The Response of Pacific Salmon and their Prey to Changing Ocean Conditions and Acidification

By Laura Tessier
IYS Coordinator, North Pacific Region
2019 NPAFC Intern

Laura Tessier was born and raised in Peterborough, Ontario. She developed her love of fishing and water by spending time with her Grandparents at their house on Chemong Lake. Laura earned her HBSc from Trent University in 2013 and completed an honours thesis in a Fish Ecology lab. From there, Laura moved to Waterloo, ON and completed her MSc at Wilfrid Laurier University (WLU) working in a Physiology and Aquatic Toxicology lab. Laura's MSc research focused primarily on investigating metabolic scaling physiology of invasive sea lamprey (*Petromyzon marinus*) exposed to lampricides in the Great Lakes. Afterwards, Laura continued her research at WLU and began working on investigating how the chemistry of the gill microenvironment (pH and alkalinity) of rainbow trout (*Oncorhynchus mykiss*) and juvenile lake sturgeon (*Acipenser fulvescens*) influenced the speciation, uptake, clearance and toxicity of lampricides. When she wasn't in the lab, Laura was often volunteering with science education and communication programs and promoting aquatic research. Laura served on the Board of Directors for the International Association of Great Lakes Research (IAGLR) from 2017–2019, while also assisting with WLU's AquaSONG project, encouraging students to learn about freshwater ecosystems, field sampling and laboratory analysis. In the middle of her internship at NPAFC, Laura moved into the position of International Year of the Salmon (IYS) Coordinator, North Pacific Region. She is passionate about fisheries, the Great Lakes, freshwater and marine ecosystems and enjoys work related to environmental conservation and restoration.

Pacific salmon are an important cultural and economic resource around the Pacific Rim. In British Columbia (BC) they are a crucial economic resource both provincially and globally and are also relied upon by First Nation and coastal communities as a high priority food source. Economically, BC fisheries generate 1.0 billion CAD annually, from combined sources of aquaculture, wild stocks, commercial and recreational fisheries. Unfortunately, many vital wild salmon populations are currently at risk and average returns are dwindling. In particular, Fraser River coho (*Oncorhynchus kisutch*) and Okanagan Chinook (*O. tshawytscha*) salmon have been listed as threatened, while Cultus and Sakinaw sockeye salmon (*O. nerka*) are endangered (DFO 2016).

Many factors contribute to the declines in Pacific salmon including pollution, habitat destruction (e.g., barriers to spawning areas), over-fishing, over-harvesting, and climate change. These factors are all predicted to have negative impacts on BC fisheries. However, despite knowledge of those stressors, many questions about the responses of Pacific salmon to extreme climate variability remain unknown. As global temperatures continue to rise and unprecedented changes in the environment are observed, information regarding these questions is crucial. Many scientists throughout the North Pacific are working to find answers. The North Pacific Anadromous Fish Commission (NPAFC) is currently working on a multi-vessel high seas expedition plan in 2021 to investigate Pacific salmon distribution, migration, growth, and fitness under present oceanic conditions. This endeavor may help to elucidate responses to climate change of these vitally important fish and what this will mean for the individuals and communities that depend on them.

To predict how Pacific salmon and their prey will respond to climate change, an understanding of how climate change and ocean acidification affect seawater habitats is required. The ocean is a dynamic and complex environment, especially along the west coast of Canada. This region is sensitive to acidification because its pH is already relatively low (Haigh et al. 2015). Multiple seawater parameters are affected by changing ocean conditions including temperature, salinity, dissolved oxygen, primary production, pH, and alkalinity. Coastal regions are especially vulnerable, as they are subjected to the cumulative effects of freshwater and marine variations, urbanization, and waste disposals (Hare and Mantua 2000; Overland et al. 2006). Temperatures in the Strait of Georgia have been rising > 1°C per century, and the Fraser River has also been experiencing an increase in the number of days that temperatures exceed the limit for safe salmon migrations (> 18°C; Riche et al. 2014). It would be remiss not to briefly mention the North Pacific marine heatwave of 2014, colloquially termed 'The Blob,' where sea surface temperatures rose 3°C above normal levels (Bond et al. 2015). It is predicted that anomalies such as this will occur more frequently and generate even more extreme conditions—due to greenhouse gas emissions—as climate change progresses.

Increases in temperature affect the amount of oxygen than can be dissolved into sea water. The partial pressure of oxygen, commonly referred to as P_{O2} (mm hg), is an accurate way to determine oxygen levels in the water, not influenced by temperature or solubility. Oxygen diffuses more readily into cooler water than warm. Therefore, increasing ocean temperatures resulting from climate change can reduce the overall amount of oxygen available to aquatic organisms. Increases in ocean temperatures can also impact coastal and freshwater salmon habitats.

Decreases in oxygen saturation are positively correlated to higher salmonid embryo mortality rates (Malcolm et al. 2010). This is vital information concerning the development of salmonid embryos which subsequently affect the success of hatch rates and fry survival. Salmonid eggs are buried and incubated in redds for a period of 58 to 260 days (Sparks et al. 2019), with northern and southern salmon populations spawning at different times to optimize the conditions the eggs will be exposed to during the gestation period (Brannon 1987; Hodgson and Quinn 2002; Brannon et al. 2004). Additionally, an increase in temperature may shorten the development time of the salmonid embryos (Sparks et al. 2019) by increasing metabolic rates and activities to adapt to increasing temperatures, but this is not necessarily favourable. The shorter incubation time may lead to more synchronized spawning and decrease the portfolio effects of salmon—a diverse "portfolio" with variable spawn and hatch time increases resilience to climate change, similar to a diverse investment stock portfolio (Adelfio et al. 2019). Additionally, higher temperatures during incubation of pink salmon resulted in smaller fry and alevins compared to lower temperatures (Murray and Beacham 1985). However, temperature selection may also drive changes in developmental phenology. Warmer waters could result in a shift in spawning phenology so that the fry hatch when conditions are most favourable for their survival (Sparks et al. 2019). However, optimal temperature and oxygen conditions may not be the only factor involved in fry survival. Other factors that impact hatch rates and fry survival include pH, yolk-to-egg ratios, food availability, and predation.

Temperature is not the only variable that is being influenced by climate change. Since pre-industrial times, the concentration of atmospheric carbon dioxide (CO_2) has been increasing exponentially, driving ocean acidification. Carbon dioxide reached the highest recorded levels, approximately 400 ppm, after 800,000 years, in 2015 (Luthi et al. 2008; Dlugokencky and Tans 2015). These levels are predicted to reach over 900 ppm by 2100 (Meinshausen et al. 2011). A significant amount of this excess CO_2 has been absorbed by the ocean, which has thus far acted as a carbon sink and reduced further consequences of climate change from occurring. However, by removing CO_2 from the atmosphere, the partial pressure (P_{CO2}) of marine systems is increased. As a result, ocean pH decreases, driving ocean acidification and environmental degradation (Doney 2010).

It is essential to measure ocean pH to monitor the rate of ocean acidification as climate change progresses. However, the additional ions present in saltwater make measuring and reporting pH significantly more complex than in freshwater (Brewer 2013), and the chemistry of the ocean's carbon state must be considered when examining ocean acidification. The carbon state refers to the concentration of each chemical in the form of dissolved inorganic carbon (DIC). Atmospheric CO_2 (> 1%) dissolves into the ocean where it forms carbonic acid (H_2CO_3) in the presence of H_2O. H_2CO_3 will further dissociate into bicarbonate (HCO_3^-) and a proton (H^+), lowering the ocean pH and increasing the partial pressure of CO_2 (P_{CO2}). At the most acidic end, HCO_3^- forms carbonate ions (CO_3^{2-}) and H^+ (Figure 1). Quantifying the ocean's carbon state requires knowing temperature and salinity along with two of the following four variables: DIC, pH, total alkalinity, and P_{CO2}. Including phosphate and silicic acid concentrations would further improve the accuracy of this measurement (Dickson et al. 2007).

As pH decreases, marine organisms that use $CaCO_3$ to build and maintain carbonate structures (e.g., seashells) will be negatively impacted, as less is available to them (Haigh et al. 2015). Aragonite is a soluble form of $CaCO_3$, commonly used by marine calcifiers to build their shells or other structures. The effects that ocean acidification will have on their ability to build and maintain these structures is based on the aragonite saturation state (Ω).This can be calculated using the following equation:

$$\Omega = \frac{[Ca^{2+}][CO_3^{2-}]}{K_{sp}}$$

In this equation, $[Ca^{2+}]$ is the concentration of calcium in the water, multiplied by the concentration of carbonate $[CO_3^{2-}]$ and divided by the equilibrium constant, K_{sp}. When Ω decreases to 3 or below, shelled organisms become stressed. At levels of $\Omega < 1$, their shells will begin to dissolve (Figure 1). In the Bering Sea, aragonite undersaturation is expected to exceed historic variability by 2044, and by 2062 it will become chronic (Mathis et al. 2015 as cited by Crozier 2016).

Carbonate ion concentrations can be quantified, making it a useful measurement for tracking ocean acidification. The aragonite saturation state is closely linked to pH, decreasing as pH decreases. The impacts of ocean acidification are not only experienced by calcifying organisms. Though they possess no shells at risk of dissolving, with increasing ocean acidification, other marine organisms such as fish, will need to expend more energy to remove metabolic waste products such as CO_2. The removal of these waste products is partially dependent on diffusion and ambient P_{CO2} gradients (Hoffmann et al. 2013). Thus, with an increase in P_{CO2} in the water, the gradient will be decreased—and in severe cases—CO_2 may not readily diffuse across the gill into the ambient water as easily. As a result, acid-base regulation becomes a challenge and fishes may experience difficulties with cardiorespiratory control as well (Ishimatsu et al. 2008).

Freshwater systems are known to have larger pH variations than oceanic systems. Freshwater pH ranges from 6.5–9.0, whereas the typical pH range of marine environments is more strictly regulated, varying between 7.8–8.1. Ocean pH generally decreases as DIC and P_{CO2} increase with depth (Haigh et al. 2015), although the North West Pacific Ocean is known for its upwelling regions which contribute to increasing pH variability by transporting cooler, deep water to the ocean surface (Feely et al. 2010; Figure 2). There is also a seasonal variation in pH, as it is typically lower in the winter and higher in summer. In marine ecosystems, normal variation is expected, and water must not be outside of 0.2 pH units from its typical range (USEPA 1976). However, overall CO_3^{2-} has decreased by 16% and in open ocean surface waters by approximately 0.1 pH units (Orr et al. 2005). This trend is predicted to continue, with approximately 50% CO_3^{2-} and 0.3–0.4 pH unit decreases estimated to occur by the end of this century alone (Orr et al. 2005).

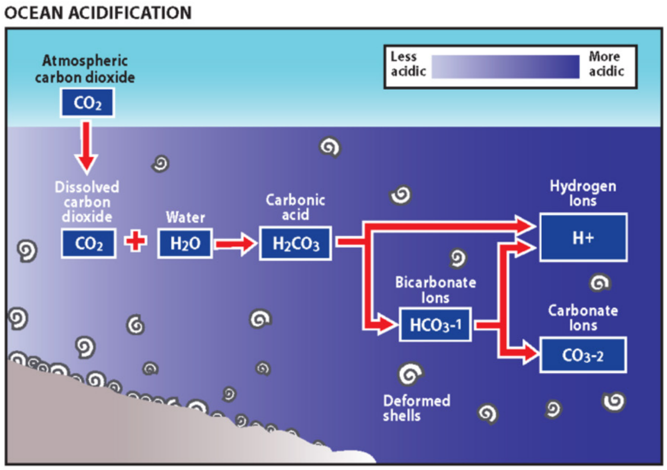

Figure 1. *Carbon state and the process of ocean acidification. Dissolved inorganic carbon (DIC) in the oceans is in the form of aqueous CO_2, carbonic acid (H_2CO_3), bicarbonate ions and carbonate ions. In the presence of H_2O, the carbonic acid dissociates into HCO_3^- and a proton (H^+). The bicarbonate further dissociates into carbonate ions and another proton. Increasing protons result in decreasing pH, and the ocean becomes more acidic. Figure from the Oregon Conservation Strategy (2016).*

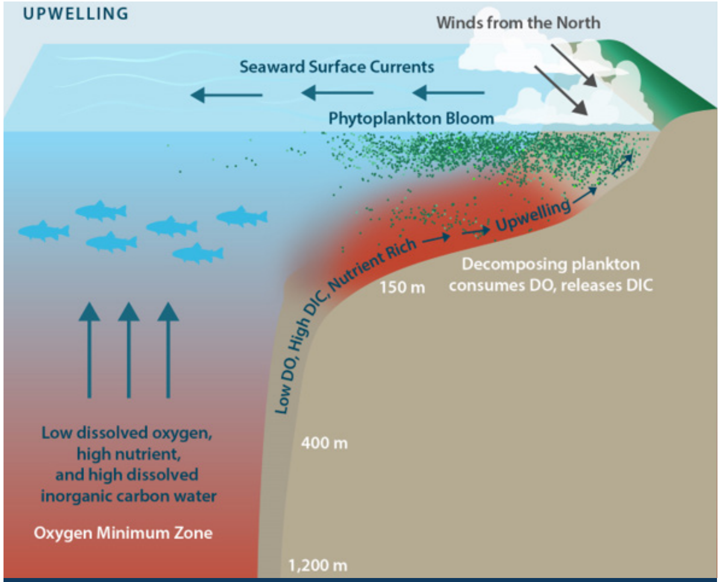

Figure 2. *Northern winds and seaward surface currents draw cooler water with low levels of dissolved oxygen, high nutrients and DIC moves up from the deep ocean towards the shelf. As the water approaches the shelf, plankton species further increase hypoxia as they consume the limited DO (dissolved oxygen) and release DIC (dissolved inorganic carbon), which can lead to toxic algae blooms depending on the circumstances. The dynamic upwelling systems, therefore, can contribute to ocean acidification and adds to the variability of ocean pH (Figure by Chan et al. 2019 where it was modified from Gewin (2011) by Moni Kovacs).*

Changes in freshwater pH systems may have important implications for salmon during their early life stages, as well as the success of their spawning periods, due to their complex life cycles. After hatching and developing as fry, the juvenile salmon must undergo smoltification to prepare for their next life stage in a marine ecosystem. Typically, the juveniles will begin their seaward migration and move back and forth as they acclimatize to increasing salinity until they reach the ocean. The effects of pH disruptions may become especially relevant during this sensitive life stage. These sublethal effects can include reduced growth, yolk-to-tissue conversion, and maximal O_2 uptake capacity (Ou et al. 2015). Additionally, increased exposure to CO_2 has been shown to reduce juvenile growth rates in Atlantic salmon (Fivelstad et al. 2015), although some models have alternatively predicted ocean acidification to have a neutral or positive effect for Pacific salmon in the high seas (Reum et al. 2015). However, those models fail to consider the physical responses of Pacific salmon when exposed to aquatic acidification.

Ocean acidification may have the capability to disrupt additional physiological processes beyond smoltification. The ion gradients that control cognitive signaling and behavior are extremely sensitive to water chemistry, and those neural membranes may become damaged when exposed to conditions outside of the normal range (Schild and Restrepo 1998; Tierney et al. 2010). The olfactory cues in salmonids are also sensitive to disruptions in pH, particularly when caused by increases in CO_2 (Williams et al. 2018). A previous study by Williams et al. (2018) determined that juvenile coho salmon exposed to elevated CO_2 experienced significantly disrupted neural pathways on a physiological level. This has potential implications for a salmon's ability to home to its natal stream for spawning following the oceanic developmental phase of the life cycle (Dittman and Quinn 1996; Gerlach et al. 2007). Adult salmon unable to locate their natal streams may "stray" to new territories. Wild fish that stray into hatchery territory will have their eggs and milt collected, which increases the genetic diversity of the hatchery-origin fish. However, straying of hatchery fish into wild populations increases the chances of them breeding with wild salmon and can lead to decreased genetic diversity and fitness of the next generation of wild fish. Additionally, damage to the olfactory bulb of juvenile coho salmon caused by excessive CO_2 exposure has been shown to decrease their ability to respond to alarm cues (Williams et al. 2018). The failure to elicit an avoidance response to an alarm cue may make juveniles more susceptible to predators as well as increasing challenges experienced in locating and capturing prey (Dixson et al. 2010; Cripps et al. 2011; Williams et al. 2018).

In addition to affecting a salmonid's ability to successfully capture prey, ocean acidification also threatens the survival of the prey species. For example, Pacific salmon typically feed on pteropods, whose swarming behavior allows salmon to feed on large clusters without having to exert much energy to find them (Armstrong et al. 2005, 2008). Ocean acidification decreases pteropod populations by limiting their ability to grow and maintain their shells. As P_{CO2} and temperatures increase, pteropods allocate more resources into a protective coating that prevents shells from being dissolved in waters that are undersaturated with aragonite (Byrne et al. 1984; Lischka and Riebesell 2012). Even so, reduced calcification under these conditions takes a toll on pteropod populations. In the Gulf of Alaska, there is a clear relationship between pteropod abundance and pink salmon survival (Doubleday and Hopcroft 2015). Therefore, under these conditions of heightened ocean acidification and decreased prey abundance, salmon must spend more time and energy foraging, which in turn reduces growth rates and ultimately survival.

Climate change may also increase competition for prey with other species, although more research is required to confirm the correlation between changes to inter-species and intra-species competition for Pacific salmon as a direct result of variables associated with changing ocean conditions. The previously described decrease in pteropod prey abundance due to ocean acidification will increase competition for all Pacific salmon that rely on them. Other organisms also compete with Pacific salmon for resources, although how climate change will influence their populations remains unclear. For example, during the International Year of the Salmon (IYS) winter 2019 Gulf of Alaska Expedition, a notable increase in northern sea nettles population (*Chrysaora melanaster*) was detected (Hunt et al. unpublished), likely originating from the Aleutian shelf. Their dry weight was approximately five times that of Pacific salmon, and since this sea nettle species are known to feed on zooplankton, they are likely a source of competition to Pacific salmon during the critical winter period for the salmon life cycle. How their responses to climate change may influence their competition for prey with Pacific salmon should be investigated, along with interactions between other species.

Invasive species are now common within aquatic communities and their introductions and survival in new ecosystems may be facilitated by the effects of climate change. In the Columbia Basin, invasive zooplankton have outcompeted native species in both reservoirs (Emerson et al. 2015) and the estuary (Bowen et al. 2015). The effects these invasive planktonic crustaceans have within the food web once they become established remain unclear. The invasive Asian copepod *Pseudodiaptomus forbesi* are now the dominant zooplankton during late summer in the Lower Columbia River (Adams et al. 2015). The invasive zooplankton are still prey for the Chinook salmon, but not the preferred prey (Adams et al. 2015) and may not have the same caloric content and benefits as the native zooplankton population. When preferred prey species are in decline, predatory fish may also switch to preying on smaller juvenile salmon (Willette et al. 2001). Additionally, in freshwater systems, increasing temperatures may also lead to increased predation on young salmon. The habitat range of predatory smallmouth bass is predicted to expand and overlap with that of Chinook juveniles with increasing aquatic temperature (Lawrence et al. 2015).

The ecosystem-based threats ocean acidification poses are amplified by those of economic importance. Shelled organisms are not only prey for salmon but are often harvested by humans for consumption as well. Thus, geoducks, oysters, and clams specifically, will negatively impact aquatic-based economies as their populations decline due to ocean acidification (Figure 3). Along with shelled organisms, salmon are contributors to the Canadian economy. Commercially and recreationally harvested wild salmon species include Chinook, coho, sockeye, pink and chum, but unfortunately more data is needed to understand the full extent of how ocean acidification will affect their populations (Figure 3). Concerning pink salmon, it is predicted that decreasing ocean pH will likely have a negative impact, due to its impacts on their pteropod prey.

Due to the economic and conservational consequences of ocean acidification, there are water quality guidelines to assist policy managers in making decisions to decrease the effects of ocean acidification. Unfortunately, air pollution is a major source of CO_2 emissions that are driving ocean acidification. This makes regulating water quality guidelines a challenge since it is air quality that must first be addressed. Air quality is impacted through a variety of anthropogenic activities, such as driving cars and burning fossil fuels. Regulations to control emissions must be enforced on a global scale in order to have the greatest impact on preventing further ocean acidification. In the meantime, there are federal laws in Canada and the United States, such as the Clean Air Act which regulate the sources of air pollution, along with the Clean Water Act which regulate water pollutants (Craig 2015). However, as previously noted, clean water and air are intricately linked and may influence each other.

Regulations tend to focus on guidelines for single parameters, forming guidelines based on individual standards. It is important to consider the cumulative effects of multiple stressors on organisms, as they may become more sensitive to changes in water quality parameters when more than one condition is outside of their typical range. While an organism may be more tolerant to changes in water quality separately (e.g., temperature stress), if this happens in occurrence with another stressor (e.g., pH), then the combined stress of temperature and pH may have a synergistic effect with a greater impact than predicted. The United States Environmental Protection Agency (USEPA) now recognizes pH as one of its water quality standards, along with a variety of other regulations such as specific contaminate levels. As one of its water quality standards, this means that there is an acceptable range that must be maintained, and this value is region-specific with seasonal variations. In marine

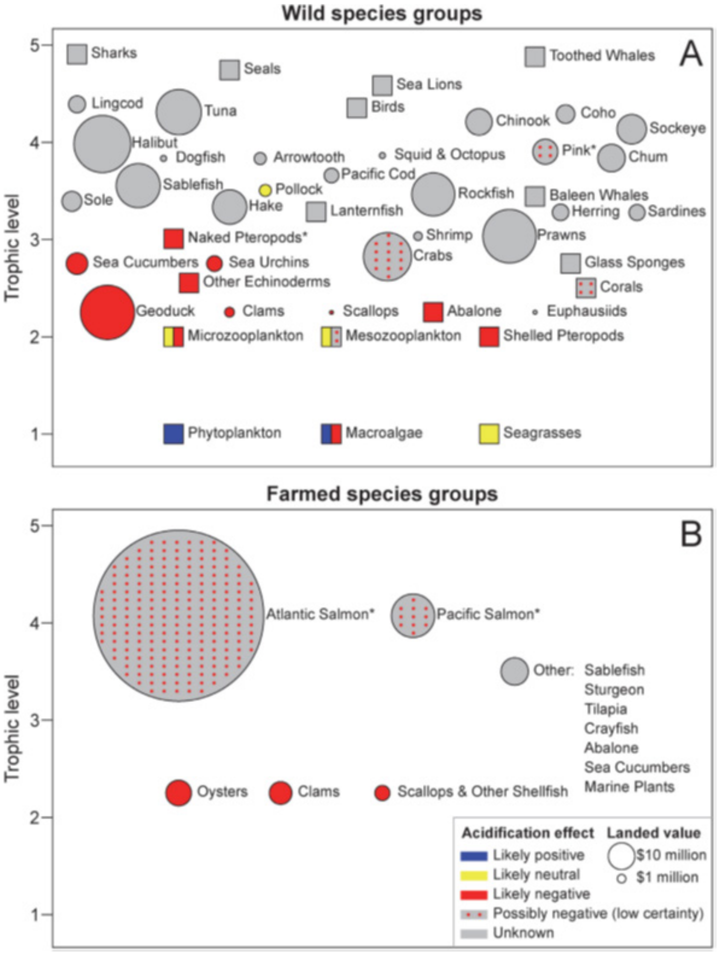

Figure 3. *The impacts of ocean acidification and estimated economic value for species that are harvested either (A) in the wild or (B) are a farmed species. The size of the circle represents the species value, while squares are species that may be impacted by ocean acidification but are not commercially harvested. The effects of ocean acidification are represented by solid colours, while uncertainty is shown by stippling. The asterisks (*) representants indirect effects on that species. Figure from Haigh et al. 2015, where the trophic level was adapted from Preikshot 2007 (Madrone Environmental Services, Duncan, BC), and landed value for economic estimated were based on data from BC Ministry of Agriculture (2012) and DFO (2013) for euphausiids. Refer to Haigh et al. (2015) for the R code that was used to generate this figure.*

ecosystems, normal variation is expected, but water must not vary more than 0.2 pH units from the typical range of 6.5–8.5 (USEPA 1976). Above or below this range can result in damage to the ecosystem, which could include bleaching corals, a variety of physiological impacts to fish and/or shelled organisms, or risks of toxic algal blooms.

Rapidly developing environmental changes, like ocean acidification and climate change, have the potential to negatively impact our oceans and underline the imperative need to increase our understanding of the implications they may have on Pacific salmon. The anadromous nature of these already threatened fish may make them more susceptible to climate change and the resulting lower ocean pH, since they rely on both freshwater and marine ecosystems to complete their life cycles (Crozier et al. 2008). Southern populations, such as the declining Puget Sound Chinook, are not doing well and many salmon are decreasing their ranges along the California Current System as they cannot survive the increased temperatures (Cheung et al. 2015). However, there are some positive salmon populations and production trends worth mentioning. Pacific salmon species in Northern regions are found to be increasing in areas that were previously unfavourable for them (Logerwell et al. 2015) and there may be phenological changes that would favour migration (Kovach et al. 2015; Sergeant et al. 2015; Stich et al. 2015; Crozier 2016) and spawn timing (Lyons et al. 2015) under these new conditions. Predicting how Pacific salmon will respond to their changing environment presents a formidable challenge, and thus it is imperative that we understand the mechanisms behind those responses to effectively make decisions for their conservation and sustainability.

References

Adams, J. B., S. M. Bollens, and J. G. Bishop. 2015. Predation on the Invasive Copepod, *Pseudodiaptomus forbesi*, and Native Zooplankton in the Lower Columbia River: An Experimental Approach to Quantify Differences in Prey-Specific Feeding Rates. PLoS One. 10(11).

Adelfio, L.S., S.M. Wondzell, N.J. Mantua, and G.H. Reeves. 2019. Warm winters reduce landscape-scale variability in the duration of egg incubation for coho salmon (*Oncorhynchus kisutch*) on the Copper River Delta, Alaska. Can. J. Fish. Aquat. Sci. 76(8): 1362–1375.

Armstrong, J.L., J.L. Boldt, A.D. Cross, J.H. Moss, N.D. Davis, K.W. Myers, R.V. Walker, D.A. Beauchamp, and L.J. Haldorson. 2005. Distribution, size and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon *Oncorhynchus gorbuscha*. Deep Sea Res. II. 52(1-2): 247–265.

Armstrong, J.L., K.W. Myers, D.A. Beauchamp, N.D. Davis, R.V. Walker, J.L. Boldt, J.J. Piccolo, L.J. Haldorson, and J.H. Moss. 2008. Interannual and spatial feeding patterns of hatchery and wild juvenile pink salmon in the Gulf of Alaska in years of high and low survival. Trans. Am. Fish. Soc. 137: 1299–1316.

Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. 42(9): 3414–3420.

Bowen, A., G. Rollwagen-Bollens, S. M. Bollens, and J. Zimmerman. 2015. Feeding of the invasive copepod *Pseudodiaptomus forbesi* on natural microplankton assemblages within the lower Columbia River. J. Plankton Res. 37(6): 1089–1094.

Brannon, E.L. 1987. Mechanisms stabilizing salmonid fry emergence timing. Can. Spec. Publ. Fish. Aquat. Sci. 96: 120–124.

Brannon, E.L., M.S. Powell, T.P. Quinn, and A. Talbot. 2004. Population structure of Columbia River basin Chinook salmon and steelhead trout. Rev. Fish Sci. 12: 99–232.

Brewer, P.G. 2013. A short history of ocean acidification science in the 20th century: a chemist's view. Biogeosciences. 10: 7411–7422.

Byrne, R.H., J.G. Acker, P.R. Betzer, R.A. Feely, M.H. Cates. 1984. Water column dissolution of aragonite in the Pacific Ocean. Nature. 312: 321–326.

Chan, F., J.A. Barth, K.J. Kroeker, J. Lubchenco, and B.A. Menge. 2019. The dynamics and impact of ocean acidification and hypoxia. Oceanography. 32(3): 62–71.

Cheung, W. W. L., R. D. Brodeur, T. A. Okey, and D. Pauly. 2015. Projecting future changes in distributions of pelagic fish species of Northeast Pacific shelf seas. Prog. Oceanogr. 130: 19–31.

Craig, R.K. 2015. Dealing with Ocean Acidification: The Problem with the Clean Water Act, and State and Regional Approaches. Wash. L. Rev. 1583: 387–466.

Cripps, I. L., P.L. Munday, and M.I. McCormick. 2011. Ocean acidification affects prey detection by a predatory reef fish. PLoS One. 6(7): e22736.

Crozier, L. 2016. Impacts of Climate Change on Salmon of the Pacific Northwest: a review of the scientific literature published in 2015. NOAA. 23 pp.

Crozier, L.G., A. Hendry, P.W. Lawson, T. Quinn, N. Mantua, J. Battin, R.G. Shaw, and R. Huey. 2008. Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. Evol. Appl. 1(2): 252–270.

Dickson, A.G., C.L. Sabine, and J.R. Christian (Editors). 2007. Determination of dissolved organic carbon and total dissolved nitrogen in sea water. In: Guide to best practices of ocean CO_2 measurements. PICES Special Publication 3, 191 pp.

Dittman, A., and T. Quinn. 1996. Homing in Pacific salmon: Mechanisms and ecological basis. J. Exp. Biol. 199(1): 83–91.

Dixson, D.L., P.L. Munday, and G.P. Jones. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. Ecol. Lett. 13(1): 68–75.

Dlugokencky, E., and P. Tans. 2015. Trends in atmospheric carbon dioxide. Natl. Ocean. Atmos. Adm. Earth Syst. Res. Lab. (Available at www.esrl.noaa.gov/gmd/ccgg/trends/)

Doney, S. C. 2010. The growing human footprint on coastal and open-ocean biogeochemistry. Science. 328: 1512–1516.

Doubleday, A.J., and R. R. Hopcroft. 2015. Interannual patterns during spring and late summer of larvaceans and pteropods in the coastal Gulf of Alaska, and their relationship to pink salmon survival. J. Plankton Res. 37(1): 134–150.

Emerson, J.E., S. M. Bollens, and T.D. Counihan. 2015. Seasonal dynamics of zooplankton in Columbia-Snake River reservoirs, with special emphasis on the invasive copepod *Pseudodiaptomus forbesi*. Aquat. Invasions. 10(1): 25–40.

Feely, R.A., S.R. Alin, J. Newton, C.L. Sabine, M. Warner, A. Devol, C. Krembs, and C. Maloy. 2010. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. Esturar. Coast. Shelf Sci. 88(4): 442–449.

Fivelstad, S., K. Kvamme, S. Handeland, M. Fivelstad, A. B. Olsen, and C. D. Hosfeld. 2015. Growth and physiological models for Atlantic salmon (*Salmo salar* L.) parr exposed to elevated carbon dioxide concentrations at high temperature. Aquaculture. 436: 90–94.

Fisheries and Oceans Canada (DFO). 2016. Species at Risk Act and Pacific salmon. (Available at http://www.pac.dfo-mpo.gc.ca/pacific-smon-pacifique/sara-lep-eng.html)

Gerlach, G., J. Atema, M.J. Kingsford, K.P. Black, and V. Miller-Sims. 2007. Smelling home can prevent dispersal of reef fish larvae. Proc. Natl. Acad. Sci. 104(3): 858–863.

Haigh, R., D. Ianson, C.A. Holt, H.E. Neate, and A.M. Edwards. 2015. Effects of Ocean Acidification on Temperate Coastal Marine Ecosystems and Fisheries in the North Pacific. PLoS One. 10(2): e0117533.

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47: 103–145.

Hodgson, S., and T.P. Quinn. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Can. J. Zool. 80(3): 542–555.

Hofmann, A.F., E.T. Peltzer, and P.G. Brewer. 2013. Kinetic bottlenecks to chemical exchange rates for deepsea animals—Part 2: Carbon dioxide. Biogeosciences. 10: 2409–2425.

Hunt, B., A. Somov, A. Kanzeparova, E.A. Pakhomov, and V. Radchenko. 2019. Mega-swarm of northern sea nettles (*Chrysaora melanaster*) in the Gulf of Alaska in the winter of 2019. PICES Annual Meeting, Victoria BC. (Available at https://meetings.pices.int/publications/book-of-abstracts)

Ishimatsu, A., M. Hayashi, and T. Kikkawa. 2008. Fishes in high-CO_2, acidified oceans. Mar. Ecol. Prog. Ser. 373: 295–302.

Kovach, R. P., S. C. Ellison, S. Pyare, and D. A. Tallmon. 2015. Temporal patterns in adult salmon migration timing across southeast Alaska. Global Change Biol. 21(5): 1821–1833.

Lawrence, D.J., D.A. Beauchamp, and J.D. Olden. 2015. Life-stage-specific physiology defines invasion extent of a riverine fish. J. Anim. Ecol. 84(3): 879–888.

Lischka, S., and U. Riebesell. 2012. Synergistic effects of ocean acidification and warming on overwintering pteropods in the Arctic. Glob. Change Biol. 18: 3517–3528.

Logerwell, E., M. Busby, C. Carothers, S. Cotton, J. Duffy-Anderson, E. Farley, P. Goddard, R. Heintz, B. Holladay, J. Hornead, S. Johnsonc, B. Lautha, L. Moultone, D. Neff, B. Norcross, S. Parker-Stetterd, J. Seigleg, and T. Sformoh. 2015. Fish communities across a spectrum of habitats in the western Beaufort Sea and Chukchi Sea. Progr. Oceanogr. 136: 115–132.

Luthi, D., M. Le Floch, B. Bereiter, T. Blunier, J-M. Barnola, U. Siegenthaler, D. Raynaud, J. Jouzel, H. Fischer, K. Kawamura, and T.F. Stocker. 2008. High-resolution carbon dioxide concentration record 650,000–800,000 years before present. Nature. 453: 379–382.

Lyons, J., A.L. Rypel, P.W. Rasmussen, T.E. Burzynski, B.T. Eggold, J.T. Myers, T.J. Paoli, and P.B. McIntyre. 2015. Trends in the Reproductive Phenology of two Great Lakes Fishes. Trans. Am. Fish. Soc. 144(6): 1263–1274.

Malcolm, I.A., C.A. Middlemas, C. Soulsby, S.J. Middlemas, and A.F. Youngson. 2010. Hyporheic zone processes in a canalised agricultural stream: implications for salmonid embryo survival. Fund. Appl. Limnol., Arch. Hydrobio. 176(4): 319–336.

Meinshausen, M., S.J. Smith, K. Calvin, J.S. Daniel, M.L.T. Kainuma, J. Lamarque, K. Matsumoto, S.A. Montzka, S.C.B. Raper, K. Riahi, A. Thomson, G.J.M. Velders, and D.P.P van Vuuren. 2011. The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. Clim. Change. 109: 213–241.

Murray, C.B., and T.D. Beacham. 1985. Effect of varying temperature regimes on the development of pink salmon (*Oncorhynchus gorbuscha*) eggs and alevins. Can. J. Zool. 64: 670–676.

Oregon Conservation Strategy. 2016. Factors Affecting Nearshore Strategy Species and Habitats. (Available at https://www.oregonconservationstrategy.org/oregon-nearshore-strategy/factors-stressors-affecting-species-and-habitat/)

Orr, C.J., V.J. Fabry, O. Aumont, L. Bopp, S.C. Doney, R.A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, R.M. Key, K. Lindsay, E. Maier-Reimer, R. Matear, P. Monfray, A. Mouchet, R.G. Najjar, G.K. Plattner, K.B. Rodgers, C.L. Sabine, J.L. Sarmiento, R. Schlitzer, R.D. Slater, I.J. Totterdell, M.F. Weirig, Y. Yamanaka, A. Yool. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature. 437: 681–686.

Ou, M., T.J. Hamilton, J. Eom, E.M. Lyall, J. Gallup, A. Jiang, J. Lee, D.A. Close, S-S. Yun and C.J. Brauner. 2015. Responses of pink salmon to CO_2-induced aquatic acidification. Nat. Clim. Change. 5: 950–955.

Overland, J.E., D.B. Percival, and H.O. Mofjeld. 2006. Regime shifts and red noise in the North Pacific. Deep-Sea Res. I 53: 582–588.

Reum, J.C.P., B.E. Ferriss, P.S. McDonald, D.M. Farrell, C.J. Harvey, T. Klinger, and P.S. Levin. 2015. Evaluating community impacts of ocean acidification using qualitative network models. Mar. Ecol. Prog. Ser. 536: 11–24.

Riche, O., S.C. Johannessen, and R.W. Macdonald. 2014. Why timing matters in a coastal sea: Trends, variability and tipping points in the Strait of Georgia, Canada. J. of Marine Systems. 131: 36–53.

Schild, D., and D. Restrepo. 1998. Transduction mechanisms in vertebrate olfactory receptor cells. Physiol. Rev. 78(2): 429–466.

Sergeant, C.J., J.B. Armstrong, and E.J. Ward. 2015. Predator-prey migration phenologies remain synchronised in a warming catchment. Freshwater. Biol. 60(4): 724–732.

Sparks, M.M., J.A. Falke, T.P. Quinn, M.D. Adkison, D.E. Schindler, K. Bartz, D. Young, and P.A.H. Westley. 2019. Influences of spawning timing, water temperature, and climatic warming on early life history phenology in western Alaska sockeye salmon. Can. J. Aquat. Sci. 76: 123–135.

Stich, D.S., M.T. Kinnison, J.F. Kocik, and J.D. Zydlewski. 2015. Initiation of migration and movement rates of Atlantic salmon smolts in fresh water. Can. J. Fish. Aquat. Sci. 72(9): 1339–1351.

Tierney, K.B., D.H. Baldwin, T.J. Hara, P.S. Ross, N.L. Scholz, C.J. Kennedy. 2010. Olfactory toxicity in fishes. Aquat. Toxicol. 96(1): 2–26.

US Environmental Protection Agency (USEPA). 1976. Quality Criteria for Water (Redbook). Washington, DC. 20460 pp.

Willette, T.M., R.T. Cooney, V. Patrick, D.M. Mason, G.L. Thomas, and T.D. Scheel. 2001. Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. Fish Oceanogr. 10: 14–41.

Williams, C.W., A.H. Dittman, P. McElhany, D.S. Busch, M.T. Maher, T.K. Bammler, J.W. MacDonald, and E.P. Gallagher. 2018. Elevated CO_2 impairs olfactory-mediated neural and behavioral responses and gene expression in ocean-phase coho salmon (*Oncorhynchus kisutch*). Glob. Change Biol. 25: 963–977.