. **Average annualized habitat compression** throughout the year is also calculated for regions. Note that this averages across all days of the year with and without compression, and the result is therefore much lower than the average during the period of compression, which is more representative of a typical day during compression.

4. Frequency and persistence of habitat compression is addressed through two additional metrics: a) planar plots of the number of cumulative days annually for each part of the study area which help distinguish geographic differences in potential exposure; and b) time-series plots of compressed habitat volume for each region, proving additional detail on the seasonal nature of compression events and persistence and magnitude of individual events within that time period for the specific region. These summary plots help interpret how much of that year-integrated compression reflects recurring or persistent events. The two results are particularly useful when considered together for regions outside of Hood Canal, where compression is often localized to a small number of inlets and bays, and daily time series help indicate whether those localized events are brief, recurring, or persistent during the part of the season they occur. Considered together, these metrics may be helpful to indicate for specific inlets whether compression may persist long enough to warrant further evaluation of chronic exposure, growth, reproduction, or other sublethal effects at those locations, given their spatial relevance.

5. Remaining aerobic refuge is a metric that quantifies the inverse of habitat compression: how much, where, and when suitable aerobic habitat remains available. Refuge should be interpreted alongside the compression metrics because the biological importance of compression depends on whether suitable refuge habitat also remains available to access. For pelagic species such as Chinook salmon, this means evaluating whether oxygenated refuge remains elsewhere in the water column or nearby horizontally when compression occurs. For benthic species such as Dungeness crab and English sole, refuge areas are the suitable bottom habitat that remains nearby or elsewhere within the region.

6. Secondary effects and cumulative risk: Aerobic habitat compression may also produce secondary effects as species are displaced into refuge waters, beyond direct metabolic stress addressed in this study. These include altered overlap with prey, predators, and fisheries, with attendant population impacts. Changes in predator-prey overlap have been documented in the U.S. East Coast (Eby and Crowder, 2002) but were not observed in Hood Canal (Moriarty et al., 2020). Froehlich et al. (2014) demonstrated habitat shifts of Dungeness crab in response to low oxygen in Hood Canal, where crab shoaled to shallow depths when deep-water oxygen levels approached ca. 5.0 kPa, which was above the estimated p_{crit} level (4.28 kPa), and speculated that this could increase vulnerability to fishing. Although a full cumulative-risk assessment is beyond the scope of this study, the spatially explicit estimates of habitat compression and where oxygenated refuge remains can serve as inputs to one – providing a basis for comparison with fisheries, predation risk, climate-related stress, or other stressors to evaluate where low oxygen and temperature stress may be most consequential for populations and management.

Temporal and spatial patterns

The extent of Dungeness crab aerobic habitat was modeled for 2014 across all of Puget Sound and the Straits, delineated into the six regional boundaries of the study area. Areas were identified where aerobic habitat compression ($\Phi < 1$) was predicted (times when there is potentially not enough oxygen to meet a species' routine metabolic activity needs at that location). The following results describe the spatial extent and timing of this compression under existing (2014) conditions, as well as differences observed across regions. The specific proportion of this compression that is attributable to nitrogen from human activities in Washington State is examined in the section following.

Spatially, habitat compression was predicted predominantly in the Hood Canal region, with shorter and more intermittent events in the terminal inlets and embayments across the other five regions: Discovery Bay (Strait of Juan de Fuca (SJF) and Admiralty); Bellingham Bay and Eastsound Bay (Strait of Georgia (SOG) and Northern Bays); Penn Cove and Port Susan (Whidbey Basin); Sinclair Inlet (Main Basin); and Case Inlet, Carr Inlet, and Budd Inlet (South Sound).

Throughout Puget Sound and the Straits, considering potential habitat < 80 m (3,021 km^2), the annualized daily average compressed habitat in 2014 was 27 km^2 by area, leaving 2,994 km^2 of habitat remaining as refuge throughout the year (equivalent to 99.1% of potential Dungeness crab habitat) (Table 3.1.1).

Table 3.1.1. Annualized daily average area and percent of habitat during 2014 when routine Φ < 1 for Dungeness crab for existing and reference conditions, as well as the difference between the two.

		km^2	**%**
All Regions	**Total available habitat**	**3,021**	**n/a**
Average habitat compression throughout the year	2014 existing conditions	27	0.88%
	2014 reference conditions	23	0.75%
	Due to nitrogen from human activities in WA	4	0.13%
Average refuge remaining throughout the year	2014 existing conditions	2,994	99.1%

Within regions, differences in the temporal and spatial patterns of habitat compression were predicted. Habitat compression occurs predominantly during the summer and fall, with a longer duration in Hood Canal extending into the winter.

In Hood Canal, habitat compression spanned from mid-June through December (Figure 3.1.3). while the inlets and embayments where compression occurred in other regions had a shorter window of compression (July–October) with correspondingly smaller spatial extent, volume, and duration.

By area, the Main Basin had the smallest compression of any region, which is expected given that much of the Main Basin is too deep to provide suitable habitat for Dungeness crab (Figure 3.1.2), while Hood Canal had the largest average area during the period of compression of any region (34 km^2). The 34 km^2 compressed is equal to 17% of the Hood Canal available potential habitat, while compression in all other regions remained ≤ 3.3% of their respective potential habitat (Table 3.1.2).

Hood Canal was by far the largest contributor regionally to the total compression throughout Puget Sound and the Straits for all species. For example, Hood Canal contributed 75% of annualized average crab habitat compression (Appendix 4). This relative contribution of Hood Canal, as well as differences between regions, can also be interpreted visually in the time series plots of daily compression – by examining differences in the corresponding area under the curve for each regional plot (e.g., Figure 3.1.3 for crab).

Throughout Puget Sound and the Straits, the maximum extent of Dungeness habitat compression occurred in late September, with 151 km^2 compressed below the metabolic threshold (5.0% of the potential habitat). Hood Canal had the largest maximum extent by area at 72 km^2 in late November (35% of the region's potential habitat); see existing conditions in Table 3.1.3). The timing and persistence of the maximum extent event for each region can be identified in Figure 3.1.1. The second largest maximum extent was in Whidbey Basin at 46 km^2 (17% of the region's potential habitat). SOG and Northern Bays also reached a maximum extent of 46 km^2 in early September, with the majority concentrated in Bellingham Bay and representing much less of a regional potential habitat compression (4.7%). Within the remaining regions, the maximum extent was $\leq$ 3.5% of Dungeness crab's potential habitat per region.

The calculated maximum extent values represent the largest modeled habitat compression within the 2014 existing-conditions scenario on the "worst day" of the year, not a long-term worst-case condition across years. Because dissolved oxygen and temperature vary substantially among years, the 2014 results should be interpreted in the context of what is published in the literature for the regional marine conditions during that year. The regional monitoring record indicates that 2014 had warmer-than-average conditions in much of Puget Sound and late-season oxygen stress in some basins (PSEMP Marine Waters Workgroup, 2015; Bond, 2014; Khangaonkar et al., 2021). Therefore, the maximum extent of 151 km^2 of Dungeness crab habitat compressed across Puget Sound and the Straits in 2014 can be interpreted as conservative relative to average-year conditions, but not necessarily as the absolute worst-case estimate across the longer interannual record. The same context applies to the maximum extent results reported for the other focal species.

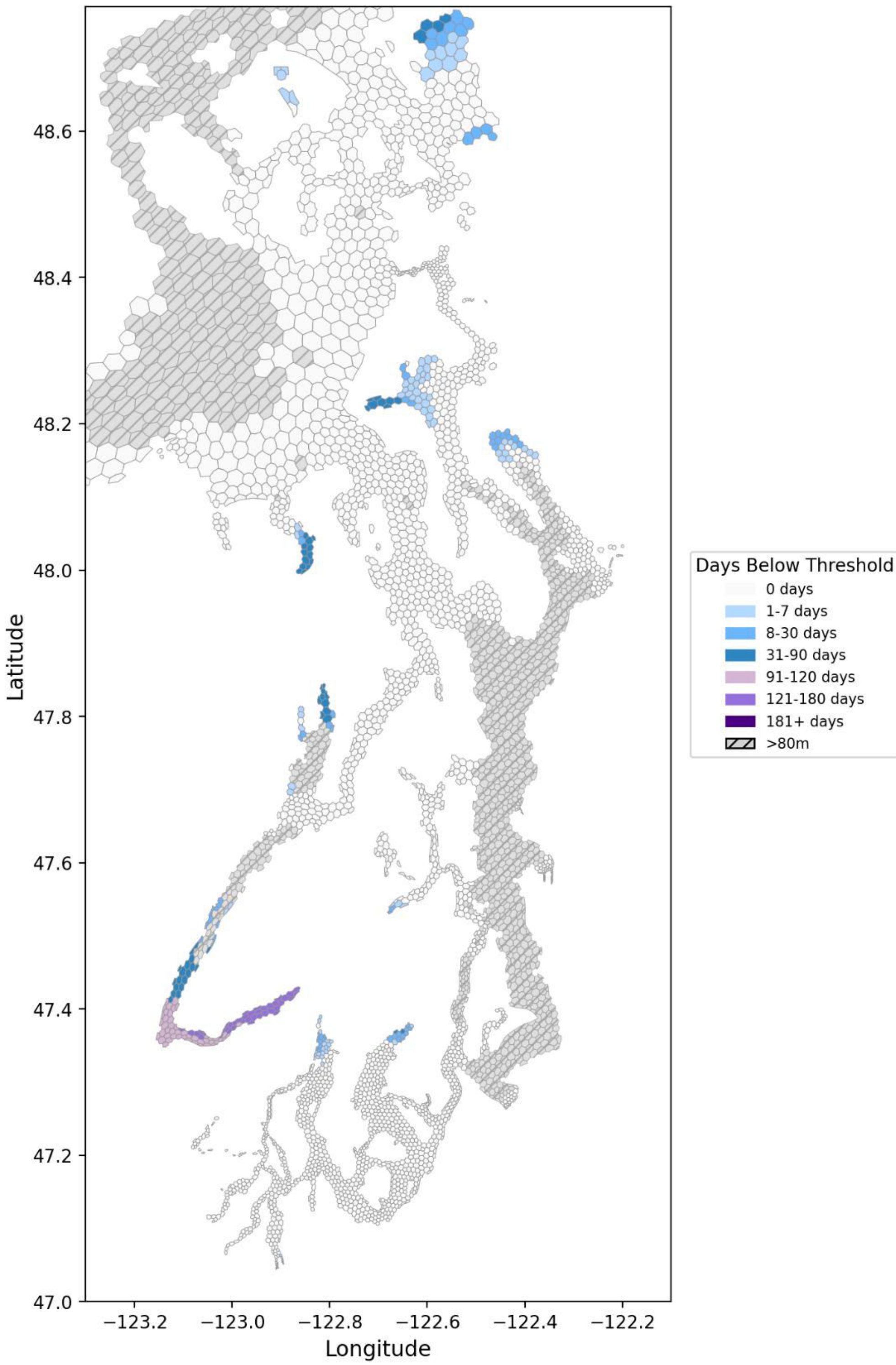


Figure 3.1.2. Spatial extent and number of days during 2014 when routine $\Phi < 1$ for Dungeness crab in bottom waters <80 m.

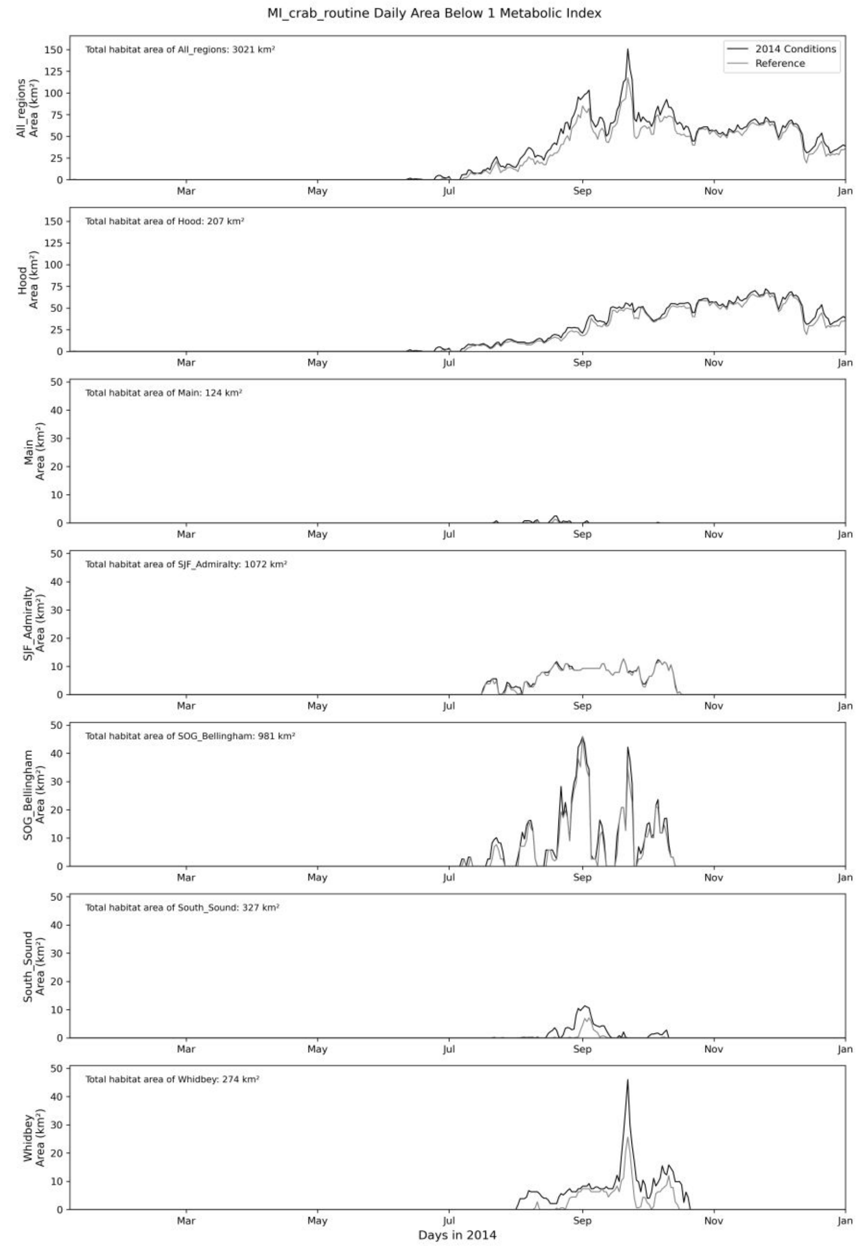


Figure 3.1.3. Daily time series of bottom water area <80 m during 2014 when routine $\Phi < 1$ for Dungeness crab, by region, for existing and reference conditions.

Table 3.1.2. Average area and percent of habitat during the period of compression in each region in 2014 when routine Φ < 1 for Dungeness crab, for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Area	2014 Existing Conditions Average Area Φ < 1		2014 Reference Conditions Average Area Φ < 1		Difference Between Existing & Reference Conditions	
	km^2	**km^2**	**% of Habitat**	**km^2**	**% of Habitat**	**km^2**	**% of Habitat**
Hood Canal	207	34	17%	33	16%	0.9	0.46%
Main Basin	124	0.22	0.2%	0.24	0.19%	<0.20	<0.1%
US Portion of SJF & Admiralty Basin	1072	7.1	0.7%	6.8	0.63%	0.34	<0.1%
US Portion of SOG & Northern Bays	981	11	1.1%	9.0	0.92%	1.8	0.19%
South Sound	327	1.9	0.6%	0.83	0.25%	1.1	0.34%
Whidbey Basin	274	9.1	3.3%	5.2	1.9%	3.9	1.4%
All Regions	**3021**	**47**	**1.6%**	**43**	**1.4%**	**3.7**	**0.12%**

Table 3.1.3. The maximum extent of habitat in 2014 with routine Φ < 1 for Dungeness crab, by region, for existing and reference conditions.

Region	Total Habitat Area	2014 Existing Conditions Max. Area Φ < 1			2014 Reference Conditions Max. Area Φ < 1			Difference Between Existing & Reference Conditions	
	km^2	**km^2**	**% of Habitat**	**Day**	**km^2**	**% of Habitat**	**Day**	**km^2**	**% of Habitat**
Hood Canal	207	72	35%	11/25	67	33%	11/25	4.7	2.3%
Main Basin	124	2.4	2.0%	08/19	1.3	1.0%	08/19	1.2	1.0%
US Portion of SJF & Admiralty Basin	1072	13	1.2%	09/20	13	1.2%	09/20	<0.20	<0.1%
US Portion of SOG & Northern Bays	981	46	4.7%	09/01	46	4.7%	09/01	<0.20	<0.1%
South Sound	327	11	3.5%	09/02	7.1	2.2%	09/04	4.3	1.3%
Whidbey Basin	274	46	17%	09/22	26	9.4%	09/22	20	7.4%
All Regions	**3021**	**151**	**5.0%**	**09/22**	**117**	**3.9%**	**09/22**	**33**	**1.1%**

Potential influence of nitrogen from human activities in Washington State on Dungeness crab aerobic habitat.

Habitat compression from seasonal dissolved oxygen reductions is attributable to both natural causes and nitrogen from human activities. In this study, a large proportion of habitat loss due to declining dissolved oxygen levels was found to occur under reference conditions independent of nitrogen inputs related to human activity in Washington State. Comparing the results of different model scenarios allows these two components to be distinguished (shown in grey and orange, respectively, in Figure 3.1.4. The habitat compression that is specifically due to anthropogenic nitrogen was examined by comparing the Salish Sea Model's modeled existing conditions for 2014 to a reference conditions scenario (a prior historic estimate) where all land-based human-sourced nitrogen loads from Washington State were excluded, while holding temperature and hydrodynamics constant for both (Table 3.1.1, Table 3.1.2, and Table 3.1.3). The difference presented for these scenarios represents the maximum potential improvement possible from nitrogen management efforts if all nitrogen from human activities in Washington is removed. It should be noted that the influence of climate change on incoming (and within-system) DO and temperature, as well as hydrodynamic and mixing processes, were not specifically addressed in this study and are identified as a future research priority.

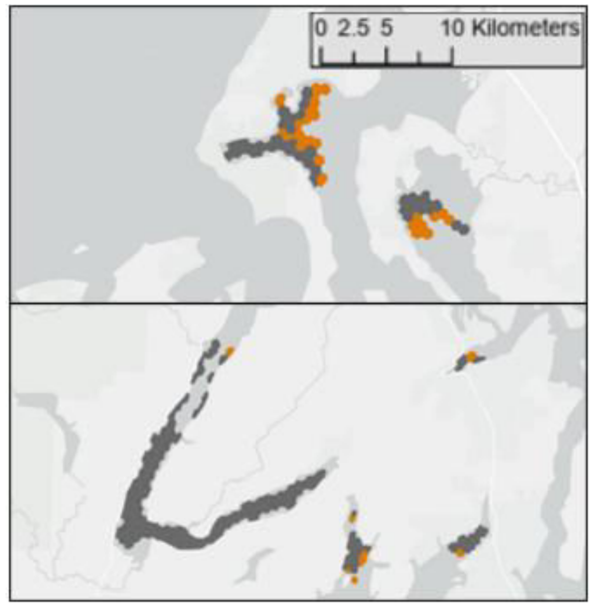


Figure 3.1.4. Spatial extent during 2014 when routine Φ < 1 for Dungeness crab in bottom waters <80 m, showing cells where the threshold was exceeded on at least one day, for the reference scenario (grey) overlaying the larger existing scenario extent with 2014 nitrogen loads (orange). The top panel shows Whidbey and the bottom panel shows Hood Canal and parts of South and Central Sound regions. See Appendix 4 for all locations.

Results show extensive areas where Dungeness crab aerobic habitat is compressed in the reference condition scenario (reference conditions Φ < 1, shown in grey in Figure 3.1.4). These areas of compression increased when nitrogen from human activities was added (existing conditions in 2014 Φ < 1, shown in orange in Figure 3.1.4), with results from this scenario extending outside of the grey reference area. These additional compressed areas are generally located seaward of the extent compressed by natural causes, on the outer margins of inlets and embayments (Figure 3.1.4). The increase in area quantifies the extent to which crab aerobic habitat is predicted to have been further compressed through the addition of nitrogen from human activities.

To quantify the contribution of nitrogen from human activities to habitat compression, the reference scenario results were subtracted from the existing conditions scenario for each model cell daily (Table 3.1.1), and both the average area during the period of compression (Table 3.1.2), and the worst day/maximum extent were calculated for each region (Table 3.1.3). Figure 3.1.5 also shows the places where nitrogen from human activities extended compression, and how many days throughout the year were compressed in each area.

For the reference condition, considering all of Puget Sound and the Straits, the average habitat area compressed during the period when compression occurred was 47 km^2 (Table 3.1.1). Comparing results between existing and reference scenarios, this is equivalent to a 3.7 km^2 lost due to nitrogen from human activities in Washington State, or a 0.12% loss of potential habitat. Within regions, the equivalent potential habitat loss due to nitrogen from human activities was greatest in Whidbey (1.4% of potential habitat; 3.9 km^2 by area), followed by Hood Canal (0.46%) and ≤ 0.34% for all other regions. In terms of change in the number of days of habitat compression, nitrogen from human activities in Washington added fewer than 31 days to any cell area in any regions (Figure 3.1.5). Outside of the southern Hood Canal, these additional days were often concentrated landward within inlets and embayments, never exceeding 7 days at their seaward margins.

The maximum extent represents the single worst day of the year in terms of compressed Dungeness crab habitat. When nitrogen loads from human activities are removed (reference conditions in Table 3.1.3), the maximum extent event occurred in late September across Puget Sound and the Straits, which resulted in a loss of 33 km^2 of habitat (1.1% of potential habitat). Whidbey Basin contributed the largest regional proportion of compression (Figure 3.1.3; Appendix 4) reaching its annual maximum on September 22, with 20 km^2 attributable to nitrogen from human activities (7.4% of the region's potential habitat). In Hood Canal, the maximum extent occurred later in the season on November 25, with a 4.7 km^2 loss due to human-sourced nitrogen (2.3% of the region's potential habitat). In South Sound, the maximum extent occurred a few days earlier under existing rather than reference conditions, with 4.3 km^2 attributed to nitrogen from human activities (1.3% of the region's potential habitat). In all remaining regions, habitat loss due to nitrogen from human activities was less than 1% of the region's potential habitat.

The presence or absence of nitrogen from human activities made little discernible change in the maximum extent of compression observed in two regions: the SJF and Admiralty Basin (limited to Discovery Bay), and the SOG and Northern Bays (predominantly in Bellingham Bay). In both regions, most cells fell below the threshold for fewer than 7 additional days relative to reference conditions (lightest blue in Figure 3.1.2). Therefore, compression in these areas is likely driven by nitrogen sources that are constant across both scenarios. In Discovery Bay, exogenous oceanic nitrogen rather than Washington State land-based sources likely dominates. Bellingham Bay is similarly influenced by oceanic and Strait of Georgia inputs (including Canadian sources held constant), as well as natural river nitrogen (e.g., Nooksack River) retained in the reference scenario.

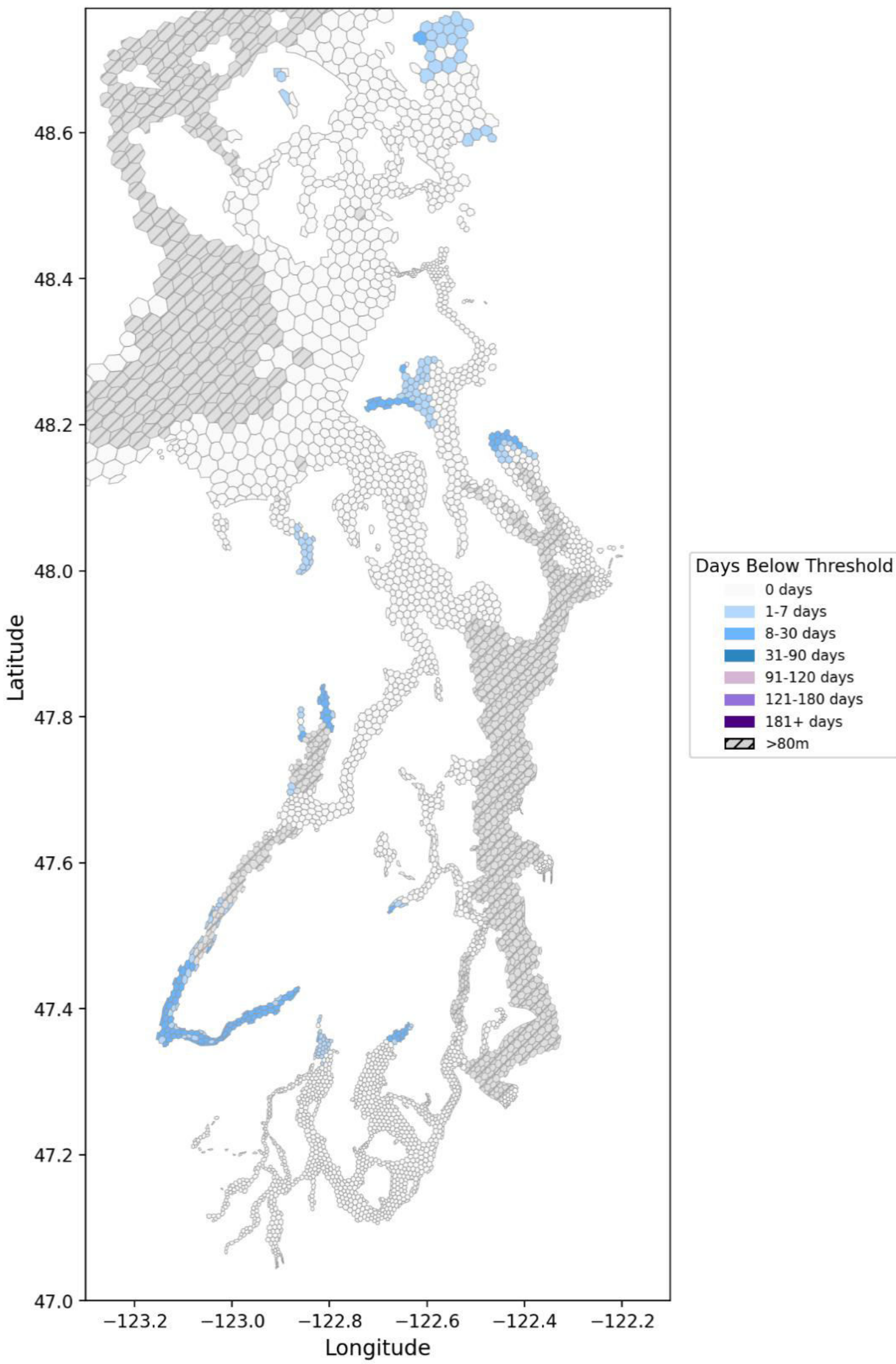


Figure 3.1.5. Change in number of days when routine Φ < 1 for Dungeness crab in bottom waters <80 m between existing and reference conditions during 2014. Positive values indicate additional days below the threshold, showing habitat loss attributable to nitrogen from human activities in Washington State.

3.2 English sole aerobic habitat

Temporal and spatial patterns

The existing extent of English sole aerobic habitat was modeled for 2014 across all regions of Puget Sound and the Straits, following the same procedure as Dungeness crab, and showed similar spatial and seasonal patterns. Predicted aerobic habitat compression for English sole was evaluated quantitatively by area, reflecting its benthic nature as a bottom-dwelling species. As with Dungeness crab, habitat compression ($\Phi < 1$) for English sole occurred from late June to the mid-October in terminal inlets and extended through December in Hood Canal. In contrast to Dungeness crab, English sole habitat compression was smaller in spatial extent and occurred for fewer days within affected cell locations (Figure 3.2.1), and with correspondingly smaller calculated area of bottom layer waters within English sole habitat (Figure 3.2.1) compared to crab (Figure 3.1.2). This is consistent with expectations based on differences in both the species' physiology and potential habitat: sole's lower oxygen sensitivity (p_{crit} 3.37 vs. 4.04 kPa) and larger potential habitat area (6,378 vs 3,021 km²) act to reduce on the absolute habitat compression as well as the portion of potential habitat that is compressed. Together, this results in a lower absolute average area during the period of compression throughout Puget Sound and the Straits (41 vs. 47 km²) (Table 3.2.2 and Table 3.1.1 respectively), and a higher proportion of potential habitat remaining (99.7% vs. 99.1%) than crab (Table 3.2.1 and Table 3.1.1 respectively).

Table 3.2.1. Annualized daily average area and percent of habitat during 2014 when routine Φ < 1 for English sole, for existing and reference conditions, as well as the difference between the two.

		km²	**%**
All Regions	**Total available habitat**	**6,378**	**n/a**
Average habitat compression throughout the year	2014 existing conditions	22	0.34%
	2014 reference conditions	18	0.28%
	Due to nitrogen from human activities in WA	3.8	<0.10%
Average refuge remaining throughout the year	2014 existing conditions	6,356	99.7%

Seasonal and spatial patterns within regions for English sole were also similar to Dungeness crab, with most of the compression occurring in Hood Canal (Figure 3.2.2). In Hood Canal, the maximum extent of habitat compression was slightly larger for English sole (84 km²) than crab (72 km²) on the worst day for each species (Table 4.2); this is notable as the one exception to the overall pattern of sole showing less absolute area compressed than crab, due to their larger potential habitat area (290 vs 207 km²) in Hood Canal. This still represented a smaller percentage of potential habitat for English sole compared to crab (29% vs 35%) in Hood Canal.

In the remaining regions, English sole experienced maximum habitat compression around the same time as Dungeness crab, but with a smaller area. English sole also experienced habitat compression for fewer days overall (Figure 3.2.1) relative to Dungeness crab (Figure 3.1.2).

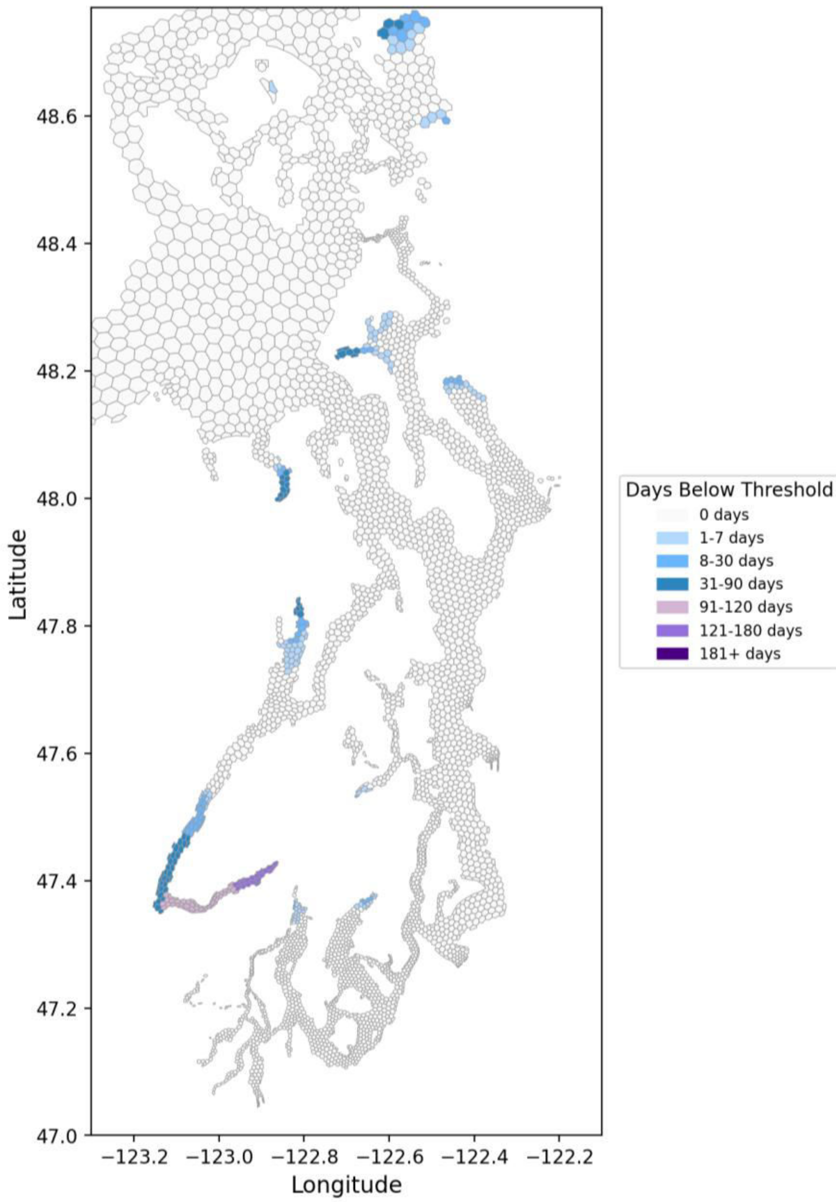


Figure 3.2.1. Spatial extent and number of days during 2014 when routine Φ < 1 for English sole in bottom waters.

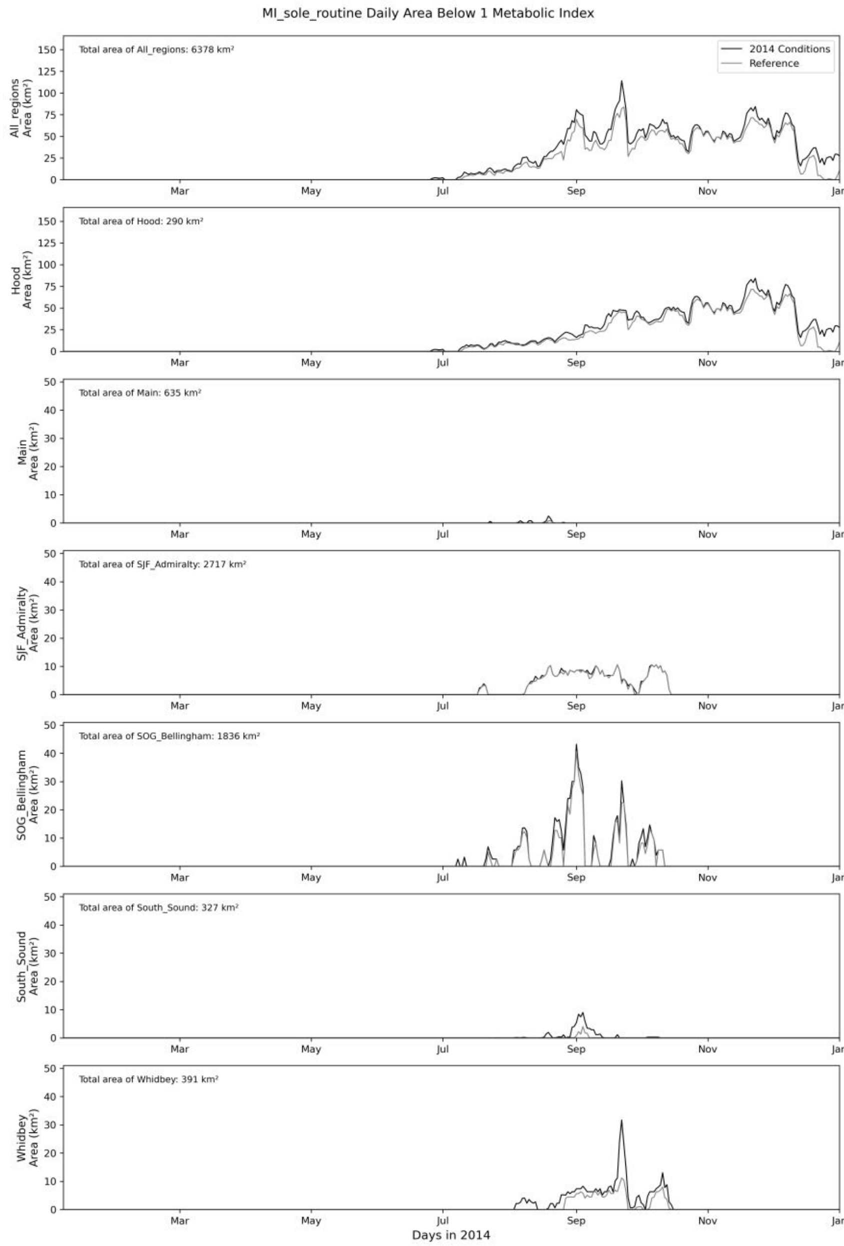


Figure 3.2.2. Daily time series of bottom water area during 2014 when routine Φ < 1 for English sole, by region, for existing and reference conditions.

Table 3.2.2. Average area and percent of habitat during the period of compression in each region in 2014 when routine Φ < 1 for English sole, for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Area	2014 Existing Conditions Average Area Φ < 1		2014 Reference Conditions Average Area Φ < 1		Difference Between Existing & Reference Conditions	
	km^2	km^2	% of Habitat	km^2	% of Habitat	km^2	% of Habitat
Hood Canal	290	32	11%	27	9.5%	4.6	1.6%
Main Basin	635	0.25	<0.1%	0.59	0.09%	-0.34	<0.1%
US Portion of SJF & Admiralty Basin	2717	5.4	0.20%	5.1	0.19%	0.22	<0.1%
US Portion of SOG & Northern Bays	1836	7.3	0.40%	7.0	0.38%	0.33	<0.1%
South Sound	327	0.88	0.27%	1.5	0.45%	-0.57	<0.1%
Whidbey Basin	391	5.7	1.5%	4.4	1.1%	1.3	0.34%
All Regions	**6378**	**41**	**0.64%**	**34**	**0.54%**	**6.7**	**0.11%**

Table 3.2.3. The maximum extent of habitat in 2014 with routine Φ < 1 for English sole, by region, for existing and reference conditions.

Region	Total Habitat Area	2014 Existing Conditions Max. Area Φ < 1			2014 Reference Conditions Max. Area Φ < 1			Difference Between Existing & Reference Conditions	
	km^2	km^2	% of Habitat	Day	km^2	% of Habitat	Day	km^2	% of Habitat
Hood Canal	290	84	29%	11/23	71	25%	11/22	13	4.4%
Main Basin	635	2.4	0.39%	08/19	0.77	0.12%	08/19	1.7	0.26%
US Portion of SJF & Admiralty Basin	2717	11	0.39%	09/20	11	0.39%	09/20	<0.20	<0.1%
US Portion of SOG & Northern Bays	1836	43	2.4%	09/01	41	2.2%	09/01	2.5	0.14%
South Sound	327	9.0	2.8%	09/04	4.0	1.2%	09/04	5.0	1.5%
Whidbey Basin	391	32	8.1%	09/22	11	2.9%	09/22	21	5.3%
All Regions	**6378**	**114**	**1.8%**	**09/22**	**84**	**1.3%**	**09/23**	**30**	**0.48%**

Potential influence of nitrogen from human activities in Washington State on English sole aerobic habitat.

Comparison of the Salish Sea Model modeled existing conditions for 2014 to a reference conditions scenario indicates that nitrogen from human activities in Washington State may lead to habitat loss for English sole, primarily in Hood Canal (Figure 3.2.2). A total of 4.6 km^2 of average habitat compression in Hood Canal was attributable to nitrogen from human activities during the period compression occurred (representing a loss of 1.6% in that region), while all remaining regions showed minimal changes (Table 3.2.2). In terms of change in the number of days of habitat compression, nitrogen from human activities in Washington added fewer than 31 days to any cell area in any regions (Figure 3.2.3), similar to Dungeness crab.

Throughout Puget Sound and the Straits, 30 km^2 of habitat was lost due to nitrogen from human activities in Washington State during the worst day (representing a loss of 0.48% of potential habitat) (Table 4.2). Within regions, Whidbey Basin showed the largest change at 21 km^2 (representing a loss of 5.3% of the region's potential habitat), driven by a short-lived event around September 22 were there was a large difference in existing and reference scenario results. Hood Canal showed the next largest change at 13 km^2 (representing a loss of 4.4% of the region's potential habitat), consistent with the sustained seasonal compression pattern. South Sound lost 5.0 km^2 (1.5% of the basin's potential habitat), while changes in all remaining regions were each <0.26 % of potential habitat, including SJF and Admiralty Basin showing the smallest change (<0.1% of potential habitat).

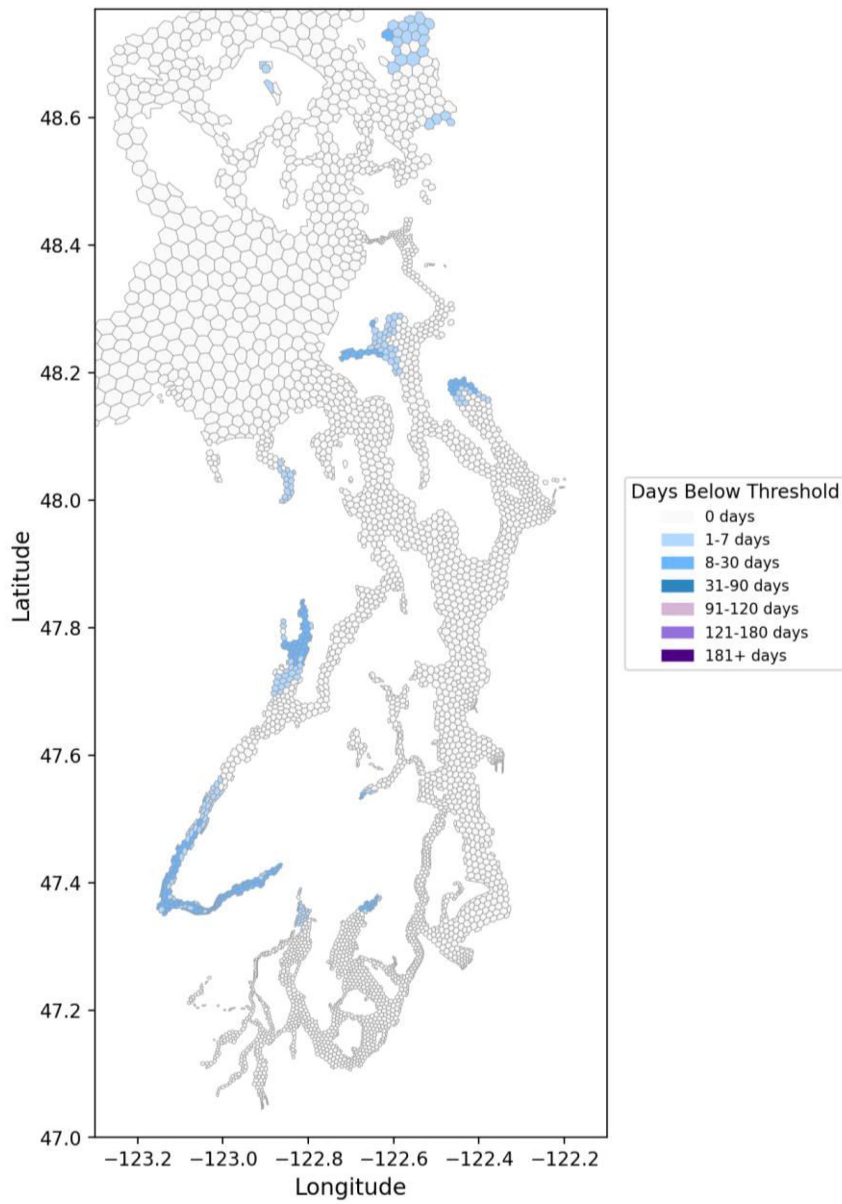


Figure 3.2.3. Change in the number of days when routine Φ < 1 for English sole in bottom waters between existing and reference conditions during 2014. Positive values indicate additional days below the threshold, showing habitat loss attributable to nitrogen from human activities in Washington State.

3.3 Chinook salmon aerobic habitat

Vertical mobility and water column refuge during bottom layer events

The extent of Chinook salmon aerobic habitat was modeled for all regions of Puget Sound and the Straits in 2014. Adult marine Chinook salmon are predominantly found within the top 100 m of the water column in Puget Sound (Freshwater et al., 2024), often inhabiting the upper 44 m or less (Smith et al., 2015), as discussed further in the methodology section. Although bottom waters within this 100m depth range were identified in some locations to experience periodic events where $\Phi < 1$ (Figure 3.3.1), salmon can move vertically and laterally to potentially avoid these locally stressful conditions identified. This mobility is in contrast with benthic species such as Dungeness crab and English sole primarily on the sea floor. Accordingly, habitat compression for Chinook salmon was evaluated using habitat volume rather than benthic area, reflecting compression across both depth and horizontal space (Table 3.3.1, Table 3.3.2, and Table 3.3.3).

Because Chinook salmon are highly mobile, vertical habitat compression (where deep waters fall below the metabolic index threshold shown in the left panel of Figure 3.3.1) does not eliminate access to oxygenated refuge. Even when bottom waters were predicted to be compressed, refuge with sufficient oxygen was always present in the overlying water column at the same location (right panel of Figure 3.3.1). Therefore, based on the results presented here, it is predicted that at least some refuge is always present above compressed areas, across all potential Chinook habitat in Puget Sound (waters shallower than 100 m).

Additional water column results and habitat assessment considerations are presented in Appendix 6. Across the inlets of Puget Sound, most habitat compression occurs within the bottom water layer. Hood Canal represents an exception, where habitat compression was also predicted to persist also in deep layers above the bottom layer of the SSM outputs, reflecting more extensive vertical exposure in this region. Outside of Hood Canal, habitat compression that does occur above the bottom layer is limited in spatial extent, occurs for fewer days, and is generally confined to the more landward portions of each inlet.

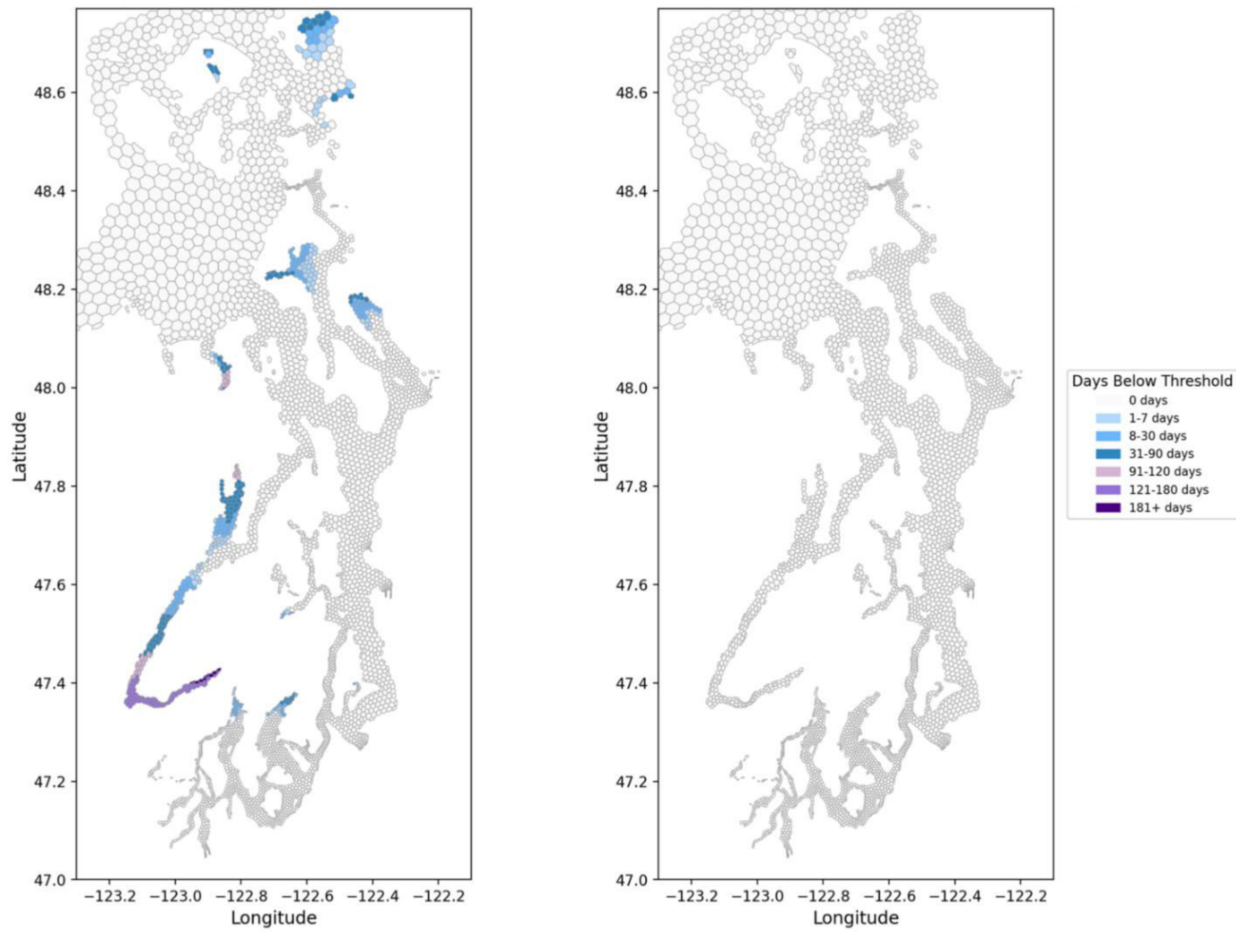


Figure 3.3.1. Spatial extent and number of days during 2014 when routine Φ < 1 for Chinook salmon in bottom waters that fall within the 100m habitat range (left panel) and surface waters (right panel). Bottom waters contain almost all calculated habitat compressed (discussed in the accompanying text), and additional plots and analysis of parts of the water column are presented in Appendix 6.

Temporal and spatial patterns in Chinook aerobic habitat.

Throughout Puget Sound and the Straits, on average, 99.8% of Chinook's potential habitat had sufficient oxygen to support routine activities throughout the year (Φ > 1). Hood Canal was the largest contributor regionally to the total compression throughout Puget Sound and the Straits for Chinook (Figure 3.3.2; Appendix 6).

Table 3.3.1. Annualized daily average volume and percent of habitat during 2014 when routine Φ < 1 for Chinook salmon, for existing and reference conditions, as well as the difference between the two.

		km^3	**%**
All Regions	**Total available habitat**	**459**	**n/a**
Average habitat compression throughout the year	2014 existing conditions	0.78	0.17%
	2014 reference conditions	0.65	0.14%
	Due to nitrogen from human activities in WA	0.13	<0.10%
Average refuge remaining throughout the year	2014 existing conditions	459	99.8%

In Hood Canal, the period of compression spanned from early June to the end of December, during which the average volume of 1.3 km^3 $\Phi < 1$ (6.3% of Chinook salmon's potential habitat in the region) (Table 5.1). Hood Canal reached a maximum extent of 3.6 km^3 of habitat compression (18% of potential habitat) in mid-October, although oxygen-sufficient surface refuge remained available near the surface during this event. (Table 3.3.3).

Outside of Hood Canal, areas where Chinook aerobic habitat was compressed ($\Phi < 1$) were restricted to June to October. It was also at the same locations as crab and sole, with the addition of Quartermaster Harbor. Specifically, the deeper waters in Discovery Bay in the US Portion of SJF & Admiralty Basin, Bellingham Bay and Eastsound Bay in the US Portion of SOG and Northern Bays, Penn Cove and Port Susan in Whidbey Basin, Sinclair Inlet and Quartermaster Harbor in Main Basin, Case Inlet, Carr Inlet, and Budd Inlet in the South Sound. During the period of compression in each of these regions, the average compression was ≤ 0.07 km^3 (less than $\leq 0.33\%$ of potential Chinook habitat in each region) (Table 5.1). Even on the worst day of the year in these regions (Table 5.2), the habitat compression was considerably less than in Hood Canal. Whidbey Basin had the next largest maximum extent as a proportion of potential habitat at 0.32 km^3 (1.4%)—an order of magnitude smaller than Hood Canal—with all other remaining regions at $\leq 0.50\%$ of potential habitat. During all of these predicted events, oxygen-sufficient surface refuge remained available above the deeper waters where habitat compression occurred (Figure 3.2.1). However, the extent to which salmon actively avoid or are impacted in these areas is the subject of further research, which is of particular importance given that current results show that the longest periods below the threshold generally also occur in some of the shallowest parts of inlets, with less water column total depth (Figure 3.2.1; Appendix 6).

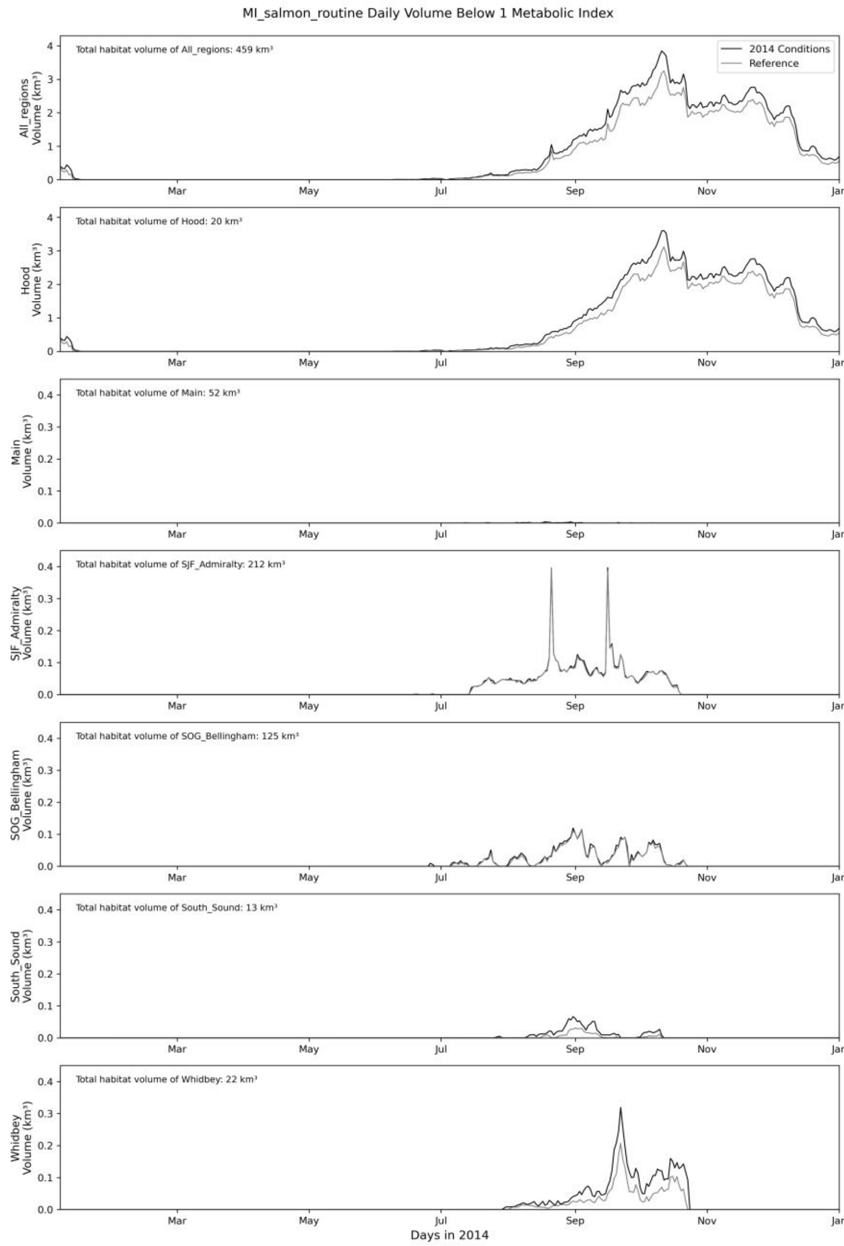


Figure 3.3.2. Daily time series of water column volume during 2014 when routine Φ < 1 for Chinook salmon, by region, for existing and reference conditions.

Table 3.3.2. Average volume and percent of habitat during the period of compression in each region in 2014 when routine Φ < 1 for Chinook salmon, for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Volume	2014 Existing Conditions Average Volume Φ < 1		2014 Reference Conditions Average Volume Φ < 1		Difference Between Existing & Reference Conditions	
	km^3	km^3	% of Habitat	km^3	% of Habitat	km^3	% of Habitat
Hood Canal	207	1.3	6.3%	1.1	5.4%	0.19	0.93%
Main Basin	124	<0.02	<0.1%	<0.02	<0.1%	<0.02	<0.1%
US Portion of SJF & Admiralty Basin	1072	0.06	<0.1%	0.05	<0.1%	<0.02	<0.1%
US Portion of SOG & Northern Bays	981	0.03	<0.1%	0.03	<0.1%	<0.02	<0.1%
South Sound	327	<0.02	0.11%	<0.02	<0.1%	<0.02	<0.1%
Whidbey Basin	274	0.07	0.33%	0.04	0.19%	0.03	0.14%
All Regions	**3021**	**1.3**	**0.29%**	**1.1**	**0.25%**	**0.21**	**<0.1%**

Table 3.3.3. The maximum extent of habitat in 2014 with routine Φ < 1 for Chinook salmon, by region, for existing and reference conditions.

Region	Total Habitat Volume	2014 Existing Conditions Max. Volume Φ < 1			2014 Reference Conditions Max. Volume Φ < 1			Difference Between Existing & Reference Conditions	
	km^3	km^3	% of Habitat	Day	km^3	% of Habitat	Day	km^3	% of Habitat
Hood Canal	20	3.6	18%	10/12	3.1	16%	10/12	0.48	2.4%
Main Basin	52	<0.02	<0.10%	08/18	<0.02	<0.10%	08/19	<0.02	<0.10%
US Portion of SJF & Admiralty Basin	212	0.40	0.19%	09/16	0.40	0.19%	08/21	<0.02	<0.10%
US Portion of SOG & Northern Bays	125	0.12	0.10%	08/31	0.11	<0.10%	09/04	<0.02	<0.10%
South Sound	13	0.07	0.50%	08/31	0.03	0.23%	09/01	0.04	0.26%
Whidbey Basin	22	0.32	1.4%	09/22	0.21	0.94%	09/22	0.11	0.51%
All Regions	**459**	**3.8**	**0.84%**	**10/11**	**3.3**	**0.71%**	**10/12**	**0.59**	**0.13%**

Potential influence of nitrogen from human activities in Washington State on Chinook salmon aerobic habitat

Comparison of existing conditions (2014) to a reference scenario with human-sourced nitrogen loads removed indicates that across Puget Sound and the Straits some deeper water habitat loss in bottom waters may occur for salmon if they do not move to refuge areas identified as available during these periods (>99% of refuge habitat available; Table 3.3.1). The average volume during the period of compression that was attributable to land-based human nitrogen inputs from Washington State was 0.21 km^3 of the 1.3 km^3 volume compressed, with the remaining 1.1 km^3 also occurring under modeled reference conditions (Table 3.3.2). A volume of 0.21 km^3 is equivalent to <0.1% of the total potential salmon habitat.

By region, Hood Canal saw the greatest change in worst day (maximum area extent) due to nitrogen from human activities, with an additional loss of 0.48 km^3, equivalent to 2.4% of the region's potential habitat (Table 3.3.3 and Appendix 6). In other regions, nutrients from human activities did not change the maximum extent appreciably (a loss of $\leq$ 0.11 km^3 or $\leq$ 0.51%) of each region's potential habitat.

Lastly, results show that in scenarios both with and without human-sourced nitrogen, oxygen-sufficient surface refuge remained available in the upper part of the water column in all locations and for all events (discussed earlier).

4 CONCLUSIONS

This study demonstrates that species-specific aerobic habitat impacts can be incorporated into water quality assessments in Puget Sound, using currently available water quality models and physiological data to quantify differences in location, time, and intensity of impact under different scenarios.

This was achieved by applying the metabolic index framework to available biogeochemical model scenario outputs for 2014, evaluating when modeled conditions supported or constrained routine metabolic demand for Dungeness crab, Chinook salmon, and English sole. The metabolic index was applied conservatively, including use of the routine rather than basal metabolic index threshold and daily minimum oxygen conditions. However, results should therefore be interpreted as a prediction of potential constraints on species-specific routine metabolic demand, not as a threshold that ensures protection of all growth, reproduction, behavior, or ecological functions. Key findings are presented below and in Table 3.3.1.

Benthic species' aerobic habitat (Dungeness crab and English sole):

- Throughout Puget Sound and the Straits, a relatively small fraction of Dungeness crab and English sole habitat was compressed with ≥95% remaining as refuge at the worst time of year.
- Dungeness crab habitat compression in Puget Sound and the Straits reached a maximum of 151 km² in late September, leaving 95% of refuge habitat available. Of this, 117 km² was also present under reference conditions, with nitrogen from human activities in Washington contributing 33 km² of habitat loss (representing 1.1% of Dungeness crab potential habitat).
- English sole habitat compression in Puget Sound and the Straits reached a maximum extent of 114 km² also in late September, leaving 98% of refuge habitat available. Of this, 84 km² was also present under reference conditions, with nitrogen from human activities in Washington contributing 30 km² of habitat loss (representing 0.48% of sole potential habitat).
- Seasonal habitat compression was limited to the bottom waters of some terminal inlets during the warmer summer and fall months for Dungeness crab, with Hood Canal experiencing much greater and more persistent compression that also extended into the winter. Specifically, habitat was compressed in: Discovery Bay (U.S. portion of SJF and Admiralty Basin); Bellingham Bay and Eastsound Bay (U.S. portion of SOG & Northern Bays); Penn Cove and Port Susan (Whidbey Basin); Sinclair Inlet (Main Basin); and Case Inlet, Carr Inlet, and Budd Inlet (South Sound), as well as Hood Canal.
- Hood Canal had the largest and most sustained regional Dungeness crab habitat compression, with daily levels of habitat compression that were often many times higher than the worst day of the year in other regions. Habitat compression ($\Phi < 1$) reached a maximum of 72 km² (35% of the habitat in Hood Canal) in late November, which left 65% of the habitat available as refuge on that day. Of this, the majority (67 km²) was also present under reference conditions, with nitrogen from human activities in Washington contributing the remaining 4.7 km² of additional habitat loss (representing 2.3% of habitat in Hood Canal).

- Whidbey Basin had the next-largest Dungeness crab habitat compression by region, reaching a maximum of 46 km^2 on the worst day (17% of the habitat in Whidbey Basin). However, this event was short-lived, and the daily average area compression during the period was 9.1 km^2 (3.3% of habitat); similar in magnitude and percentage habitat to other regions outside of Hood Canal.
- English sole seasonal and spatial patterns closely follow those of Dungeness crab, with compression concentrated in Hood Canal and the same terminal inlets, though occurring for fewer days of the year and affecting a smaller proportion of potential habitat. Throughout Puget Sound and the Straits 0.64% of sole habitat was compressed, compared to 1.6% for crab during the period of compression. Two factors drive the lower percentage of potential habitat compression observed for English sole. First, sole have a lower p_{crit} (3.37 kPa) than crab (4.04 kPa), which means they can maintain routine functions in slightly lower oxygen conditions than crab. Second, sole have a larger potential habitat area (6,378 vs 3,021 km^2), as their habitat includes all bottom areas, while crab habitat is limited to bottom areas shallower than 80 m.

Pelagic species' aerobic habitat (Chinook salmon):

- Chinook salmon always have access to oxygen-sufficient refuge in the water column in all locations in Puget Sound and the Straits throughout the year. This is because the seasonal habitat compression was restricted to deeper waters, closer to the bottom of salmon's habitat range in some inlets and Hood Canal.
- Unlike Dungeness crab and English sole, Chinook salmon are pelagic, with mobility to move laterally as well as vertically to occupy various depths within the upper 100 meters of the water column. This includes any overlying waters that provide refuge during low-oxygen events in deeper water. However, salmon would likely experience impacts on their routine metabolic activities if they stayed in these deeper waters long enough during events. Chinook salmon also have greater oxygen sensitivity than crab and sole. Analysis of salmon habitat compression ($\Phi < 1$) throughout the water column indicates that oxygen-sufficient refuges were available throughout the year, at all locations.
- Throughout Puget Sound and the Straits, habitat compression reached a maximum extent of 3.8 km^3 on the worst day of the year in early October, leaving >99% of refuge habitat available. Of this, 3.3 km^3 was also present under reference conditions, with nitrogen from human activities in Washington contributing 0.59 km^3 of habitat loss (representing 0.13% of Chinook salmon potential habitat).
- Like Dungeness crab and English sole, Chinook salmon habitat compression was primarily restricted to deeper waters of the same terminal inlets during the warmer summer and fall months, with the addition of Quartermaster Harbor. Compression in Hood Canal also extended into the winter for salmon, and was much greater than other regions.

- By region, Chinook salmon potential habitat compression was greatest in Hood Canal (18%) on the worst day, compared to < 2% within all other regions. For Hood Canal, this reached 3.6 km^3 of habitat compression at its maximum extent, leaving 82% of refuge habitat available on that day. This compression was an order of magnitude greater than all remaining regions—none of which exceeded 0.40 km^3. Of this, most was also present under reference conditions, with nitrogen from human activities in Washington contributing 0.48 km^3 of additional habitat loss (representing 2.4% of Hood Canal's potential habitat).

- Comparing anthropogenic contributions to habitat compression across regions indicates that potential responses to nutrient management strategies vary considerably across Puget Sound. Outside of Hood Canal, these effects were concentrated in specific inlets and time periods and varied in magnitude and duration across those inlets. Differences in regional drivers (e.g., oceanic versus riverine influences on hydrodynamic exchange, temperature, and nutrient loading) represent a priority for future research to better understand region-specific and inlet-scale responses to nutrient management. This indicates that nutrient management strategies will be more effective if they focus on addressing these region- and inlet-specific responses and highlights the value of future work that better characterizes local physical and biogeochemical controls on low dissolved oxygen and temperature.

Table 3.3.1. Summary of available aerobic habitat available to three Puget Sound species. Habitat metrics (rows) of aerobic habitat compression (Φ < 1) and mean refuge under 2014 existing and reference conditions are shown for each species (columns) for each of the two model scenarios, as well as the calculated loss due to nitrogen from human activities in Washington State (existing-reference scenario). The percent of habitat for each metric is based on the species-specific total habitat available (shown in grey on row 3).*

Habitat metric	**Scenario**	**Dungeness crab**		**English sole**		**Chinook salmon**	
		km^2	**%**	**km^2**	**%**	**km^3**	**%**
	Total available habitat	**3,021**	**n/a**	**6378**	**n/a**	**459**	**n/a**
Average habitat remaining throughout the year (i.e., not compressed)	2014 existing conditions	2,994	99.1%	6,356	99.7%	459	99.8%
Average during the period of compression	2014 existing conditions	47	1.6%	41	0.64%	1.3	0.29%
	2014 reference conditions	43	1.4%	34	0.54%	1.1	0.25%
	Loss due to nitrogen from human activities in WA	3.7	0.12%	6.7	0.11%	0.21	0.04%
Worst day (day of the year when maximum compression occurs)	2014 existing conditions	151	5.0%	114	1.8%	3.8	0.84%
	2014 reference conditions	117	3.9%	84	1.3%	3.3	0.71%
	Loss due to nitrogen from human activities in WA	33	1.1%	30	0.48%	0.59	0.13%

* Percent remaining uses three significant figures for resolution near 100%, while others are rounded to two (see methodology).

5 FUTURE RESEARCH AND APPLICATION BUILDING ON THE CURRENT STUDY

1. A risk-based framework that assesses the probability that water quality surpasses a critical threshold — and the extent to which anthropogenic nitrogen alters that probability — would advance the science available for decision making. Oxygen thresholds are difficult to translate from the lab to *in situ* environments, and adverse effects of oxygen depletion could be felt before routine metabolism becomes constrained. Moreover, metabolic index parameters are estimated with considerable uncertainty for species that lack extensive laboratory studies, such as Dungeness crab and English sole. A risk-based framework can embrace these and other uncertainties to better characterize how human activity may be affecting marine life through oxygen depletion.
2. Empirical studies examining how episodic vertical habitat compression affects Chinook salmon routine activities and behavioral responses in Puget Sound are important for translating the findings of this study and any future management applications. This could include quantifying how far away vertically and horizontally the “refuge waters” (sufficient dissolved oxygen) are from the waters where habitat is compressed during such events, and improved empirical data on how well salmon access them. This would determine the degree to which episodic compression may pose a meaningful biological risk to this mobile species.
3. Refuge waters and below-threshold habitat volumes are sensitive to the Salish Sea Model representation of the timing and persistence of vertical dissolved oxygen stratification. Additional validation using available continuous dissolved oxygen profile observations above and below the pycnocline would refine habitat compression and refuge volumes, complementing recommendations in prior evaluations (Mazzilli et al., 2024).
4. Additional research into the impact of low oxygen throughout the life cycle of these and other species would improve our understanding of aerobic habitat compression risk, particularly given the temporal differences and habitat-specific nature of the current results. Furthermore, expanding this application to other species and life stages that are key to ecosystem functioning in Puget Sound would broaden the applicability of the approach applied.
5. Some areas that fall below the threshold occur near river mouths, such as the inner extent of the unmasked area of the Salish Sea Model in Bellingham Bay. River inlets and estuarine deltas may exhibit $\Phi < 1$ in the shallow masked zones currently excluded from this study, such as the Stillaguamish River's entrance in Port Susan in the Whidbey Basin. Such estuarine waters may be of particular importance to juvenile Chinook salmon, given the variation in “smoltification” timing and estuary residence strategies (ranging from days to many months) that may overlap with the habitat compression periods identified in this study. In addition, higher-resolution bathymetry (and confidence in the resulting Salish Sea Model outputs in those locations) would be required to unmask and better evaluate near-shore areas, including wetting/drying zones of river mouths and terminal inlets. This is important because these areas encompass ecologically important nearshore and estuarine habitats where short-duration exposure events can be consequential.

6. The anthropogenic contribution to habitat compression modeled in this study estimates how available aerobic habitat changes under modeled 2014 conditions with and without Washington State modern-day anthropogenic nitrogen loads. A more advanced application would require consideration of differences in climate change on hydrodynamic forcing and mixing, and incoming and ambient dissolved oxygen and temperature in model scenarios (among other considerations). Such a study would benefit from partitioned exogenous loadings to Puget Sound, including quantifying pre-settlement loadings from Canada rather than the modern-day levels of marine treatment plants and rivers that were used in the current available reference condition scenario. This underscores the need to attribute habitat compression to anthropogenic loading under evolving climate and broader transboundary conditions.

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7 APPENDICES

APPENDIX 1 METABOLIC INDEX METHODOLOGY

Code Documentation[1]

1. Biogeochemical and Hydrodynamic Model Data Processing: Script used to extract Salish Sea Model outputs between current conditions (2014 baseline) and reference conditions (estimated pre-industrial nutrient loadings) scenarios across all 10 depth layers.
2. Metabolic Index Calculations: Python script to calculate metabolic index using phylogenetic trait imputation parameters, incorporating daily minimum dissolved oxygen, maximum temperature, and associated partial pressure conditions from SSM outputs.
3. Species-Specific Parameter Application: Script to apply taxa-specific physiological parameters (V, Eo, n) and biological characteristics (body mass, depth distributions) for Chinook salmon, Dungeness crab, and English sole.
4. Risk Threshold Analysis: Python script to categorize metabolic index results into likely risk ($\varphi < 1$), and unlikely risk ($\varphi \geq 1$) categories for both basal and routine metabolic rates.
5. Regional Statistics and Exposure Analysis: Script to calculate regional statistics including exposure frequency, duration, and spatial distributions of low metabolic index events across Puget Sound basins.
6. Spatial Mapping and Visualization: Python script to create maps. For example, showing annual minimum metabolic index, average duration of likely risk exposures, and days per year of likely risk for each taxon.
7. Area- and Volume-Based Habitat Assessment: Script to calculate available habitat area and volume within species depth ranges and quantify anthropogenic changes in habitat quality between current and reference conditions.

References [1] https://github.com/UW-PSI/SalishSeaModel-analysis

Phylogenetic trait imputation application – reference values and variance-covariance matrix by species

Following Essington et al., (2006) the following fixed and references parameters are applied: w_ref is reference weight (5g, model reference parameter); T_ref is reference temperature (15°C, model reference parameter), and k_B is Boltzmann constant (8.617×10^{-5} eV K^{-1}).

Table A1. Variance-Covariance Matrices by Species. Parameter uncertainty matrices showing statistical relationships between model coefficients. Rows represent: intercept uncertainty (row 1), size effect uncertainty (row 2), temperature effect uncertainty (row 3), and metabolic mode uncertainty (row 4).

Chinook Salmon

Parameter	β_0 (log(V))	β_1 (n)	β_2 (Eo)	β_3 (beta method)
β_0	0.173846857	1.326809e-02	-0.073963952	6.287643e-03
β_1	0.013268092	8.014129e-03	-0.004246992	1.119302e-05
β_2	-0.073963952	-4.246992e-03	0.035758738	-2.752385e-03
β_3	0.006287643	1.119302e-05	-0.002752385	2.331340e-02

Dungeness Crab

Parameter	β_0 (log(V))	β_1 (n)	β_2 (Eo)	β_3 (beta method)
β_0	0.160201361	0.006825386	-0.043946093	0.005911341
β_1	0.006825386	0.006126607	-0.003405334	-0.000179495
β_2	-0.043946093	-0.003405334	0.026743298	-0.001186574
β_3	0.005911341	-0.000179495	-0.001186574	0.023313400

English Sole

Parameter	β_0 (log(V))	β_1 (n)	β_2 (Eo)	β_3 (beta method)
β_0	0.133984605	-0.000759200	-0.034233516	0.002470956
β_1	-0.000759200	0.005736930	-0.001583776	-0.000338378
β_2	-0.034233516	-0.001583776	0.025289992	-0.000539733
β_3	0.002470956	-0.000338378	-0.000539733	0.023313400

APPENDIX 2: METHODOLOGY PLOTS

Both the basal and routine metabolic index results are based on the maximum likelihood predictions from the phylogenetic trait imputation (Essington et al., 2026), and upper and lower bounds of the 95% prediction interval for each are presented. Thus, our calculations of the daily metabolic index capture the uncertainty resulting from parameter uncertainty for each (Figure A2.1). Additionally, we capture variation from environmental variability by repeating the calculations for all days of the year.

Figure A2.1 shows examples of a daily time series of basal (top panel) and routine (bottom panel) metabolic index for Dungeness crab in bottom waters at 3 locations. The left panel shows results at a location in Southern Hood Canal (left panels) with the dashed line indicating the threshold (Φ = 1) in each. Chinook Salmon results are shown in Figure A2.2.

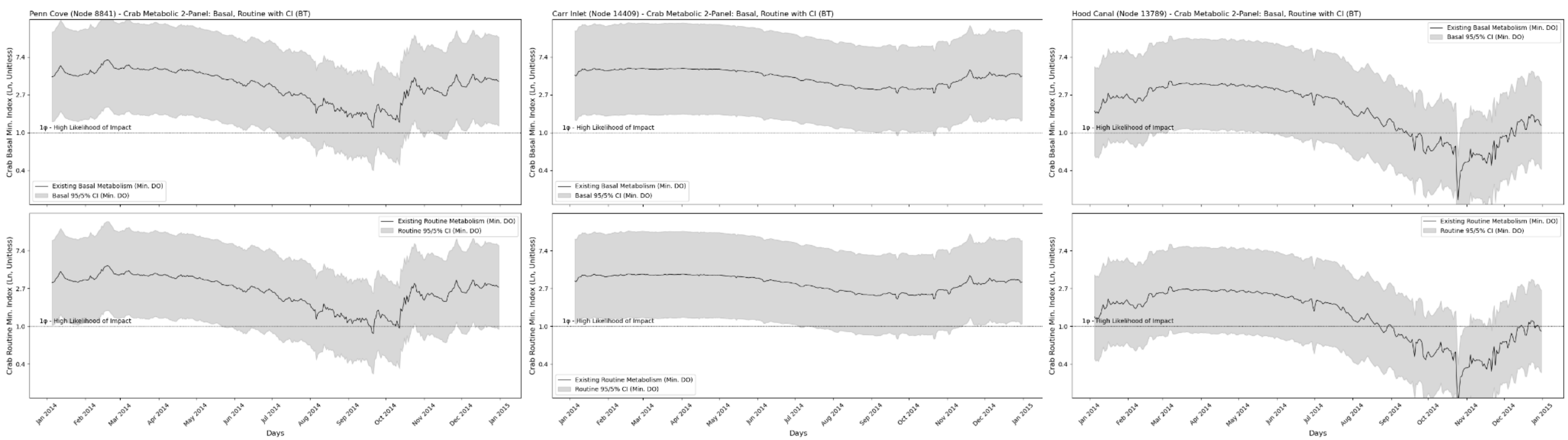

Figure A2.1. Example of a daily time series of basal (top panel) and routine (bottom panel) metabolic index for Dungeness crab in bottom waters at 3 locations. Predicted results (black line) using median input parameters for crab show at what time of the year there is a potential high likelihood of impact dropping below the modeled threshold (dashed line indicating Φ = 1). The lower and upper bounds to results using 5%, and 95% input parameters.

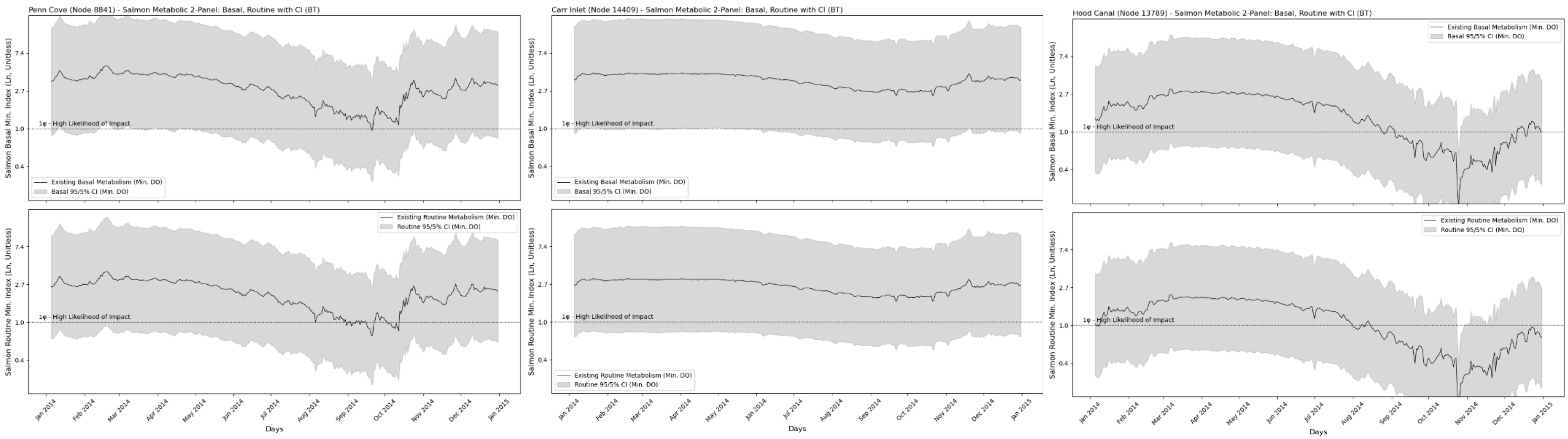

Figure A2.2 Example of a daily time series of basal (top panel) and routine (bottom panel) metabolic index for Chinook salmon in bottom waters at 3 locations (See Figure A2.1 for further information).

APPENDIX 3 MODELED RESULTS BELOW NUMERICAL CRITERIA FOR WASHINGTON STATE

Table A3.1. Average daily volume in each basin that the model predicts to fall below the numeric criteria in 2014. Depending on the cell, the numeric criteria falls between 4 to 7 mg/L.

		2014 Existing Conditions		2014 Reference Conditions		Difference Between Existing & Reference Conditions	
Region	**Total Volume (km^3)**	**Average Volume (km^3)**	**Average Volume (%)**	**Average Volume (km^3)**	**Average Volume (%)**	**Average Volume (km^3)**	**Average Volume (%)**
Hood Canal	19.9	14.1	71.0	13.9	70.0	0.2	70.0
Main Basin	70.8	35.5	50.1	34.5	48.8	0.9	48.8
US Portion of SJF & Admiralty Basin	260.0	233.1	89.7	232.9	89.6	0.2	89.6
US Portion of SOG & Northern Bays	153.9	130.5	84.8	130.3	84.6	0.2	84.6
South Sound	13.4	4.1	30.3	3.8	28.6	0.2	28.6
Whidbey Basin	23.3	7.4	31.9	7.0	30.1	0.4	30.1
SJF/SOG Border Basin	22.2	20.0	89.9	20.0	89.8	0.0	0.1
All Regions	**563.5**	**444.7**	**78.9**	**442.5**	**78.5**	**2.2**	**78.5**

Table A3.2. Minimum daily volume in each basin that the model predicts to fall below the numeric criteria in 2014 and the associated date. Depending on the cell, the numeric criteria falls between 4 to 7 mg/L.

		2014 Existing Conditions			2014 Reference Conditions		
Region	**Total Volume (km^3)**	**Date of Minimum Volume**	**Minimum Volume (km^3)**	**Minimum Volume (%)**	**Date of Minimum Volume**	**Minimum Volume (km^3)**	**Minimum Volume (%)**
Hood Canal	19.9	03/21	5.5	27.5	03/21	5.2	25.9
Main Basin	70.8	02/21	0.0	0.0	02/03	0.0	0.0
US Portion of SJF & Admiralty Basin	260.0	02/19	184.6	71.0	02/18	184.3	70.9
US Portion of SOG & Northern Bays	153.9	03/07	94.4	61.3	03/07	93.8	60.9
South Sound	13.4	01/08	0.0	0.0	01/07	0.0	0.0
Whidbey Basin	23.3	01/05	0.0	0.0	01/05	0.0	0.0
SJF/SOG Border Basin	22.2	03/10	16.2	72.9	03/09	16.1	72.6
All Regions	**563.5**	**02/19**	**307.6**	**54.6**	**02/19**	**306.7**	**54.4**

Table A3.3. Maximum daily volume in each basin that the model predicts to fall below the numeric criteria in 2014 and the associated date. Depending on the cell, the numeric criteria falls between 4 to 7 mg/L.

		2014 Existing Conditions			**2014 Reference Conditions**		
Region	**Total Volume (km^3)**	**Date of Maximum Volume**	**Maximum Volume (km^3)**	**Maximum Volume (%)**	**Date of Maximum Volume**	**Maximum Volume (km^3)**	**Maximum Volume (%)**
Hood Canal	19.9	10/09	19.3	96.8	10/09	19.2	96.7
Main Basin	70.8	10/09	69.3	97.9	10/09	69.2	97.8
US Portion of SJF & Admiralty Basin	260.0	10/12	258.1	99.3	10/12	258.1	99.3
US Portion of SOG & Northern Bays	153.9	10/09	148.6	96.5	10/09	148.6	96.5
South Sound	13.4	10/09	12.3	91.7	10/09	12.1	90.3
Whidbey Basin	23.3	10/09	21.9	94.0	10/09	21.9	93.8
SJF/SOG Border Basin	22.2	09/23	21.6	97.1	09/23	21.6	97.1
All Regions	**563.5**	**10/09**	**550.6**	**97.7**	**10/09**	**550.2**	**97.6**

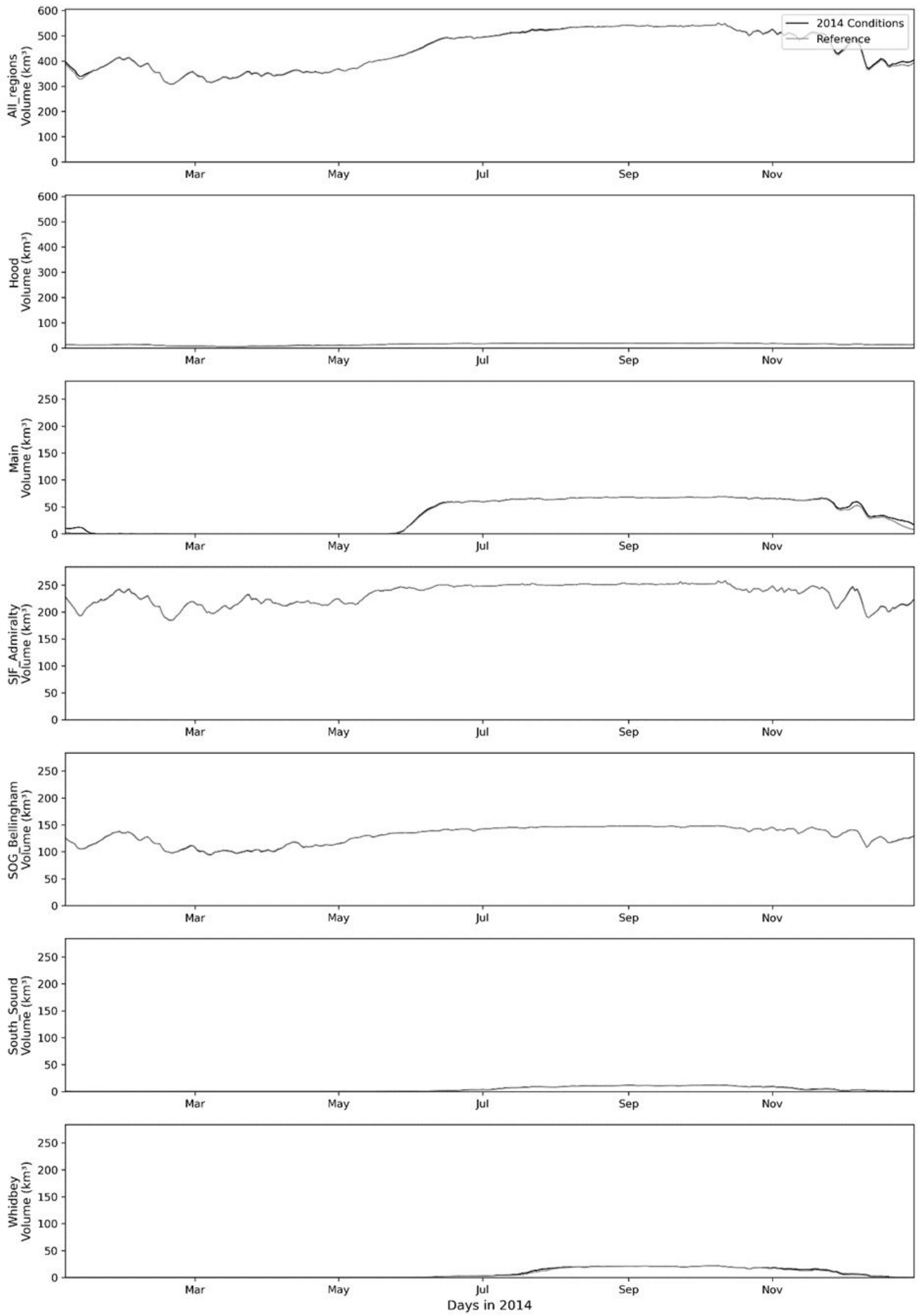

Figure A3.1. Daily time series of water column volume below numerical criteria for Washington State by basin during 2014. Daily volumes were calculated from the total water column volume of cells where the minimum daily dissolved oxygen concentration fell below the numerical criteria for at least 1 hour in any layer.

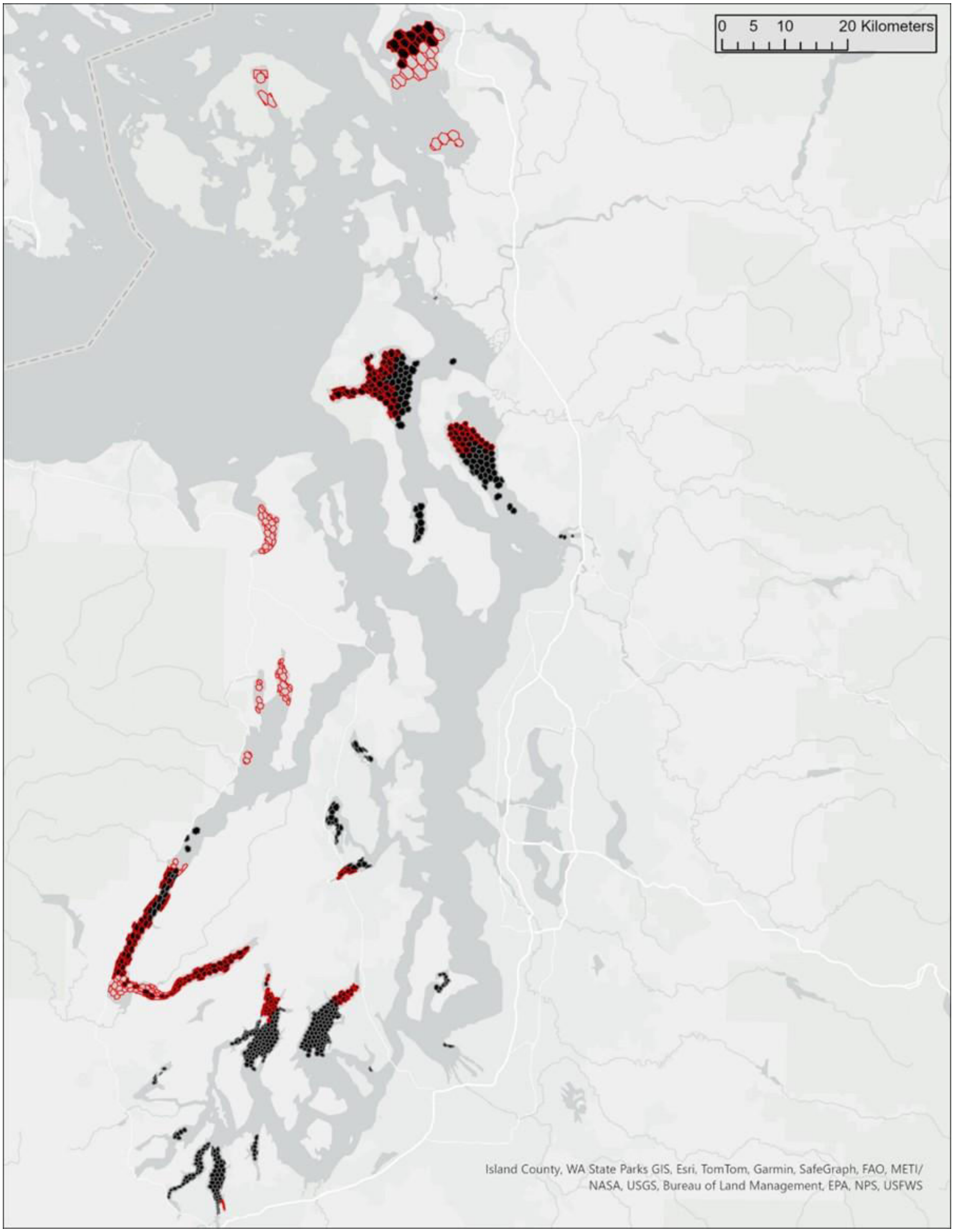

Figure A3.2. Spatial extent of Dungeness crab routine Φ < 1 in bottom waters during 2014, showing all cells where the threshold was exceeded on at least one day (red outline). Spatial extent of non-compliance with water quality standards in 2014, showing all cells where Ahmed et al. (2021) predicted non-compliance on at least one day (black fill).

APPENDIX 4 DUNGENESS CRAB

Table A4.1. Annualized daily average area and percent of habitat during 2014 when basal Φ < 1 for Dungeness crab for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Area	2014 Existing Conditions Average Area Φ < 1		2014 Reference Conditions Average Area Φ < 1		Difference Between Existing & Reference Conditions	
	km^2	km^2	% of Habitat	km^2	% of Habitat	km^2	% of Habitat
Hood Canal	207	12	5.7%	10	5.0%	1.4	0.70%
Main Basin	124	<0.20	<0.10%	<0.20	<0.10%	<0.20	<0.10%
US Portion of SJF & Admiralty Basin	1072	0.69	<0.10%	0.64	<0.10%	<0.20	<0.10%
US Portion of SOG & Northern Bays	981	1.0	0.10%	0.77	<0.10%	0.3	<0.10%
South Sound	327	<0.20	<0.10%	<0.20	<0.10%	<0.20	<0.10%
Whidbey Basin	274	0.58	0.21%	0.36	0.13%	0.23	<0.10%
All Regions	**3021**	**14**	**0.47%**	**12**	**0.40%**	**2.0**	**<0.10%**

Table A4.2. The maximum extent of habitat in 2014 with basal Φ < 1 for Dungeness crab, by region, for existing and reference conditions.

Region	Total Habitat Area	2014 Existing Conditions Max Area Φ < 1			2014 Reference Conditions Max Area Φ < 1			Difference Between Existing & Reference Conditions	
	km^2	km^2	% of Habitat	Day	km^2	% of Habitat	Day	km^2	% of Habitat
Hood Canal	207	59	28%	11/23	58	28%	11/22	0.87	0.42%
Main Basin	124	1.6	1.3%	08/18	0.77	0.62%	08/19	0.79	0.64%
US Portion of SJF & Admiralty Basin	1072	7.2	0.67%	08/18	7.2	0.7%	10/04	<0.20	<0.10%
US Portion of SOG & Northern Bays	981	28	2.9%	09/01	26	2.7%	09/02	2.1	0.22%
South Sound	327	4.3	1.3%	09/03	0.52	0.16%	09/03	3.8	1.15%
Whidbey Basin	274	10	3.8%	09/22	7.3	2.7%	09/21	3.1	1.13%
All Regions	**3021**	**69**	**2.3%**	**09/22**	**58**	**1.9%**	**11/22**	**12**	**0.39%**

Table A4.3 Annualized daily average area and percent of habitat during 2014 when routine Φ < 1 for Dungeness crab for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Area	2014 Existing Conditions Average Area Φ < 1		2014 Reference Conditions Average Area Φ < 1		Difference Between Existing & Reference Conditions	
	km²	**km²**	**% of Habitat**	**km²**	**% of Habitat**	**km²**	**% of Habitat**
Hood Canal	207	19	9.3%	17	8.4%	2.0	0.97%
Main Basin	124	<0.20	<0.10%	<0.20	<0.10%	<0.20	<0.10%
US Portion of SJF & Admiralty Basin	1072	1.8	0.17%	1.7	0.16%	<0.20	<0.10%
US Portion of SOG & Northern Bays	981	3.0	0.30%	2.4	0.25%	0.53	<0.10%
South Sound	327	0.44	0.13%	<0.20	<0.10%	0.32	<0.10%
Whidbey Basin	274	2.0	0.74%	0.97	0.35%	1.1	0.38%
All Regions	**3021**	**27**	**0.88%**	**23**	**0.75%**	**4.0**	**0.13%**

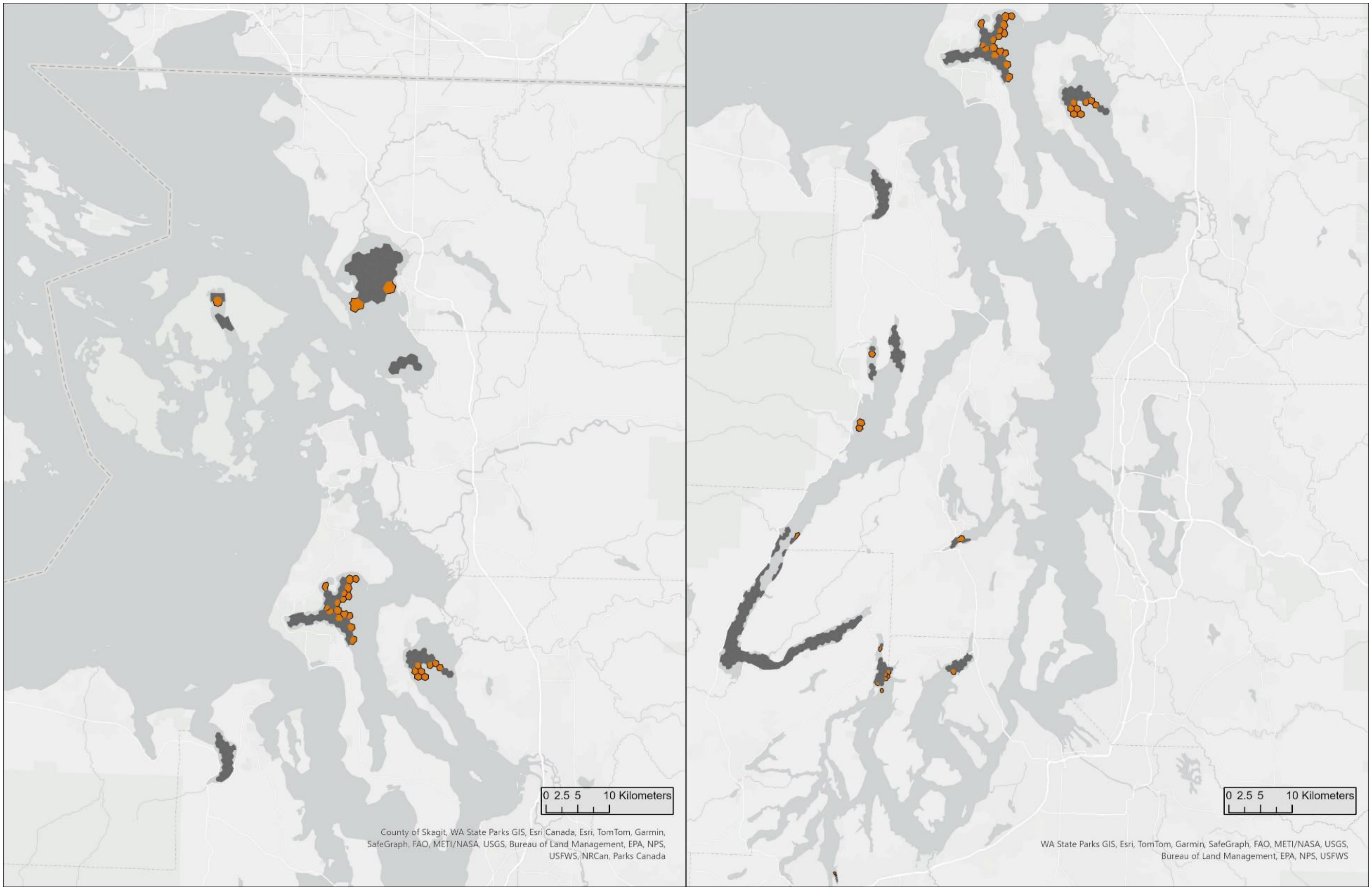

Figure A4.1. Spatial extent of Dungeness crab routine Φ < 1 in bottom waters during 2014, showing all cells where the threshold was exceeded on at least one day, for the reference scenario (grey) overlayed by the existing scenario with 2014 nutrient loads (orange). The left panel shows northern portion of the study area, and the right panel shows the southern.

APPENDIX 5 ENGLISH SOLE

Table A5.1. Annualized daily average area and percent of habitat during 2014 when basal Φ < 1 for English sole for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Area	2014 Existing Conditions Average Area Φ < 1		2014 Reference Conditions Average Area Φ < 1		Difference Between Existing & Reference Conditions	
	km²	km²	% of Habitat	km²	% of Habitat	km²	% of Habitat
Hood Canal	290	10	3.5%	8.8	3.0%	1.4	0.48%
Main Basin	635	<0.20	<0.10%	<0.20	<0.10%	<0.20	<0.10%
US Portion of SJF & Admiralty Basin	2717	0.41	<0.10%	0.37	<0.10%	<0.20	<0.10%
US Portion of SOG & Northern Bays	1836	0.63	<0.10%	0.44	<0.10%	0.20	<0.10%
South Sound	327	<0.20	<0.10%	<0.20	<0.10%	0.20	<0.10%
Whidbey Basin	391	0.44	0.11%	0.19	<0.10%	0.25	<0.10%
All Regions	**6378**	**12**	**0.18%**	**9.8**	**0.15%**	**1.9**	**<0.10%**

Table A5.2. The maximum extent of habitat in 2014 with basal Φ < 1 for English sole, by region, for existing and reference conditions.

Region	Total Habitat Area	2014 Existing Conditions Max Area Φ < 1			2014 Reference Conditions Max Area Φ < 1			Difference Between Existing & Reference Conditions	
	km²	km²	% of Habitat	Day	km²	% of Habitat	Day	km²	% of Habitat
Hood Canal	290	59	20%	11/22	56	19%	11/22	2.4	0.83%
Main Basin	635	0.77	0.12%	08/05	0.22	<0.10%	08/19	0.55	**<0.10%**
US Portion of SJF & Admiralty Basin	2717	6.5	0.24%	10/09	5.6	0.21%	09/01	0.90	**<0.10%**
US Portion of SOG & Northern Bays	1836	25	1.3%	09/02	19	1.0%	09/02	5.9	0.32%
South Sound	327	1.7	0.51%	09/03	<0.20	<0.10%	01/05	1.7	0.51%
Whidbey Basin	391	7.3	1.9%	09/20	5.6	1.4%	09/21	1.7	0.44%
All Regions	**6378**	**59**	**0.92%**	**11/22**	**56**	**0.88%**	**11/22**	**2.4**	**<0.10%**

Table A5.3. Annualized daily average area and percent of habitat during 2014 when routine Φ < 1 for English sole for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Area	2014 Existing Conditions Average Area Φ < 1		2014 Reference Conditions Average Area Φ < 1		Difference Between Existing & Reference Conditions	
	km^2	**km^2**	**% of Habitat**	**km^2**	**% of Habitat**	**km^2**	**% of Habitat**
Hood Canal	290	17	5.8%	14	4.9%	2.7	0.92%
Main Basin	635	<0.20	<0.10%	<0.20	<0.10%	<0.20	<0.10%
US Portion of SJF & Admiralty Basin	2717	1.3	<0.10%	1.3	<0.10%	<0.20	<0.10%
US Portion of SOG & Northern Bays	1836	1.9	0.11%	1.6	<0.10%	0.36	<0.10%
South Sound	327	0.20	<0.10%	<0.20	<0.10%	0.16	<0.10%
Whidbey Basin	391	1.2	0.30%	0.60	0.15%	0.56	0.14%
All Regions	**6378**	**22**	**0.34%**	**18**	**0.28%**	**3.8**	**<0.10%**

APPENDIX 6 SALMON

Methodological Considerations for Pelagic Species: Water Column Averaging and Vertical Distribution of Chinook Salmon

There is an added complexity to interpreting results when considering pelagic species that can move freely through the water column, unlike benthic species. Further investigation, using an average water-column Φ calculated as a surrogate for impacts on salmon throughout the water column also shows no likely impairment ($\Phi > 1$) anywhere in Puget Sound during 2014. However, using an averaged metric to represent the water column misses the impact on routine metabolic activities that can occur if species do stay in deeper waters at locations and times that are $\Phi > 1$, and was therefore not used as a metric in this report. Looking at the volumes ($\Phi < 1$) throughout Puget Sound and the Straits the total water column maximum extent reached 3.8 km^3 on 10/11 (Table 3.3.3). Looking at the volumes by layer in the SSM, the bottom layer represents 14.6% of the water column and the remaining layers above represent 85.4% everywhere in the model domain, regardless of depth.

Ultimately, the extent of habitat actually used in the water column requires future research focus to better quantify impact at specific locations, and is currently unknown for Puget Sound for Chinook salmon beyond existing studies identified (Section 3.3). Metrics from this current work can be further developed to compare to such geographic-specific field studies, quantifying the depths within the water column (and relative thickness) of individual cells that are likely impaired ($\Phi > 1$). Currently this is limited to cumulative volume calculations by region (Table 3.3.2 and 3.3.3 for routine, and Table A6.1 and A6.2 for basal results).

Table A6.1. Annualized daily average volume and percent of habitat during 2014 when basal Φ < 1 for Chinook salmon for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Volume	2014 Existing Conditions Average Volume Φ < 1		2014 Reference Conditions Average Volume Φ < 1		Difference Between Existing & Reference Conditions	
	km^3	km^3	% of Habitat	km^3	% of Habitat	km^3	% of Habitat
Hood Canal	20	0.28	1.4%	0.22	1.1%	0.064	0.32%
Main Basin	52	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
US Portion of SJF & Admiralty Basin	212	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
US Portion of SOG & Northern Bays	125	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
South Sound	13	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
Whidbey Basin	22	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
All Regions	**459**	**0.29**	**<0.10%**	**0.23**	**<0.10%**	**0.067**	**<0.10%**

Table A6.2. The maximum extent of habitat in 2014 with basal Φ < 1 for Chinook salmon, by region, for existing and reference conditions.

Region	Total Habitat Volume	2014 Existing Conditions Max Volume Φ < 1			2014 Reference Conditions Max Volume Φ < 1			Difference Between Existing & Reference Conditions	
	km^3	km^3	% of Habitat	Day	km^3	% of Habitat	Day	km^3	% of Habitat
Hood Canal	20	1.5	7.7%	10/17	1.3	6.6%	10/17	0.22	1.12%
Main Basin	52	<0.020	<0.10%	08/18	<0.020	<0.10%	08/18	<0.020	<0.10%
US Portion of SJF & Admiralty Basin	212	0.051	<0.10%	09/19	0.046	<0.10%	08/19	<0.020	<0.10%
US Portion of SOG & Northern Bays	125	0.065	<0.10%	08/31	0.062	<0.10%	08/31	<0.020	<0.10%
South Sound	13	0.020	0.15%	09/01	<0.020	<0.10%	09/03	<0.020	0.11%
Whidbey Basin	22	0.084	0.38%	09/21	0.029	0.13%	09/21	0.06	0.25%
All Regions	**459**	**1.6**	**0.35%**	**10/10**	**1.3**	**0.28%**	**10/17**	**0.29**	**<0.10%**

Table A6.3. Annualized daily average volume and percent of habitat during 2014 when routine Φ < 1 for Chinook salmon for existing and reference conditions, as well as the difference between the two.

Region	Total Habitat Volume	2014 Existing Conditions Average Volume Φ < 1		2014 Reference Conditions Average Volume Φ < 1		Difference Between Existing & Reference Conditions	
	km^3	km^3	% of Habitat	km^3	% of Habitat	km^3	% of Habitat
Hood Canal	20	0.73	3.7%	0.61	3.1%	0.11	0.58%
Main Basin	52	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
US Portion of SJF & Admiralty Basin	212	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
US Portion of SOG & Northern Bays	125	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
South Sound	13	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
Whidbey Basin	22	<0.020	<0.10%	<0.020	<0.10%	<0.020	<0.10%
All Regions	**459**	**0.78**	**0.17%**	**0.65**	**0.14%**	**0.13**	**<0.10%**

APPENDIX 7 DURATION OF AEROBIC HABITAT COMPRESSION

The biological significance of aerobic habitat compression depends not only on where and how extensively oxygen conditions fall below a species' routine threshold, but also on how long those conditions persist. For example, considering hypoxic exposure for two Puget Sound species, Vaquer-Sunyer & Duarte (2008) reported a median lethal time for starry flounder of 23 minutes, while priapulids can withstand more than 816 hours. Understanding how the duration of exposure to conditions where routine $\Phi < 1$ influences biological impact remains an active area of research, and the metrics presented here are intended to provide a foundation for comparison as that understanding develops.

For computational efficiency and to increase confidence in results, Salish Sea Model daily minimum as well as maximum values for each cell-layer combination were extracted and used in this study. These were drawn from hourly Salish Sea Model outputs. The hours inbetween would fall somewhere between these minimum and max daily values . Given that the median lethal time under hypoxia for many benthic species is less than one day (Vaquer-Sunyer & Duarte, 2008), finer hourly resolution of duration metrics may be warranted in future analyses. For now, two complementary duration metrics bracket the range of potential exposure:

- **Gross duration** counts the number of consecutive days on which the daily minimum oxygen conditions fall below the routine $\Phi < 1$ threshold — meaning that aerobic habitat compression occurred at least once during the day. This is the most conservative assumption, as any day with some compression is counted towards a full day of exposure. It may therefore overstate biologically relevant exposure by not accounting for periods within the same day when conditions were sufficient to support routine activity.
- **Net duration** accounts for the opportunity for recovery within a day. If the daily minimum falls below the routine threshold but the daily maximum does not, refuge was available at some point during that day, and the day is not counted toward the exposure total. This is the most optimistic assumption and may understate potential impact in situations where sub-threshold conditions, even if brief, carry biological consequences.

For both metrics, the average duration describes how long compression events typically persist at a given location across the modeled year, while the maximum duration captures the single longest uninterrupted compression event.

The distinction between gross and net duration is illustrated by Dungeness crab in Bellingham Bay, where applying the net duration metric reduces both the spatial extent of compressed habitat and the duration of compression relative to the gross metric — with maximum durations in some locations declining from 8–14 days to less than 7 days, and in other cells (more seaward), reducing to no days of compression at all. In Hood Canal, however, compression is sufficiently persistent that maximum duration exceeds one month under both metrics, reflecting the more sustained nature of aerobic habitat reduction in that region (Figure A7.1).

Regional duration results were summarized using a volume-weighted mean across all cell-layers within each region; where each cell-layer was weighted by its contribution to the total regional habitat volume.

It should be noted when examining all metric outputs for Chinook Salmon that salmon were also modeled to always have access to oxygen-sufficient refuge in the water column in all locations in Puget Sound and the Straits throughout the year - even when a layer in the cell experiences habitat compression in the deeper waters of the water column at the same cell location, as presented in A7.5 and A7.6.

Max
Gross Duration

Max
Net Duration

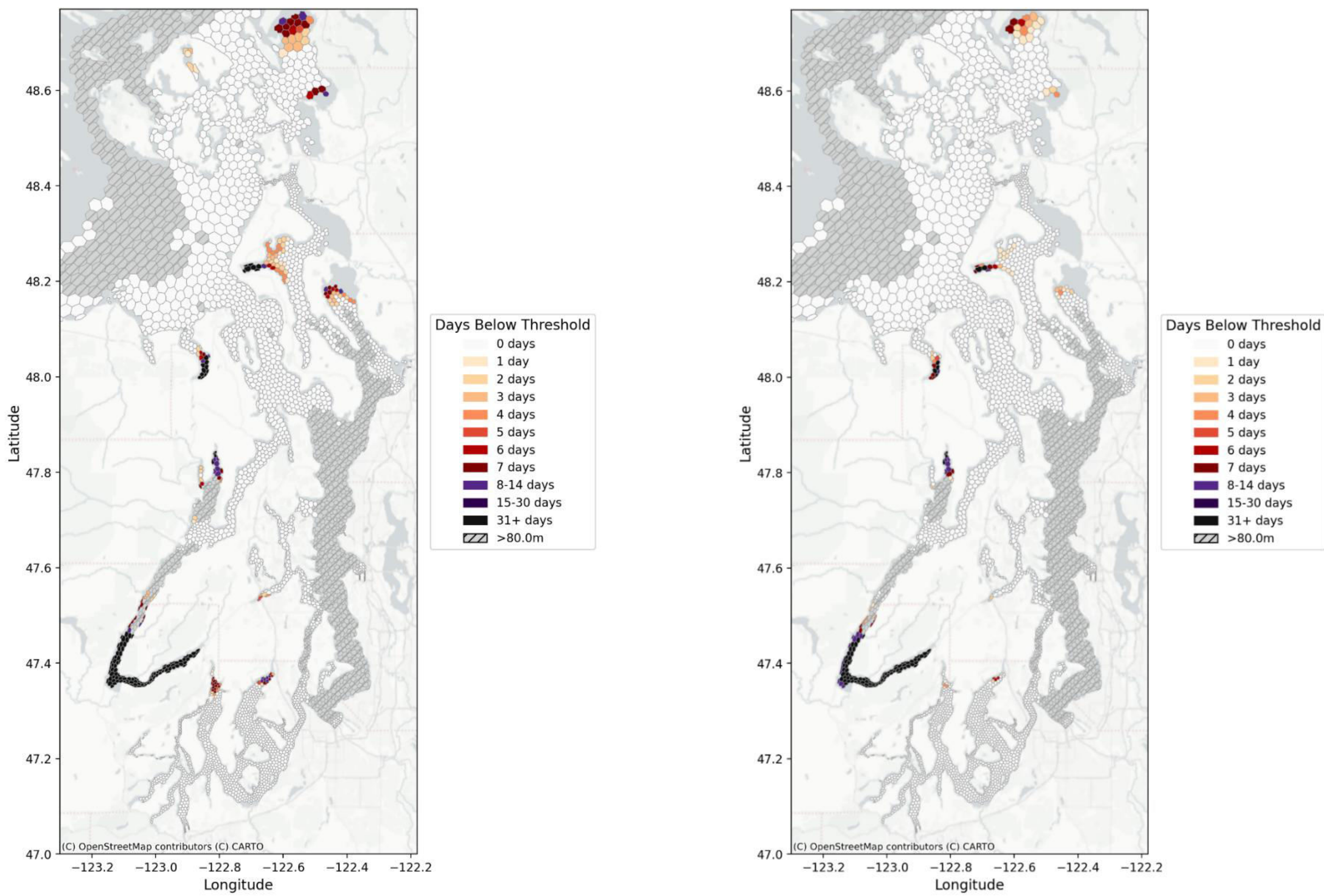

Figure A7.1 Max duration of exposure during 2014 for Dungeness crab when Φ < 1 in the bottom layer. Gross duration (left) and net duration (right).

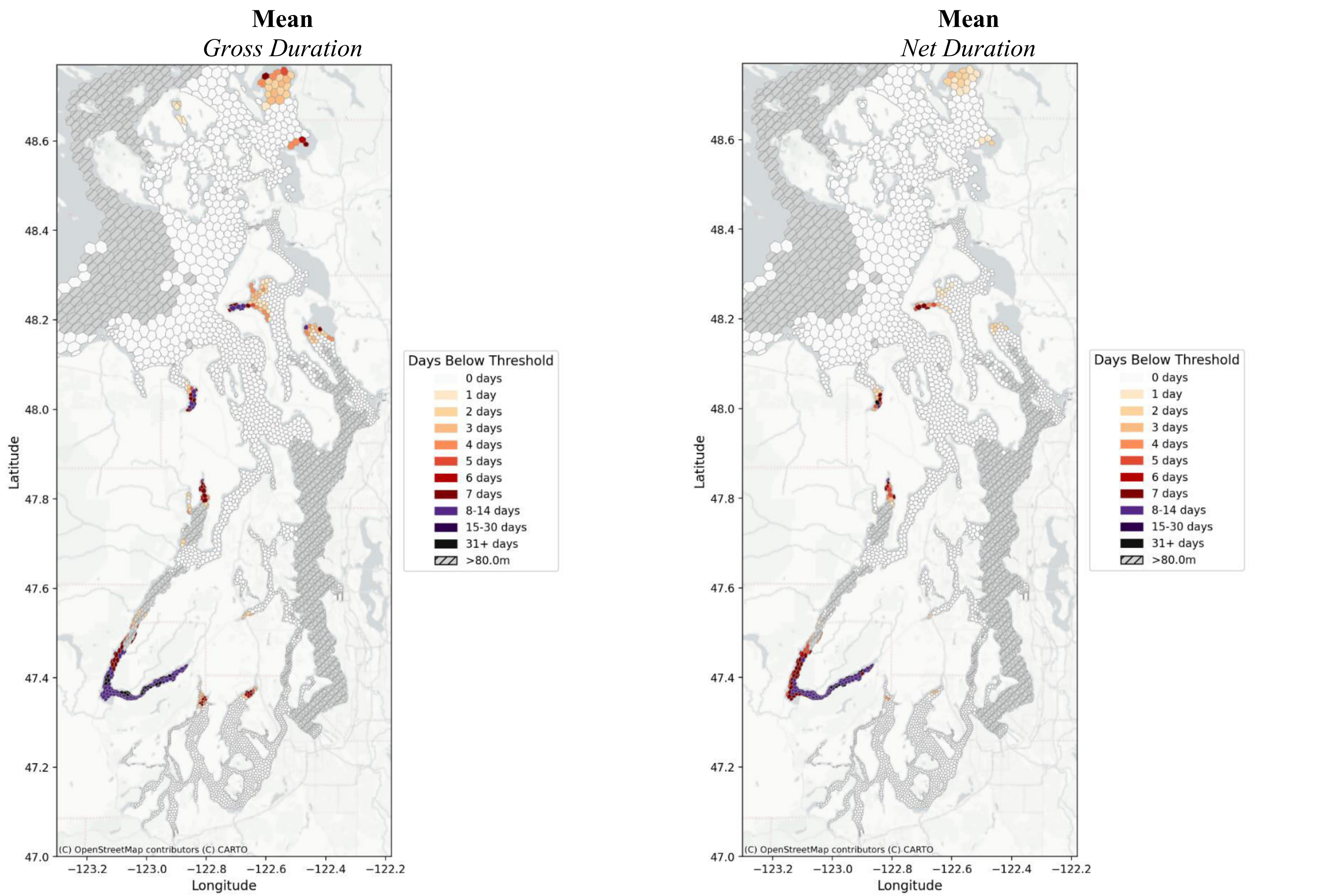

Figure A7.2. Mean duration of exposure during 2014 for Dungeness crab when Φ < 1 in the bottom layer. Gross duration (left) and net duration (right).

Table A7.1. Max duration of exposure during 2014 for Dungeness crab when Φ < 1. Aggregated for each region using a volume-weighted mean of the max duration for each cell's bottom layer for a) gross duration and b) net duration. All calculations were performed using full-precision values before rounding to the nearest day.

Region	Gross Duration			Net Duration		
	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference
Hood Canal	65	60	4	56	50	6
Main Basin	3	2	2	2		2
US Portion of SJF & Admiralty Basin	34	32	2	19	16	3
US Portion of SOG & Northern Bays	6	6	0	3	3	0
South Sound	8	4	4	4	2	2
Whidbey Basin	8	7	1	6	8	-2
All Regions	**27**	**28**	**-1**	**29**	**30**	**-1**

Table A7.2. Mean duration of exposure during 2014 for Dungeness crab when Φ < 1. Aggregated for each region using a volume-weighted mean of the mean duration for each cell's bottom layer for a) gross duration and b) net duration. All calculations were performed using full-precision values before rounding to the nearest day.

Region	Gross Duration			Net Duration		
	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference
Hood Canal	19	18	1	15	14	1
Main Basin	2	1	1	2		2
US Portion of SJF & Admiralty Basin	11	11	0	8	7	1
US Portion of SOG & Northern Bays	3	3	0	2	2	0
South Sound	5	3	1	2	2	1
Whidbey Basin	5	4	0	3	5	-2
All Regions	**9**	**9**	**0**	**8**	**9**	**-1**

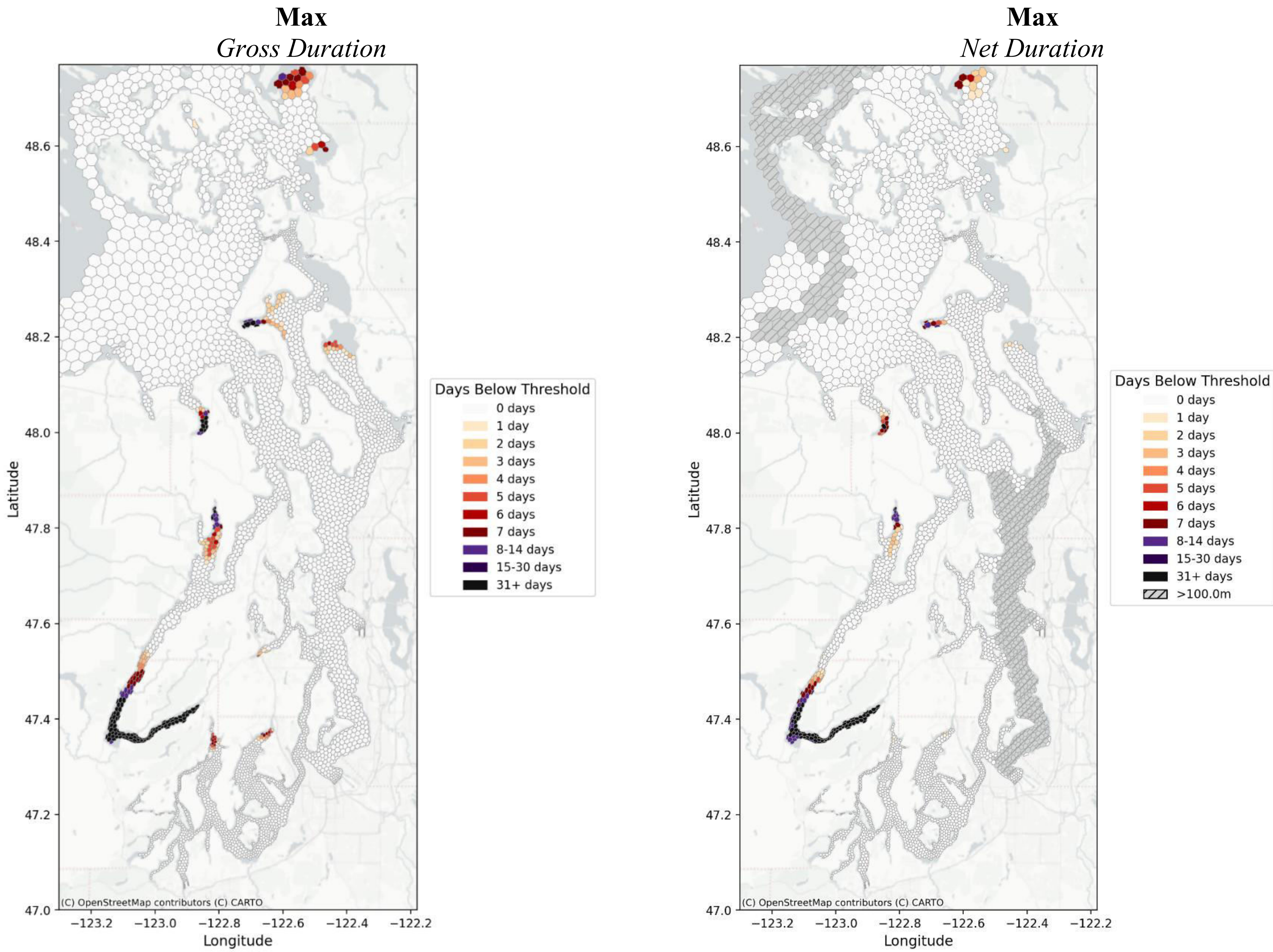

Figure A7.3. Max duration of exposure during 2014 for English sole when Φ < 1 in the bottom layer. Gross duration (left) and net duration (right).

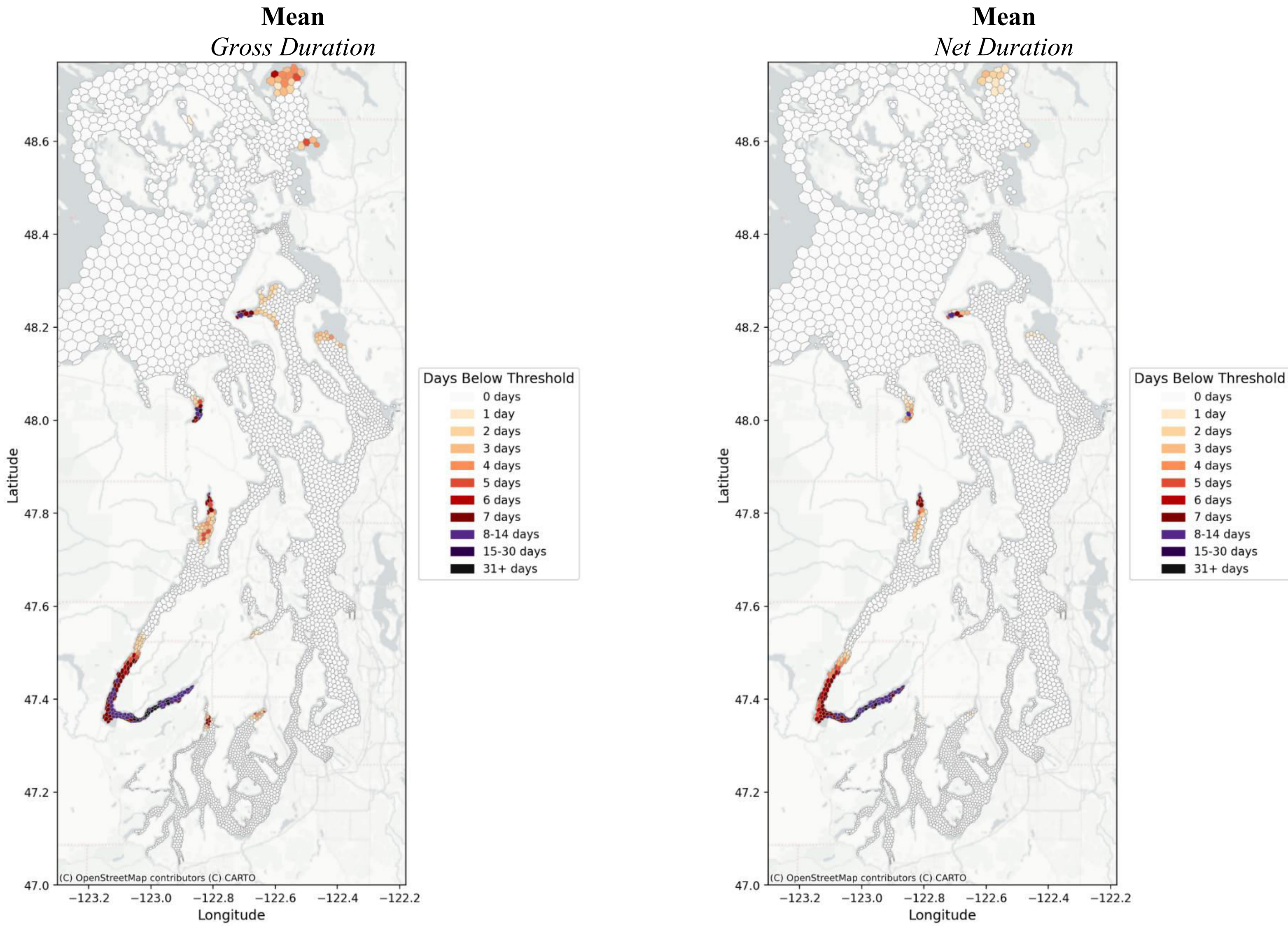

Figure A7.4. Mean duration of exposure during 2014 for English sole when Φ < 1 in the bottom layer. Gross duration (left) and net duration (right).

Table A7.3. Max duration of exposure during 2014 for English sole when Φ < 1. Aggregated for each region using a volume-weighted mean of the max duration for each cell's bottom layer for a) gross duration and b) net duration. All calculations were performed using full-precision values before rounding to the nearest day.

Region	Gross Duration			Net Duration		
	2014 Existing Conditions	**2014 Reference Conditions**	**Existing - Reference**	**2014 Existing Conditions**	**2014 Reference Conditions**	**Existing - Reference**
Hood Canal	43	42	1	38	36	2
Main Basin	2	2	0	1	0	1
US Portion of SJF & Admiralty Basin	25	24	1	9	9	0
US Portion of SOG & Northern Bays	6	5	1	3	4	-1
South Sound	5	2	3	2	0	2
Whidbey Basin	7	12	-5	9	8	1
All Regions	**24**	**27**	**-2**	**26**	**26**	**0**

Table A7.4. Mean duration of exposure during 2014 for English sole when Φ < 1. Aggregated for each region using a volume-weighted mean of the mean duration for each cell's bottom layer for a) gross duration and b) net duration. All calculations were performed using full-precision values before rounding to the nearest day.

Region	Gross Duration			Net Duration		
	2014 Existing Conditions	**2014 Reference Conditions**	**Existing - Reference**	**2014 Existing Conditions**	**2014 Reference Conditions**	**Existing - Reference**
Hood Canal	12	13	1	11	12	0
Main Basin	2	2	1	1	0	1
US Portion of SJF & Admiralty Basin	11	11	6	4	5	-1
US Portion of SOG & Northern Bays	3	3	2	2	3	-1
South Sound	3	2	2	2	0	2
Whidbey Basin	4	7	-2	5	4	2
All Regions	**8**	**9**	**0**	**8**	**9**	**-1**

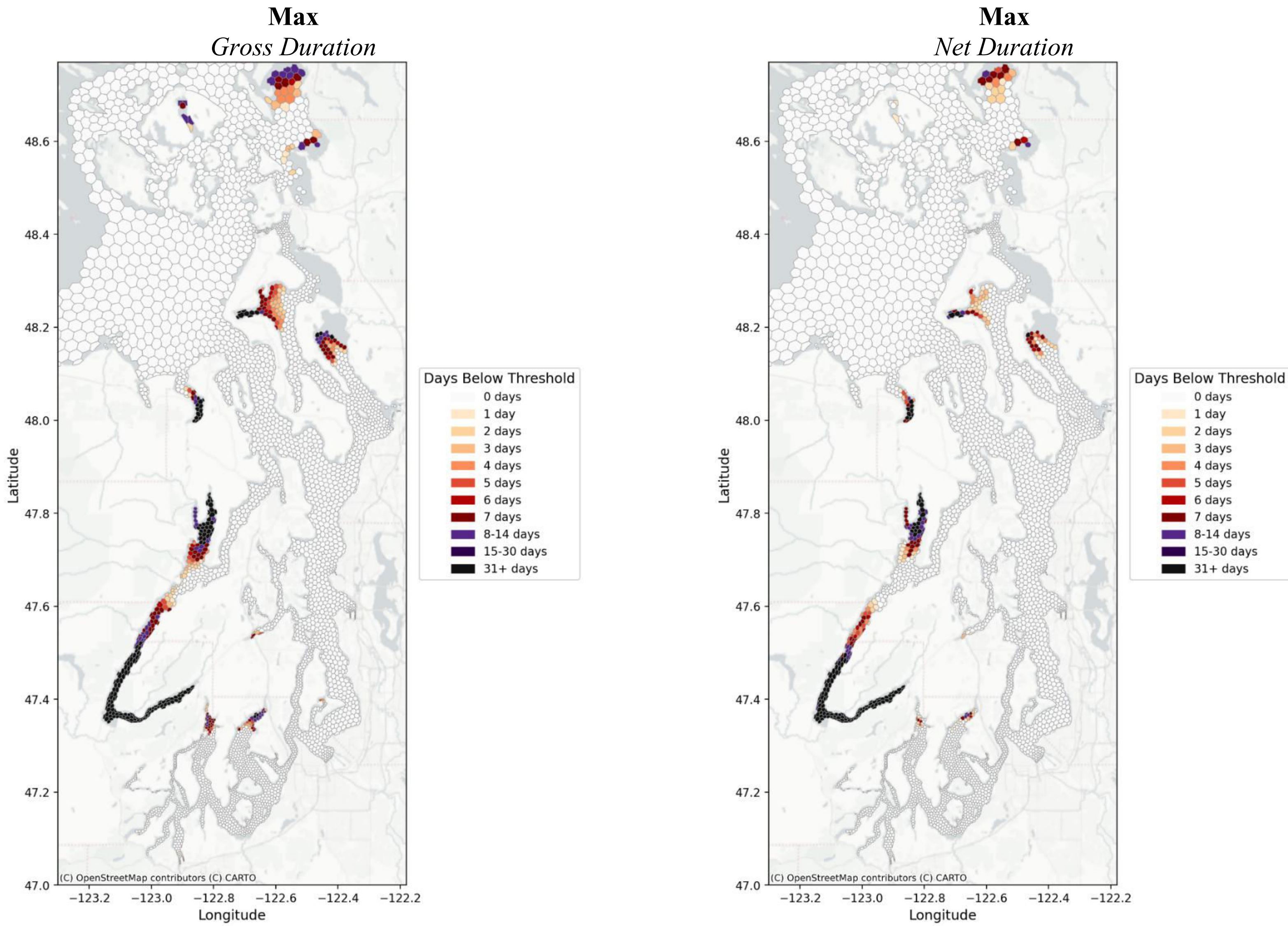

Figure A7.5. Max duration of exposure during 2014 for Chinook salmon when Φ < 1 in any layer in the cell. Gross duration (left) and net duration (right). Note: Chinook salmon always have access to oxygen-sufficient refuge in the water column in all locations in Puget Sound and the Straits throughout the year.

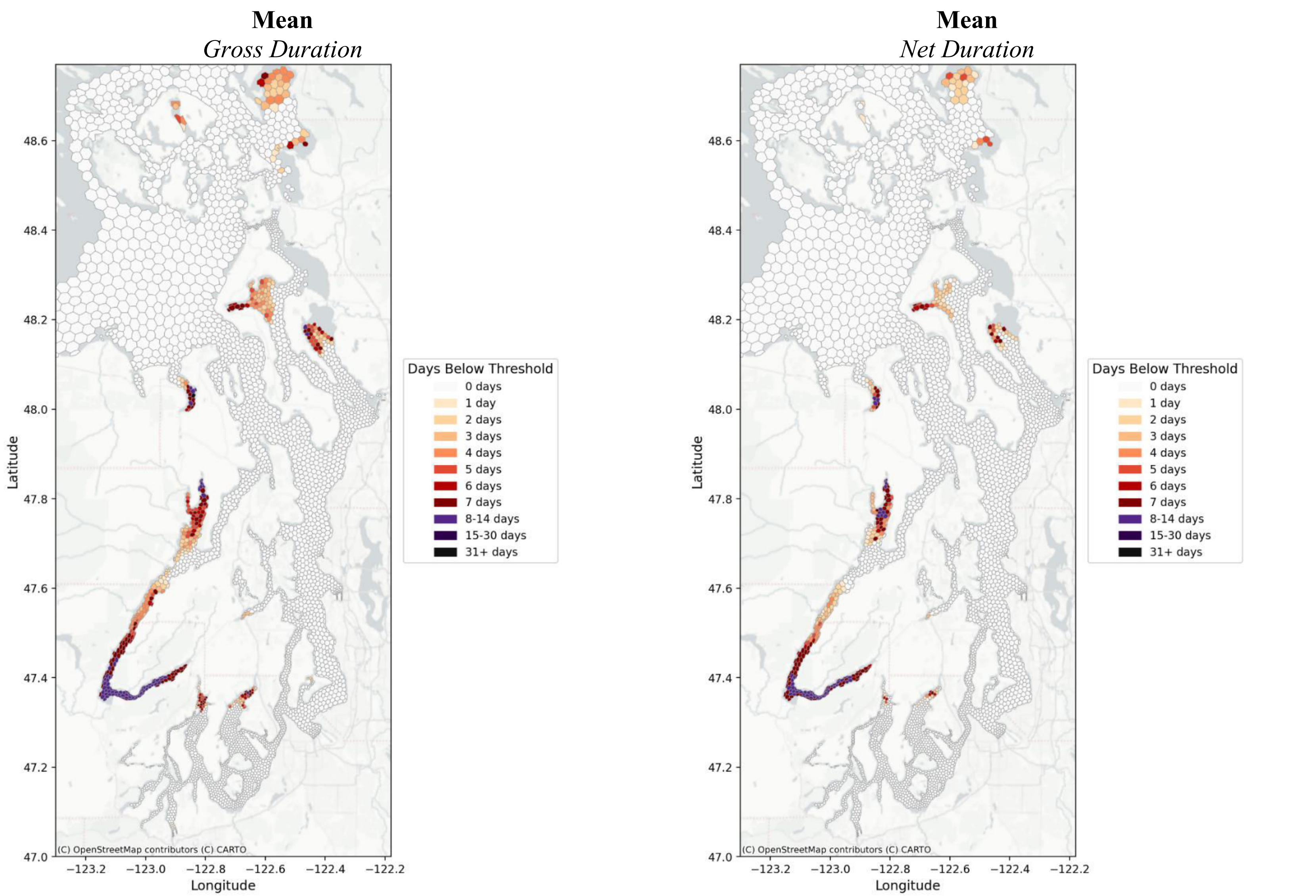

Figure A7.6. Mean duration of exposure during 2014 for Chinook salmon when Φ < 1 in any layer in the cell. Gross duration (left) and net duration (right). Note: Chinook salmon always have access to oxygen-sufficient refuge in the water column in all locations in Puget Sound and the Straits throughout the year.

Table A7.5. Max duration of exposure during 2014 for Chinook salmon when Φ < 1. Aggregated for each region using a volume-weighted mean of the mean duration for each cell-layer for a) gross duration and b) net duration. All calculations were performed using full-precision values before rounding to the nearest day. Note: Chinook salmon always have access to oxygen-sufficient refuge in the water column in all locations in Puget Sound and the Straits throughout the year.

Region	Gross Duration			Net Duration		
	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference
Hood Canal	52	50	2	45	43	2
Main Basin	5	2	2	2	0	2
US Portion of SJF & Admiralty Basin	10	10	0	30	29	1
US Portion of SOG & Northern Bays	8	8	0	5	5	0
South Sound	11	8	2	5	3	2
Whidbey Basin	11	9	2	7	6	1
All Regions	**25**	**24**	**1**	**27**	**27**	**0**

Table A7.6. Mean duration of exposure during 2014 for Chinook salmon when Φ < 1. Aggregated for each region using a volume-weighted mean of the mean duration for each cell-layer for a) gross duration and b) net duration. All calculations were performed using full-precision values before rounding to the nearest day. Note: Chinook salmon always have access to oxygen-sufficient refuge in the water column in all locations in Puget Sound and the Straits throughout the year.

Region	Gross Duration			Net Duration		
	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference	2014 Existing Conditions	2014 Reference Conditions	Existing - Reference
Hood Canal	10	10	0	9	9	0
Main Basin	3	2	1	2	0	2
US Portion of SJF & Admiralty Basin	3	3	0	8	8	0
US Portion of SOG & Northern Bays	3	3	0	3	3	0
South Sound	5	5	0	3	2	1
Whidbey Basin	5	4	1	3	3	1
All Regions	**6**	**6**	**0**	**6**	**6**	**0**