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Review of 2011-2015 NPAFC Science Plan: Forecast of Pacific Salmon Production in the Ocean Ecosystems Under Changing Climate

by

The Science Sub-Committee (SSC) and Review Panels
The Committee on Scientific Research and Statistics (CSRS)

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Review of 2011-2015 NPAFC Science Plan: Forecast of Pacific Salmon Production in the Ocean Ecosystems under Changing Climate

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Introduction

Over the past several decades, there have been significant variations in the marine production of Asian and North American anadromous populations that are linked to climate change. There is a strong need for new international cooperative research that provides better scientific information on: (1) the ecological mechanisms regulating production of anadromous populations; (2) climate impacts on salmon populations in North Pacific marine ecosystems; and (3) the utility of using salmon populations as indicators of conditions in North Pacific marine ecosystems.

Accurate forecast of returning salmon abundances is of great importance for stock managements in all member countries. Precise monitoring of abundance and biomass in the ocean may be the most reliable method for predicting changes in production of anadromous populations. Accurate stock identification methods such as genetic and otolith mark analyses are necessary to monitor stock-specific ocean distributions and abundance. Cooperative research that improves understanding of common mechanisms that regulate Pacific salmon production will increase the accuracy of short-term and long-term forecasting.

The NPAFC Science Plan is a long-term comprehensive guideline for cooperative research. The plan has been revised every 5 or 8 years (1993-2000, 2001-2005, and 2006-2010) after reviews of research progress. In 2010, the Science Sub-Committee (SSC) developed a five-year (2011-2015) Science Plan (Anonymous 2010). The goal is to be able to explain and forecast the annual variation in Pacific salmon production. To provide necessary focus to cooperative research under the 2011-2015 Science Plan, the SSC identified an overarching research theme “Forecast of Pacific Salmon Production in the Ocean Ecosystems under Changing Climate” and the following five research topics:

1) Migration and Survival Mechanisms of Juvenile Salmon in the Ocean Ecosystems;
2) Climate Impacts on Pacific Salmon Production in the Bering Sea (BASIS) and Adjacent Waters;
3) Winter Survival of Pacific Salmon in the North Pacific Ocean Ecosystems;
4) Biological Monitoring of Key Salmon Populations; and
5) Development and Applications of Stock Identification Methods and Models for Management of Pacific Salmon.

To assess the progress of cooperative research under the current 2011-2015 Science Plan, an international symposium “Pacific Salmon and Steelhead Production in a Changing Climate: Past, Present, and Future” was held in Kobe, Japan on May 17-19, 2015 (Urawa 2015a, 2016). In addition, panel members were identified for the review of the five research components (Appendix 1). This document provides an overall review of 2011-2015 Science Plan, including recommendations for developing the new Science Plan.

Research Component 1: Migration and Survival Mechanisms of Juvenile Salmon in the Ocean Ecosystems

Panel Members: M. Trudel*, A. Tompkins (Canada), T. Saito (Japan), J.K. Kim*, D.H. Lee (Korea), O. Temnykh, M. Koval (Russia), and D. Oxman (USA) (*panel leaders)

Background and Aim

A common hypothesis is that the initial period of after migration to sea is the most critical phase with respect to ocean survival of anadromous populations. Recent cooperative and national research on juvenile salmon suggests considerable inter-annual variation in abundance, growth, and survival rates of juvenile salmon in the ocean. These variations may be related to climate-induced changes in habitat environments that operate at regional and local scales. These processes are monitored annually in marine survey areas along the coasts of Asia and North America. A better understanding of these processes is needed for conservation and management of anadromous populations.

Cooperative research focused on the following issues:

1) Seasonal distribution and migration route/timing of juvenile salmon
2) Hydrological characteristics, primary production, and prey resources in the habitats
3) Trophic linkages, growth rates and predation rates of juvenile salmon
4) Ecological interactions between species, and between populations
5) Survival rate and survival mechanism of juvenile salmon
6) Population size and carrying capacity of juvenile salmon

Research Review

There has been an explosion of research on the early marine life of Pacific salmon during the last 5 years throughout their native range (Radchenko et al. 2013; Trudel and Hertz 2013; Hertz and Trudel 2014, 2015). This research has benefited from long-term monitoring and integrated epipelagic programs that are now approaching the twenty year milestone in some regions, and dating as far back as the early 1980s in Russia, as well as from short-term small-scale nearshore sampling activities. Although not all this research has been published by members of the CSRS, there is a large body of literature that need to be considered to understand the progress that has been achieved in this field, and to avoid duplication of effort.

1) Seasonal distribution and migration route/timing of juvenile salmon

The first step that is required to understand the interactions between Pacific salmon and marine ecosystems is to determine when salmon smolts enter the ocean, where they migrate to and how long they reside in different regions of the ocean. Research indicates that the downstream migration timing of salmon smolts is affected by river conditions such as temperature, water level, and discharge rate, as well as by the size of the river basin, with downstream migration occurring over a longer period of time in large river systems (Volubuez and Marchenko 2011; Kaev et al. 2012; Kolpakov et al. 2012; Kasugai et al. 2013). Sea-entry timing of salmon smolts has also been linked to body size, life-history, migration distance in freshwater (Weitkamp et al. 2012, 2015), and release date (Kasugai et al. 2013). Climatic effects on the timing of smolt migration are also apparent from long-term data set, with a shift toward earlier migration associated with increasing stream temperatures (Kovach et al. 2013). Further understanding of the factors affecting the downstream migration of salmon smolts will require an increase in the number of systems that are monitored to encompass the diversity of conditions experienced by salmon smolts (Radchenko et al. 2013).

In the marine environment, considerable effort has been allocated to investigate stock-specific migration routes of juvenile salmon using catch data (Koval and Kolomeistev 2011), otolith marking (Kasugai et al. 2011, 2016; Chistyakova and Bugaev 2013; Chistyakova et al. 2013; Saito et al. 2013; Sasaki et al. 2013), coded-wire tags (Fisher et al. 2014; Tucker et al. 2015a), acoustic tags (Moore et al. 2012; Brosnan et al. 2014), and genetic stock identification methods (Tucker et al. 2012a, b; Sato et al. 2013; Shpigalskaya et al. 2013; Beacham et al. 2014a). Overall, migration behavior of juvenile salmon has been shown to vary among species, stocks, and life-histories (Tucker et al. 2011, 2012a, b; Beacham et al. 2014a; Fisher et al. 2014; Teel et al. 2015). Migration routes may also be genetically programmed (Sharma and Quinn 2012; Tucker et al. 2012a, b; Burke et al. 2013a, b), but the distribution of juvenile salmon along their migration trajectory may be affected by multiple cues (Burke et al. 2014) such as size (Hasegawa et al. 2013; Saito et al. 2013; Beacham et al. 2014b; Freshwater et al. in press), temperature (Kasugai et al. 2011; Urawa 2015b), currents (Burke et al. 2013a), phytoplankton biomass (Bi et al. 2008; Peterson et al. 2010), and magnetic currents (Putman et al. 2014). Furthermore, migration behaviour of hatchery and wild fish appear to be different at small scales during the early marine life (Moore et al. 2012), but similar over larger scales (Tucker et al. 2011). The distribution and inshore-offshore movements of juvenile salmon may also be linked to food availability, zooplankton community succession, and the geomorphology of juvenile salmon habitat (Frenkel et al. 2013; Koval and Morozova 2013; Morozova 2013). Clearly, significant progress has been achieved to better understand the migration of juvenile salmon.

2) Hydrological characteristics, primary production, and prey resources in the habitats

Our understanding of the dynamics of zooplankton communities through the far-eastern seas and adjacent waters has been greatly enhanced by the creation of the TINRO-Center zooplankton database. Data analyses revealed that important juvenile salmon prey items such as euphausiids, amphipods, pteropods, and appendicularians, are generally higher in the western North Pacific Ocean compared to the eastern North Pacific Ocean and exhibited different trends between basins (Shuntov and Temnykh 2011a). Zooplankton biomass appeared to have varied inversely between the Bering Sea and Sea of Okhotsk (Shuntov and Temnykh 2011a). Changes in zooplankton community composition and abundance have been linked to changes in climate and ocean conditions, with larger species dominating in cooler years, and smaller species dominating in warmer years (Shuntov and Temnykh 2011a; Volkov et al. 2012a, b, c). The diet of juvenile salmon is also reflected by the variability in zooplankton communities. For instance, *Themisto libellula* dominated the diet of juvenile salmon and other nekton species following their demographic explosion in the western and eastern part of the Bering Sea (Volkov et al. 2012a, c; Volkov 2013; Pinchuk et al. 2013).

In the California Current System, changes in wind directions and intensity have been linked to salmon survival through their effects on upwelling, nutrient availability, phytoplankton and zooplankton production (Wells et al. 2012) and on zooplankton community composition and quality (Kiester et al. 2011; Bi et al. 2011; Peterson et al. 2014). In addition to winds, the hydrology of marine ecosystems may be affected by winter precipitations and air temperature through their effects on freshwater flow. This may in turn affect the availability of nutrients for primary productivity and the timing of prey productivity, and ultimately salmon survival (Borstad et al. 2011; Thomson et al. 2012; McKinnell et al. 2014). Lastly, in long fjords, tidal mixing may affect the stability of the water column, primary and secondary productivity, resulting in poor feeding and growth conditions for juvenile salmon (McKinnell et al. 2014; Ferris et al. 2014).

3) Trophic linkages, growth rates and predation rates of juvenile salmon

Bioenergetics models have been particularly useful for understanding the processes affecting juvenile salmon growth. In particular, they showed that prey quality and quantity may be more important for juvenile salmon growth and survival than temperature, and that the effect of temperature on growth is likely indirect and mediated by changes in prey quality and quantity (Trudel et al. 2002; Beauchamp 2009; Farley and Trudel 2009; Moss et al. 2009; but see Daly and Brodeur 2015). As stomach contents are expected to integrate the variability in prey availability and preferences, diet may also be a key indicator for salmon growth and survival in the marine environment (Armstrong et al. 2008; Kline et al. 2008; Kline 2010; Daly et al. 2013). Recent studies show that juvenile salmon diet is highly variable in space and time (Kim et al. 2013), and that diet variability is linked to prey availability (Volkov et al. 2012a, c; Volkov 2013), the abundance of juvenile salmon (Jenkins et al. 2013; Zavolokin 2013), and changes in ocean conditions and climate (Brodeur et al. 2007; Sweeting and Beamish 2009; Sturdevant et al. 2012a; Daly et al. 2013). In particular, although pink, chum, and sockeye salmon are generally considered planktivorous species, fish may contribute significantly to their diet in the Bering Sea during warm years (Andrews et al. 2009; Farley and Moss 2009; Farley and Trudel 2009). Further research is needed though to understand how changes in diet affect the survival of salmon.

Despite their usefulness, the validity of bioenergetics model for Pacific salmon has been questioned (Trudel et al. 2004, 2005). In particular, model parameters have frequently been borrowed from both closely and distantly-related species, potentially introducing significant biases in model predictions (Trudel et al. 2004, 2005). Furthermore, these models have generally been derived for juvenile salmon rearing in freshwater, and may not reflect the bioenergetics of salmon in sea-water, especially after undergoing physiological changes associated with smoltification. Recent effort has been devoted to derive species-specific bioenergetics parameters in juvenile Chinook salmon (Perry et al. 2015; Plumb and Moffitt 2015). This research has shown that the optimal temperature for growth was much higher than previously thought. It is important, however, to note that these parameters were also derived in freshwater. Consequently, further effort is needed to parameterize these models for juvenile salmon in the marine environment.

4) Ecological interactions between species, and between populations

Juvenile salmon may interact with other salmon species or populations through competition or predation (Hasegawa et al. 2014). Competition is expected to be more intense among species that share similar prey such as juvenile pink, chum, and sockeye salmon, and may be modulated by the presence of parasites (Godwin et al. 2015). Competition between wild and hatchery fish may be asymmetrical (Beamish et al. 2008, 2010) and is likely more intense in offshore waters as recent studies also indicate that hatchery and wild salmon often feed on different prey in the nearshore environment but on similar prey offshore (Sweeting and Beamish 2009; Daly et al. 2012; Sturdevant et al. 2012b). Stable isotope analyses have recently shown that the diet overlap between juvenile pink and chum salmon increased as their abundance increased, suggesting that competitive interactions were stronger at higher densities (Jenkins et al. 2013). In contrast, although an increase in the biomass of juvenile salmon was accompanied by changes in their feeding habits and reduced feeding rates in the Okhotsk Sea and Bering Sea, juvenile salmon growth was not negatively affected by biomass. Instead, size and growth of juvenile salmon in these waters were generally higher in years of high salmon biomass and synchronized between species (Shuntov and Temnych 2011a; Zavolokin 2013). Hence, the impact competitive interactions for juvenile salmon growth may vary among ocean basins, depending on prey availability.

Predation of Pacific salmon on other salmon species has rarely been documented, but it occasionally occur both in juvenile (Hargreaves and Lebrasseur 1985) and adult salmon (Sturdevant et al. 2012a, 2013). Cannibalism by returning adult salmon has been hypothesized to affect the cyclic dominance of salmon population (Krkošek et al. 2011a). This hypothesis, however, is not supported by empirical data (Sturdevant et al. 2013). Predation on juvenile pink and chum salmon by juvenile coho salmon may also affect the dynamic of sea lice (*Lepeophtheirus salmonis*) population, and the asymmetry of sex ratio in sea lice of their host (Connors et al. 2008, 2010). Simulation models also suggest that the differential impacts of sea lice infection on juvenile pink and chum salmon may be mediated by the preference of juvenile coho salmon for juvenile pink salmon (Peacock et al. 2014). This hypothesis has not yet been tested in the field.

5) Survival rate and survival mechanism of juvenile salmon

Estimating mortality rates of juvenile salmon in the marine environment and determining the relative importance of the factors that contribute to this mortality remains a major challenge. The miniaturization of acoustic tags now makes it possible to estimate mortality rates of juvenile salmon in a cost effective way along their migration corridor, provided 1) that the fish are sufficiently large to carry the burden of these tags without affecting their behavior, 2) that the migration corridor is relatively narrow. However, most applications to date have been performed on the largest smolts of a cohort, which may not be representative of the population (Freshwater et al, in press). In addition, there is a growing concern that marine mammals may be hearing and cuing on acoustic tags (Bowles et al. 2010; Cunningham et al. 2014; Stansbury et al. 2014), suggesting that mortality rates estimated with acoustic tags could be biased.

Wild juvenile salmon tend to have higher survival rates than their hatchery counterparts (Melnychuk et al. 2014; Goetz et al. 2015; Zimmerman et al. 2015). The specific mechanism explaining the lower survival of hatchery salmon is unknown, but may be related to physiological preparedness to sea water or to differences in foraging behaviour. In particular, hatchery fish may be more surface-oriented during their early marine life, and thus, vulnerable to both avian and fish predators.

Predation is thought to be a main source of mortality for juvenile salmon. Fish predators have been documented on either side of the North Pacific Ocean (Nagasawa 1998; Emmett and Krutzikowsky 2008; Duffy and Beauchamp 2008; Sturdevant et al. 2009, 2012a,b; Miyakoshi et al. 2013). Bird predation (Nagasawa 1998; Osterback et al. 2014; Hostetter et al. 2015; Tucker et al. 2016) and marine mammal predation on juvenile salmon (Thomas et al, in review) have also been documented. Evidence is mounting that predation on juvenile salmon is not only size-selective (Duffy and Beauchamp 2008; Tucker et al. 2016) but also condition dependent (Tucker et al. 2016). Although the impact of these predators on the survival rates of juvenile salmon remains elusive, it might be assessed through the application of ecosystem models (Ruzicka et al. 2011; Preikshot et al. 2013).

Parasites and microbes have also been hypothesized to play a role on the dynamics of juvenile salmon (Krkošek et al. 2006, 2007, 2011b). Field studies suggest that juvenile growth maybe be affected by microbes (Sandell et al. 2015), and that predators may preferentially select juvenile salmon infected with freshwater parasites (Miller et al. 2014a). The impact of sea lice (*Lepeophtheirus salmonis*) from farm salmon on the dynamics of wild salmon populations is highly debated (Brooks and Jones 2008; Krkošek et al. 2008a,b, 2011b; Riddell et al. 2008; Marty et al. 2010; Jones and Beamish 2011; Krkošek and Hilborn 2011). On the other hand, infection experiments and field observations indicated that the ectoparasitic flagellate *Ichthyobodo salmonis* causes high mortality of juvenile chum salmon when they migrate into the coastal ocean, since the heavy parasite infection disturbs the osmoregulation of juveniles (Urawa 1993, 1996, 2013).

It is generally believed that large and fast growing fish have higher survival, either because large fish are less vulnerable to gape-limited predators or can sustain starvation (i.e. winter) for longer periods of time (Beamish and Mahnken 2001). It should be noted, however, that while larger and fast growing salmon have frequently been found to have a survival advantage over small and slow-growing juvenile salmon (Duffy and Beauchamp 2011; Farley et al. 2011; Tomaro et al. 2012; Irvine et al. 2013; Zavalokin and Strezhneva 2013; Woodson et al. 2013; Miller et al. 2014b), size-selective mortality has not always been apparent during summer or winter in juvenile salmon (Welch et al. 2011; Trudel et al. 2012). Furthermore, a negative relationship between adult return and juvenile salmon growth has also been observed (Miller et al. 2013), indicating that other factors may override the effects of size and growth on the marine survival of juvenile salmon.

Survival mechanisms have also been inferred indirectly through correlational studies of smolt survival with climatic and oceanographic conditions. These analyses have been performed using simple tools such as linear regression models (Tanasichuk and Routledge 2011; Tucker et al. 2015b) as well as more sophisticated approaches such as the maximum covariance analysis (Burke et al. 2013b), Bayesian Beliefs Network (Araujo et al. 2013; Malick et al. 2015a; Hertz et al., in press), and state-space models (Ye et al. 2015). It should be remembered though, that no matter how sophisticated the analysis is, correlation should not be equated to causation (Peters 1991), and correlations often break over time (Skud 1983; Walters and Collie 1988). Nevertheless, they have helped to generate and test a number of hypotheses relating salmon survival to ocean conditions, including changes in prey availability (Tanasichuk and Routledge 2011; Wells et al. 2012; Doubleday and Hopcroft 2015; but see Shuntov and Temnyck 2011a, b; Radchenko et al. 2013), the timing of prey availability (Satterthwaite et al. 2015; Malick et al. 2015b), prey quality (Peterson et al. 2014; Tucker et al. 2015b), climate (Killduff et al. 2015; Hertz et al., in press). The fact that these correlations break over time may simply indicate that other factors that were not initially considered may contribute to the dynamics of salmon populations, and thereby contribute to the generation of new hypotheses and theories of salmon production. A more holistic approach that simultaneously accounts for the interactions of multiple factors may be necessary to understand the complex interactions between climate, marine ecosystems, and salmon.

6) Population size and carrying capacity of juvenile salmon

How many salmon can be sustained in the North Pacific Ocean is a long lasting question that has been part of the core research performed by NPAFC. This requires an estimation of not only the abundance of juvenile salmon in the marine environment, their feeding rates, the availability and production of their prey, but also the abundance and feeding rates of other species that may be eating the same prey. Research conducted by Russian scientists suggest that the size of juvenile salmon is high when their abundance is high, and small when their abundance is low, which is contrary to what is expected to occur due to density-dependent interactions when food is limiting (Shuntov and Temnykh 2011a; Zavolokin 2013). In addition, bioenergetics model calculations indicate that juvenile salmon consume only a small proportion of the zooplankton biomass, suggesting that their abundance and size may not be limited by competition (Orsi et al. 2004). In contrast to these findings, the size of juvenile pink and chum salmon was inversely related to their abundance on the west coast of North America (Jenkins et al. 2013). Hence, the intensity of competitive interactions may vary among regions of the North Pacific Ocean. Notably, the Western North Pacific Ocean is thought to be more productive than the Eastern North Pacific Ocean (Saito et al. 2011) and may therefore support higher fish biomass (PICES 2005).

Summary

Our understanding of the early marine migration and survival has increased tremendously throughout their native range during the last five years, in large part due to the application of genetic stock identification methods and to the miniaturization of acoustic tags. Linkages between ocean physics (i.e. currents), lower trophic levels, salmon diet and growth, and ultimately survival have been examined. This research, however, has been primarily based on correlation analyses using univariate and multivariate statistics. Much remains to be done to understand the actual causes of mortality for juvenile salmon and their relative importance for driving recruitment variability.

Recommendations for the new Science Plan

In recent years, there has been an increase in the abundance of salmon in northern regions, but a decrease at the southern edge of the Asian and North American continents. It may be related to climate-induced changes in habitat environments that operate at regional and local scales. The main objectives of future studies should be focused on the following areas:

- The linkage between marine survival of salmon, and changes in climate and in the ocean such as primary production, and prey resources in the habitats
- The effect of natural environmental variability on stock-specific distribution and abundance of salmon
- Predicting the potential impacts of global climate change on marine salmon habitats
- Understanding the causes of mortality in salmon during their marine life

Research Component 2: Climate Impacts on Pacific Salmon Production in the Bering Sea (BASIS) and Adjacent Waters

Panel Members: M. Trudel (Canada), S. Sato, T. Azumaya (Japan), O. Temnykh*, A. Zavolokin (Russia), and E. Farley*(USA) (*panel leaders)

Background and Aim

Climate change, and its impact on salmon carrying capacity in the Bering Sea was discussed at the BASIS Symposium held in November 2008. A current overarching hypothesis suggests that climate change will alter the current geographic distributions and behaviors of humans, marine mammals, seabirds, and fish by restructuring their habitats within the Bering Sea ecosystem (NPRB 2007). Oral presentations at the symposium highlighted evidence that increased levels of atmospheric carbon dioxide are linked to warming air and sea temperatures, reduced sea ice extent during winter, and melting of the polar cap in the Arctic region (Bond et al. 2008). However, the effect of climate change on the Bering Sea ecosystem is still debatable, with studies indicating no direct effect on the ecosystem (Shuntov and Temnykh 2009) to studies that indicate the possibility of reduced ecosystem productivity with increasing sea surface temperatures (Coyle et al. 2008, 2011).

The goal of BASIS phase II is to understand how climate change will affect productivity of Bering Sea salmon and ecologically related species. Key scientific questions are:

- How will climate change affect anadromous populations, ecologically related species, and the Bering Sea ecosystems?
- What are the key climatic and oceanographic factors affecting long-term changes in Bering Sea food production and salmon growth rates?
- How will climate change impact the available salmon habitat in the Bering Sea?
- How will climate change affect Pacific salmon carrying capacity within the Being Sea?

Cooperative research centered on the following critical issues:

1) Monitor and evaluate climate-oceanographic and biological factors related to foraging conditions, distribution, abundance and production of salmon and ecologically related species.
2) Determine and understand the role of salmon in nektonic communities and their association to Bering Sea ecosystem status.
3) Understand influence of climate-oceanographic conditions upon structure, status, population structure, migration, biological parameters and production processes of Pacific salmon populations.
4) Understand foraging dynamics, food competition and its influence on growth and survival of salmon.
5) Understand the processes that affect salmon production.
6) Study the linkage between marine survival of salmon, and climate and ocean changes.
7) Predict the potential impacts of global climate change on marine salmon habitats.

Research Review

1) Climate-oceanographic and biological factors related to foraging conditions, distribution, abundance and production of salmon and ecologically related species

Sea ice consistently covers the northern Bering Sea each year (Stabeno et al. 2012a), while ice extent and retreat timing vary annually in the southeastern Bering Sea (Stabeno et al. 2012b). As a result, conditions vary more in the southeastern Bering Sea, which is an ecotone marking the transition between the seasonally ice-covered northern Bering Sea and the largely ice-free Gulf of Alaska. The interaction of ice extent and the broad (500 km), nearly flat continental shelf makes the eastern Bering Sea spatially rich, with three cross-shelf domains (inner, middle, and outer) in the southeastern Bering Sea (Coachman 1986); a distinct northern Bering Sea domain (Grebmeier et al. 2006; Sigler et al. 2011; Stabeno et al. 2012a); and a Pribilof domain (Stabeno et al. 2008).

Changes in distribution and abundance of Pacific salmon in relation to shifts in water circulation were revealed in the western Bering Sea in the 2000s. Shift in water circulation occurred in 2007 with cyclonic gyre becoming smaller and restricted by the Commander Basin (Zavolokin and Khen 2012; Khen et al. 2013; Khen and Zavolokin 2015). Longitudinal current from Near Strait to north intensified while latitudinal current from the Aleutian Basin to the west became markedly weaker. The latitudinal current limited the flow of the dichothermal layer water to the east, and as a result, a hydrodynamic front occurred near the border of the Russian exclusive economic zone. Change in water circulation in the Bering Sea in 2007-2011 affected the intensity of feeding migrations of immature salmon to the western part of the sea. The abundance of immature chum, sockeye, and Chinook salmon then decreased while their distribution changed. In 2012, water circulation returned to a “normal” regime, with salmon abundance going back to a former state.

Climate-oceanographic conditions affected the prey base and diet of Pacific salmon (Volkov 2012a, b, c, 2014; Dulepova 2014). Pacific salmon research under BASIS covered two periods: warm (2003-2006) and cold (2007-2012). During the warm period, small- and medium-sized zooplankton dominated in the eastern Bering Sea. During the cold period, the portion of large-sized zooplankton (euphausiids, hyperiids, copepods and chaetognaths) significantly increased. These changes were reflected in Pacific salmon diets. For example, in 2003-2006, most of the diet of pink, chum and sockeye salmon juveniles comprised walleye pollock, sandlance, capelin, flounder larvae, fry of small demersal fish and crab larvae. After 2006, euphausiids, hyperiids and pteropods became the dominant salmon prey items in their diet. In contrast, there were no major changes in zooplankton community structure and salmon diet in the western Bering Sea,; the year-to-year variations were also significant in this area, but long-term trends were not observed.

Interestingly, cooling of the Bering Sea observed in 2007-2012 caused shifts in the distribution of some zooplankton species. In particular, a bloom of the large-sized hyperiid amphipod *Themisto libellula* was noted both in the western and eastern Bering Sea (Volkov 2014). The importance of *Themisto libellula* in salmon diet subsequently increased with increasing biomass of this amphipod.

2) The role of salmon in nektonic communities and their association to Bering Sea ecosystem status

During the last three decades, Pacific salmon abundance increased significantly in the Bering Sea, resulting in an increased contribution of salmon to the total consumption of food by nekton from 1-2 % in the 1980s to 8-9 % in the 2000s (Shuntov et al. 2010; Shuntov and Temnykh 2011a). However, even in recent years when Pacific salmon are the most abundant, they do not appear to play a key role in the functioning of pelagic communities. Indeed, in some regions where salmon are abundant, they can consume up to 25-30% of the food in the epipelagic layer, which could lead to density-dependent interactions. However, the carrying capacity may not necessarily be exceeded even in those areas. Carrying capacity of the western Bering Sea appears sufficient to support salmon populations (Shuntov and Temnykh 2011a; Zavolokin 2011).

Changes of in the composition and trophic structure of the nekton community in the western Bering Sea as well as the role of Pacific salmon on the dynamics of energy flow in relation to their abundance have been assessed for the last decades using the ecosystem model Ecopath (Zavolokin et al. 2014). Significant decrease of pollock abundance between 1980s and 2000s caused a twofold reduction of the total food consumption by nekton species; the increased consumption of salmons and squids in the 2000s compensated for only a small portion of the reduction in pollock abundance. However, the tenfold increase of salmon biomass affected their diet with a lowering of the prey trophic level from amphipods and squids to euphausiids, copepods, and pteropods. At present, salmon are the only abundant predators of the fourth trophic level in the upper pelagic layer of the offshore waters in the western Bering Sea. Due to their high trophic plasticity, they can feed to a wide range of prey belonging to 2–3rd trophic levels that supplies them with a large amount of food. The model suggests that the current level of forage resources is able to support their populations even by increasing salmon biomass 1.5-fold relative to the level of 2000s. Researchers have concluded that the carrying capacity of the western Bering Sea is sufficiently favorable for Pacific salmon, even during periods when salmon are highly abundant.

3) Influence of climate-oceanographic conditions upon structure, status, population structure, migration, biological parameters and production processes of Pacific salmon populations

Eisner et al. (2013) explored the distributions and community composition of pelagic species in the sub-Arctic and Arctic waters of the northern Bering and central and southern Chukchi seas during September 2007 by linking pelagic zooplankton and fish assemblages to water masses. Juvenile saffron cod, polar cod, and shorthorn sculpin were most abundant in warm, low salinity Alaska Coastal Water (ACW) of the central Chukchi Sea, characterized by low chlorophyll, low nutrients, and small zooplankton taxa. Adult Pacific herring were more abundant in the less stratified Bering Strait waters and in the colder, saltier Bering Shelf Water of the northern Bering and southern Chukchi seas, characterized by high chlorophyll, high nutrients, and larger zooplankton taxa. Juvenile pink and chum salmon were most abundant in the less stratified ACW in the central Chukchi Sea and Bering Strait. Abundances of large zooplankton were dominated by copepods (*Eucalanus bungii*, *Calanus lacialis/marshallae*, *Metridia pacifica*) followed by euphausiids (juvenile *Thysanoessa raschii*, bivalve larvae and copepods (*Centropages abdominalis*, *Oithona similis*, *Pseudocalanus* sp.). Pelagic community composition was related to environ- mental factors, with highest correlations between bottom salinity and large zooplankton taxa, and latitude and fish species. These data were collected in a year with strong northward retreat of summer sea ice and therefore provide a baseline for assessing the effects of future climate warming on pelagic ecosystems in sub-Arctic and Arctic regions.

4) Foraging dynamics, food competition and its influence on growth and survival of salmon

Inter-annual changes in body size, age composition, and intra-annual changes in the growth of Russian chum salmon were studied (Zavolokin et al. 2011; Temnykh et al. 2012). The body size of most Russian chum salmon stocks changed in a similar way. It significantly decreased from 1960 to 2000s. First-year growth of Anadyr chum salmon estimated by measuring inter-circuli distances on scales samples collected in 1962 to 2007 increased, but decreased in subsequent age classes. Based on published results, the growth of at least two salmon species (chum and pink salmon) appeared to have changed similarly in recent decades. Hence there are some large-scale factors that influenced these species and had an effect on vast areas of the North Pacific and marginal seas. Study results do not corroborate other studies that have suggested density-dependent interactions in productivities among Pacific salmon in the last 50 years. Negative correlations between some climatic indices (ocean surface temperature, ground air temperature, and heat content of North Pacific Ocean) and scale increments of Anadyr chum salmon in the second, third and fourth year zones suggest that warming of the North Pacific may have adverse impact on chum salmon growth after the first year of life. Chum salmon growth reduction after the early marine period may be the result of increasing abundance of Pacific salmon combined with a warming ocean.

5) The processes that affect salmon production

Recent production declines in Chinook salmon have had a critical impact on subsistence, commercial, and sport fisheries throughout Alaska. Estimates of juvenile Chinook salmon abundance in the northern Bering Sea are used to provide insight into when and where production declines are occurring in the Canadian-origin stock group from the Yukon River (Murphy et al. in press). Although estimates of average juvenile survival in the northern Bering Sea are relatively low (5%), juvenile abundance is significantly correlated with adult returns, indicating that much of the variability in survival has occurred during earlier life stages of Chinook salmon (freshwater and initial marine). Survival during these early life stages of Chinook has increased in 2013 and 2014 along with juvenile abundance. The number of juveniles per spawner increased by a factor of two in recent years (2013-2014) relative to the previous decade (2003-2012). The number of adults projected to return from these brood years indicates that subsistence fisheries on the Canadian-origin stock group of Chinook salmon in the Yukon River could recover in 2016 and will likely recover by 2017.

6) The linkage between marine survival of salmon, and climate and ocean changes

A warming of the southeastern Bering Sea has been accompanied by a lack or reduction of the ice extent during winter/spring and with increased returns of Bristol Bay sockeye salmon. Relative abundance and growth rates of juvenile Bristol Bay sockeye salmon are high during warm years (Farley and Trudel 2009); however, the energetic status of juvenile Bristol Bay sockeye salmon during warm years is significantly lower, leading to a higher overwinter mortality (Farley et al. 2011).

Overwinter survival of Pacific salmon is believed to be a function of size and energetic status they gain during their first summer at sea. Farley et al. (2011) tested this notion for Bristol Bay sockeye salmon, utilizing data from large-scale fisheries and oceanographic surveys conducted during mid-August to September 2002 – 2008 and from February to March 2009. The new data presented in this paper demonstrate size-selective mortality for Bristol Bay sockeye salmon between autumn and their first winter at sea. Differences in the seasonal energetic signatures for lipid and protein suggest that these fish are not starving, but instead the larger fish caught during winter apparently are utilizing energy stores to minimize predation. Energetic status of juvenile sockeye salmon was also related to marine survival indices and years with lower energetic status apparently are a function of density-dependent processes associated with high abundance of juvenile sockeye salmon. Based on new information regarding eastern Bering Sea ecosystem productivity under a climate-warming scenario, we hypothesize that sustained increases in spring and summer sea temperatures may negatively affect energetic status of juvenile sockeye salmon, potentially resulting in increased overwinter mortality.

7) The potential impacts of global climate change on marine salmon habitats

The large marine ecosystems within Alaska are rapidly changing due to climate warming. Since 2013, sea temperatures in the Gulf of Alaska have been anomalously warm, and process studies have provided critical data to illustrate that sustained periods of warming can change the trophic structure of the ecosystem, reducing energy to upper trophic level young of the year fishes, leading to increased overwinter mortality. Ongoing field research and modeling suggests that the manifestations of warming in the GOA [The Blob, strongest El Niño in recent history, shifts in run timing (later) for sockeye salmon in the Bering Sea and GOA, protracted run timing of pink salmon in the GOA, unexpected low returns of pink salmon in southern Southeast Alaska, toxic algal blooms, small-copepod-dominated community, cetacean die-offs, and temperate and tropical fish species collected off Alaska's coasts] will continue to highlight the need for research and monitoring of conditions in this region.

A northward shift in the distribution of several fish species is expected to occur in the northern hemisphere as a result of global climate change (Cheung et al. 2015). For Pacific salmon, their northward distribution is generally limited to the Bering Sea Strait due to the short growing season in the Arctic Ocean and sea ice formation. However, summer sea temperatures in the Chukchi Sea were anomalously warm in 2007 (Eisner et al. 2013). BASIS surveys conducted in the Arctic during 2007 documented relatively high abundances of juvenile pink and chum salmon in the Chukchi Sea (Moss et al. 2009). The abundant juvenile salmon returned as adults to the coastal regions of the Pacific Arctic Region in relatively high numbers during 2008 (pink salmon) and 2009/10 (chum salmon) as reported by subsistence users in coastal communities (Carothers et al. 2013; Taquilik Hepa, personal communication). These events (anomalously warm summer sea temperatures, historic summer sea ice minima, and highly abundant juvenile pink and chum salmon in the Chukchi Sea) were all "surprises" in that they were large variations from predicted anthropogenic effects on temperatures and sea ice loss from climate models (Overland 2011). While the capture of salmon in the Chukchi Sea north of known salmon producing drainages likely reflects straying and not colonization, natal populations within Canada's Mackenzie River have been documented (Irvine et al. 2009; Dunmall et al. 2013). Continued warming in marine, terrestrial and riverine environments may make it possible for additional salmon populations to become permanently established in the Arctic. Hence, we hypothesize that these "surprises" will become the norm in the near future.

Summary

The Bering Sea has experienced large changes in sea ice extent, hydrology, and zooplankton communities and quality during the last decade, especially in the eastern Bering Sea. And these changes have been reflected in the diet and survival of juvenile salmon, as well as in their distribution. Limits to the carrying capacity of the Bering Sea is unknown, though prey productivity appears to be sufficiently large to sustain an abundance of juvenile salmon, especially in the western Bering Sea. With a further melting of the polar ice caps and subsequent reduction of sea ice, these changes are expected to be more pronounced in the Bering Sea in the upcoming decades as a result of climate change, with potentially significant impacts on salmon habitat in this region. Further research is critically needed to assess the impacts of climate change on Pacific salmon in the Bering Sea.

Recommendations for the new Science Plan

The issue of climate change and its relationship with salmon and ocean ecosystems will continue to be a major concern to ocean salmon research and will be included in the new science plan. Topics related to climate change include the role of salmon in marine and ocean ecosystems, the impact of climate changes on salmon distribution, effects on salmon hatcheries and the potential impacts of climate change on salmon marine habitats will continue to be important in the coming decade.

- **The role of salmon in changing marine and ocean ecosystems**

Studies to investigate the future of salmon in areas particularly affected by climate change may mean the change in species composition of dominant species and could affect the location and timing of marine salmon fisheries.

- **Impact of climate changes on salmon living on the edge of the areal**

Summer surface waters in the northeastern Bering Sea will continue to warm and be a source of heat adverted to the Pacific Arctic Region, providing new marine habitat for juvenile salmon.

- **Efficiency of salmon hatcheries under the changing climate**

With changing marine environments, the timing of release of juvenile fish and the size of the fish at release may need modifications to optimize hatchery production.

- **The potential impacts of global climate change on marine salmon habitats**

Developing climate forecasts for salmonid marine ecology integrated ecosystem modeling to examine potential impacts of global climate change on marine salmon habitats
Developing models like 20 year climate forecasts for salmonid marine ecology integrated ecosystem modeling – IPCC Scenarios, physical oceanography, nutrient-phytoplankton-zooplankton, fish bioenergetics, distribution, etc., at several spatial scales may help in allocating resources to hatchery production and fisheries. Models will be useful to provide insight into changing ecosystem capacity for salmon and assist in apportioning scarce resources to ocean salmon surveys.

Research Component 3: Winter Survival of Pacific Salmon in the North Pacific Ocean Ecosystem

Panel Members: M. Trudel*, J. Irvine (Canada), S. Urawa (Japan), S. Naydenko* (Russia), and E. Farley (USA) (*panel leaders)

Background and Aim

Western Subarctic Gyre and Gulf of Alaska ecosystems provide the major wintering habitats for various anadromous populations. While previous research has identified this as a critical period that defines the biological characteristics and biomass of anadromous populations, open ocean field research and monitoring programs have typically been carried out only during the late spring to early fall period. Better information on the status and trends in production and condition of Pacific salmon during the late fall to early spring period is needed for conservation and management of salmon resources. Knowledge of variation in the characteristics of winter marine production in the Western Subarctic Gyre and Gulf of Alaska ecosystems is needed for conservation of salmon population resources in Asia and North America.

We have concentrated cooperative research on the following issues:

1) Winter distribution, production, and health status of salmon populations
2) Hydrological characteristics, primary production, and prey resources in the winter habitats
3) Trophic linkages, growth rate and predation of salmon at different stages
4) Winter survival rate of salmon at different stages
5) Winter carrying capacity of salmon populations
6) Effects of climate change on salmon populations during winter
7) Interactions between species, and between populations

Research Review

Beamish and Mahnken (2001) hypothesized that brood year strength of Pacific salmon was determined during two stages: a predation-based marine mortality following the first few weeks at sea and a physiologically-based mortality following their first winter at sea. They further hypothesized that juvenile salmon that failed to reach a critical size by the end of their first summer at sea would not survive through the winter.

Despite the potential importance of winter mortality in regulating the dynamics of salmon abundance, relatively little research has been conducted on the winter ecology of Pacific salmon in the marine environment, due to largely the challenges associated with conducting field work at this time of the year. The knowledge gained during the last 5 years on the winter ecology of Pacific salmon is based primarily on surveys conducted by Russia in central and western parts of Subarctic front zone (SAF) in the winter and spring 2009-2011 and by Canada on the continental shelf from the west of Vancouver Island to Southeast Alaska in the fall and winter 2000-2014, as well as a synthesis of surveys conducted by Russia in 1982-1992.

1) Winter distribution, production, and health status of salmon populations

Myers et al. (in press) reviewed winter salmon research in the high seas of the North Pacific Ocean and Bering Sea. Early high-seas research (1950s-1970s) established that salmon exhibit broad seasonal (north-south) movements, that there are stock-specific marine distributions, and identified dominant oceanographic features of winter habitat. In succeeding decades (1980-2015), new fisheries-oceanographic survey methods, stock-identification techniques, remote-sensing technologies, and analytical approaches enabled researchers to expand their knowledge of the winter distribution and ecology of salmon, although empirical data remain limited.

The winter distribution of salmon is complex and variable, depending on spatiotemporal scale and synergies among genetics, environment, population dynamics, and phenotypic plasticity. For instance, the winter distribution of Pacific salmon in the open ocean depends on the general state of the Western Subarctic Cyclonic Gyre and on position of frontal zone of the East Kamchatka current ocean branch sector (Figurkin and Naydenko 2013, 2014). New data on the vertical distribution of Pacific salmon during winter and spring indicate that they are more dispersed in the water column compared to summer and fall (Starovoytov et al. 2010a, b; Glebov et al. 2011). Pink salmon are distributed across a wide range of temperature during winter (0.5-11.5°C), whereas sockeye and coho salmon tend to occupy cooler (1.5-6.5°C) and warmer (4.0-11.5°C) waters, respectively. Most small chum salmon (<30 cm in FL) are distributed in the Subarctic front zone between 3°C and 8°C, while larger chum salmon shift in cooler water with a peak of 4.5°C (Naydenko and Temnykh, in review).

Few salmon species remain on the continental shelf during winter. On the west coast of North America, winter catches of salmon are dominated by immature Chinook and coho salmon (Trudel et al. 2007; Tucker et al. 2011, 2012a, b), though one population of sockeye salmon has been showed to remain on the continental shelf during winter(Tucker et al. 2009; Beacham et al. 2014a, b). Stock composition appears relatively stable among years despite highly variable ocean conditions, even at a small geographic scales, suggesting that their coastal distribution is genetically programed (Tucker et al. 2012a, 2015a). Unlike the open ocean, juvenile/immature salmon tend to be caught deeper in the water column during winter time (Orsi and Wertheimer 1995; Trudel and Tucker 2013).

The development of quantitative multispecies, multistage models of salmon ocean distribution linked to oceanographic features should help to identify key factors influencing winter distribution and improve understanding of potential climate change effects (Myers et al., in press).

2) Hydrological characteristics, primary production, and prey resources in the winter habitats

The biomass of zooplankton prey resources in the Pacific Ocean has been determined to be lowest in winter (Nagasawa 2000). On the other hand, drastic declines in zooplankton biomass from summer to winter have not been observed in the upper epipelagic layer of the Northwest Pacific Ocean (Naydenko and Kuznetsova 2011). Zooplankton biomass is highly variable among locations and is sufficiently high in some places to provide favorable conditions for Pacific salmon feeding in winter and spring (Naydenko and Kuznetsova 2011). Feeding studies conducted in the Northwest Pacific Ocean indicate that feeding intensity of Pacific salmon is lower in winter than in summer and fall. The feeding intensity differs among species within the same locations, and high feeding intensities are occasionally observed during winter. Feeding selectivity of salmon relates not only to composition and size of forage base, but also to the abundance and availability of these prey. There is considerable overlap in diet among salmon species during winter. Sufficient preys are available for winter salmon in the Northwest Pacific Ocean. The reduction in the feeding intensity that occurs during winter may not be due to a reduction in food availability during this period (Naydenko and Kuznetsova 2011, 2013). Salmon may require less food at lower temperatures to sustain metabolic functions (Ueno et al. 1997; Nagasawa 2000).

On the continental shelf, zooplankton biomass decreased by a factor of three between fall and winter (Middleton 2011). However, stomach contents of juvenile Chinook salmon only decreased slightly between these seasons (Middleton 2011). Considering that energy demand decreases during winter due to low water temperature, these results suggest that food supply may be sufficient to maintain growth during winter.

3) Trophic linkages, growth rate and predation of salmon at different stages

Feeding studies conducted in the Northwest Pacific Ocean indicate that pink, chum and sockeye salmon selectively feed on crustacean zooplankton and pteropods, whereas Chinook and coho salmon prey mainly small-size nekton. In addition to their preferred prey, the diet of pink, chum and sockeye salmon are chaetognaths, gelatinous plankton, squids and small-size fish during winter and spring. This plasticity allows salmon to take advantage of alternative preys when their preferred preys are less abundant (Naydenko and Kuznetsova 2011).

On the continental shelf off the west coast of Vancouver Island, stomach contents and stable isotopes analyses indicate the juvenile Chinook salmon shifted their diet from a dominance of amphipods to a dominance of euphausiids and forage fish between fall and winter (Hertz et al,. submitted).

4) Winter survival rate of salmon at different stages

Winter mortality is expected to be high and variable in juvenile salmon, and higher in smaller fish than larger fish, as smaller fish are expected to deplete their energy reserves faster than larger fish. However, life-stage specific estimates of mortality or survival are rare. Most estimates of marine mortality cover the entire period a salmon is in the ocean, from smolts leaving freshwater to adults returning (e.g. Irvine and Akenhead 2013). As a result, estimates specific to a particular life stage, such as winter (e.g. Trudel et al. 2012), are rare. Other published estimates include mortality that occurred beyond their first winter at sea. For instance, Zavolokin and Strezhneva (2013) estimated mortality rates of pink salmon during winter and spring, while Farley et al. (2011) estimated the total mortality of Bristol Bay sockeye salmon that occurred beyond their first summer at sea, and thus covered two years of their marine life. Hence, for the most part, estimates of mortality rates that are specific to the winter period are generally lacking.

Evidence for overwinter size-selective mortality is also equivocal, with both data consistent (e.g. Farley et al. 2011; Zavolokin and Strezhneva 2013) and inconsistent with this hypothesis (e.g. Middleton 2011; Trudel et al. 2012). The size of juvenile salmon in the fall has been correlated to winter and spring mortality in Okhotsk Sea pink salmon, suggesting that there is a critical size that they must achieve in order to survive winter (Zavolokin and Strezhneva 2013). However, this relationship broke down with additional data (Naydenko et al. unpublished). This suggests that size-selective mortality may be mediated by environmental conditions experienced prior to and during winter such as the concentration of lipid, winter duration, prey abundance and quality, and predator distribution and abundance.

Lipid dynamics during winter has been rarely examined in juvenile salmon. The total muscle lipid content of age 0.1 chum salmon in the Gulf of Alaska were extremely low (less than 2%), suggesting their malnutrition during winter (Kaga et al. 2006). The lipid content of pink salmon was also significantly lower in the Gulf of Alaska than in the western North Pacific Ocean during winter (Nomura et al. 2000; Kaga et al. 2006). On the other hand, larger juvenile salmon utilize a larger fraction of their energy reserves compared to smaller fish and that they are not starving during winter (Middleton 2011; Farley et al. 2011), a result which is inconsistent with the critical-size and critical-period hypothesis. Survival beyond the first summer at sea has been linked to the energy density of juvenile Bristol Bay sockeye salmon in the fall prior to their first winter, suggesting that juvenile salmon need to accumulate enough energy to survive through the winter (Farley et al 2011). However this relationship was not significant, indicating that further works are required to test the critical-size and critical-period hypothesis.

5) Winter carrying capacity of salmon populations

Overall, the dominant nekton species that occur during winter (squid, salmon, mesopelagic fish and anchovy) only consume a small fraction of the zooplankton biomass available during the winter months, providing further support that Pacific salmon are not starving during winter, and that low food abundance cannot explain the high mortality rates that are thought to occur during this period (Naydenko and Kuznetsova 2011, 2013).

6) Effects of climate change on salmon populations during winter

Little effort has been directed at assessing the impacts of climate change on salmon population during winter. In a joint PICES/NPAFC workshop held in Yeosu, Korea, Minobe and colleagues projected change in the distribution of salmon during winter using climate model outputs from the Coupled Model Intercomparison Project Phase 5 (CMIP5). They concluded that salmon would further north and west as a results of warmer temperatures. These results were qualitatively similar to those obtained by Welch et al. (1998) and more recently by Abdul-Aziz et al. (2011).

Farley et al. (2011) hypothesized that winter survival of Bristol Bay sockeye salmon would decrease as a result of warming conditions, as extended periods of warming are expected to decrease the availability of lipid-rich zooplankton and the recruitment of young-of-the-year pollock (Hunt et al. 2011; Heintz et al. 2013). As a result, juvenile sockeye would get smaller (Farley and Trudel 2009) and accumulate less lipids, and potentially experience higher size-selective mortality. This hypothesis will require further testing.

7) Interactions between species, and between populations

Not available

Summary

It has been nearly 15 years since Beamish and Mahnken (2001) proposed that winter was a critical period for juvenile salmon and that fish that did not reached a certain critical size are expected to be eliminated from the population. Some progress has been made toward testing this theory during the last 5 years. Though there is currently no consensus as to whether or not winter is a critical period for salmon or whether or not size-selective mortality occurs during winter. It is recognized that winter may be an important period for salmon, but may not be more critical than any other periods during their marine life. Changes in feeding, growth, and lipids during winter may be due to seasonal cyclic changes of physiological processes of salmon, but not necessarily due to poor food resources and prey availability in winter. It is currently difficult to determine the main factor affecting winter mortality in salmon, in part because there are too few estimates of mortality, and survival of Pacific salmon is likely determined by the complex interaction of abiotic and biotic factors.

Recommendations for the new Science Plan

Testing the critical-period and critical-size hypothesis will require an assessment of how winter mortality contributes to the overall recruitment of salmon and understand the factors affecting the variability associated with winter mortality. This will require an estimation of winter mortality itself (as opposed to winter and spring mortality for instance), which will certainly be challenging for populations that are widely dispersed in the ocean. This work would greatly benefit from genetic stock identification methods to ensure that the same populations are monitored between fall and winter (e.g. Trudel et al. 2012).

As the size and lipid concentrations reached prior to winter are expected affect winter survival through size-selective mortality processes, a better understanding of the conditions that affect marine growth and lipid dynamics during their first year at sea (from ocean entry to the end of the winter), such as the prey resources they encounter in different oceanic habitats (e.g. the community composition of zooplankton, the monthly dynamics of zooplankton biomass, caloric content of oceanic zooplankton species in different season) and feeding intensity will be required. It should be kept in mind that non size-selective mortality processes may also be operating during winter (Middleton 2011; Trudel et al. 2012) such as predation by salmon shark (Nagasawa 1998), disease or physiological imbalance, and should be examined further. Given that 60-95% of juvenile salmon may be dying during their first winter at sea (Trudel et al. 2012; Beacham et al., in press), it is certainly worth identifying the factors that may contribute to this mortality.

Research Component 4: Biological Monitoring of Key Salmon Populations

Panel Members: J. Irvine*, A. Tompkins (Canada), T. Saito*(Japan), N. Klovach, V. Volobuev (Russia), and E. Volk (USA) (*panel leaders)

Background and Aim

Salmon monitoring data can be useful indicators of the status of salmon populations and the ecosystems in which they live. The data can be collected/assembled/analyzed for various categories including abundance (e.g. numbers, weights, biomass), spatial units (fresh water, coastal, oceanic domain, North Pacific), life history phases (eggs, fry, smolts, early marine, immature, mature, spawners), and biological diversity units (multiple species, individual taxonomic species, population unit, deme). Regardless of how the data are being used, the quality of the data is dependent on accurate and precise measurements.

Because of the importance of understanding potential impacts of climate change on salmon production, there is a continuing need to maintain and improve monitoring of spawning escapement, catch, smolt production and other biological information for potential use in the forecasting of salmon return strength or ocean survival. Long time series are particularly valuable in understanding linkages between climate and Pacific salmon production. In areas where hatcheries are present, data on hatchery fish abundance should be separated from wild fish abundance. Biological information such as age composition of a population, body size, fecundity and egg size should be monitored whenever feasible.

With the potential of limiting food resources in epipelagic waters of the North Pacific Ocean as a consequence of climate change, understanding the implications of habitat utilization by Pacific Rim salmon populations at varying levels of abundance is important. The quantification of regional salmon production trends for hatchery and wild stock sources will enable researchers to better examine the effects of ocean salmon biomass on subsequent survival, size at return, and age at return for key Pacific Rim stock groups.

Cooperative research focused on the following issues:

1) Identify key populations of each salmon species as indicators of regional and basin-scale ecosystems
2) Monitor biological status of key salmon populations (abundance, age and body size at return, timing of return, fecundity, egg size, trophic condition, genetic diversity, disease and parasites)
3) Identify annual regional production of hatchery and wild salmon

Research Review

1) Key populations of each salmon species as indicators of regional and basin-scale ecosystems

Biological monitoring programs, which generally included the identification of key populations, were documented for each of the member countries in a series of recent NPAFC newsletter articles: Canada (Tompkins et al. 2014), Japan (Saito 2015), Russia (Koval et al. 2014), the Republic of Korea (Park and Hong 2013, Kang et al. 2016), and the USA (Orsi et al. 2014). In addition, salmon escapement monitoring activities are described for all countries on a new page at the NPAFC website (http://www.npafc.org/new/science_escapement.html).

It was, however, recognized that to evaluate whether biological traits of key populations were reasonable ecosystem indicators would require collaboration with scientists from outside NPAFC. In part to address this, a NPAFC-PICES (North Pacific Marine Science Organization)

Framework for Enhanced Scientific Cooperation in the North Pacific Ocean was established in 2014. The framework identified two major scientific topics of joint interest to NPAFC and PICES: 1) effects of climate change on the dynamics and production of Pacific salmon populations; and 2) oceanographic properties and the growth and survival of Pacific salmon. The framework also identified mechanisms for implementing enhanced cooperation between NPAFC and PICES, including theme sessions at PICES annual meetings, joint working groups, symposia, workshops, strategic initiatives, and continued representation at each other's meetings (NPAFC-PICES Study Group 2014). Several joint papers from the 2015 NPAFC International Symposium on Pacific Salmon and Steelhead Production in a Changing Climate from this enhanced cooperation are expected to be published in 2017.

Although the framework has improved collaboration between NPAFC and PICES scientists, the utility of using key populations and their biological traits as ecosystem indicators has not been adequately examined. Further discussion is needed to determine the priority of focusing on this topic within the next science plan.

2) Biological status of key salmon populations (abundance, age and body size at return, timing of return, fecundity, egg size, trophic condition, genetic diversity, disease and parasites)

The last major overview assessment of stock status by the NPAFC Working Group on Stock Assessment was updated in 2012 (Irvine et al. 2012a). In addition, there are numerous status assessments published by NPAFC and others, many of which are documented at http://www.npafc.org/new/science_stocks.html. In summary, Pacific salmon abundance in the North Pacific Ocean, as indexed by aggregate commercial catches, remains near all-time high levels. Total commercial catches of Pacific salmon by member countries exceeded one million metric tonnes in the recent add years (2007, 2009, 2011 and 2013). Even-year catches exceed 800 thousand tonnes, somewhat lower than odd-years, because even-year returning pink salmon are less abundant than odd-year. Although the northern North Pacific Ocean continues to produce large quantities of Pacific salmon, abundance patterns vary spatially, among species, and from year-to-year. Currently, pink and chum salmon are very abundant, particularly on the Asian side of the North Pacific. Coho and Chinook salmon are less abundant than their historical levels, while inter-annual patterns of sockeye salmon abundance vary highly among regions.

An updated review of biological traits and status of key salmon populations throughout the North Pacific is needed. The following text provides additional information on biological status, largely from area-specific reviews of catch trends. Over the long-term (1926-2010), odd-year pink salmon have become increasingly dominant over even-year fish, particularly in the southern portion of their range (Irvine et al. 2014). In Asia, Russian pink salmon catches increased since the 1990s in Chukotka (Khokhlov 2012), west and east Kamchatka (Karpenko and Koval 2012) and Sahalin-Kuril (Kaev 2012). On the other hand, Japanese pink salmon, which are near the southern extent of their distribution in the western North Pacific, have undergone remarkable declines since 2011 (Saito et al. in press).

In the eastern North Pacific, Alaskan pink salmon catches were low during 1950-1970, but rebounded strongly following the 1980s (Heard and Wertheimer 2012), and remain at high levels in recent years with some years of poor-runs (Piston and Heinl 2012). In British Columbia and Puget Sound, near the southern portion of pink salmon distribution in the eastern North Pacific, odd-year runs do better than the even-year runs in the same watershed, and show increasing trends as with populations further north and west (Irvine et al. 2012b, 2014). In the Fraser River, the total returns of pink salmon increased after the 1977 regime shift, declined after the 1989 regime shift, and increased again after 1998 (Beamish 2012a).

Chum salmon catches from the western side of the Pacific Ocean increased since the late 1970s and amounted to 250-300 thousand metric tonnes annually in the 2000s (Nagasawa 2015). Anadyr chum salmon increased in the 1930s-1940s, and again in the 1980s, showing a 40- to 50-year fluctuation in the abundance (Khokhlov 2012). During 2001-2010, chum salmon catches along the both coasts of Kamchatka have increased threehold as compared to the previous decade (Zavarina 2012). In Russia, a sharp increase in chum salmon catch occurred in the mid 2000s, and historically the second highest catch was recorded in 2010 (Temnykh et al. 2012). In particular, the increase in chum salmon catch was evident in the Amur River. The increasing trends in chum catch were common in most regions of the Far East Russia, with some exception for the Anadyr River and rivers in Primorye (Temnykh et al. 2012). In Hokkaido, return rates of chum salmon are historically high in the Okhotsk Sea regions, relatively low in the Sea of Japan region, and highly variable in the Pacific Ocean region (Miyakoshi and Nagata 2012). Such regional differences in return rates of chum salmon are also recognized in the northern part of Honshu (Saito and Nagasawa 2009). The Great East Japan Earthquake on March 11, 2011, severely damaged the 2010 brood-year chum salmon in coastal salmon hatcheries in northeastern Honshu, raising concerns of significant effects on coastal salmon fisheries and future hatchery production in the Honshu Pacific region (Watanabe et al. 2015).

Commercial chum salmon catches increased after 1990 in the Prince William Sound, and Southeast Alaska, following the start of modern hatcheries in Alaska in the late 1970s (Heard and Wertheimer 2012). In Kodiak, chum salmon catches varied widely before hatcheries were built, but subsequently increased (Heard and Wertheimer 2012). In Southeast Alaska, the commercial catches of chum salmon have been comprised primarily of hatchery fish, and estimated catches of wild chum salmon have recently declined to levels similar to those of 1970s (Piston and Heinl 2012). Population abundance of chum salmon originating in the Columbia River and southwards to Newport, Oregon, is highly variable and has fallen more than 80% from historic levels (Johnson et al. 2012).

During 1971-2010, sockeye salmon catches have increased in west and east Kamchatka (Karpenko and Koval 2012). In 2013, Russian sockeye catches reached over 50 thousand metric tonnes, which was almost a historic high level (NPAFC 2016).

In Bristol Bay, Alaska, commercial fishing has reduced sockeye salmon population diversity (Schindler et al. 2010). Decreasing trends in productivity for sockeye salmon have occurred since 1950 across a large geographic area ranging from Washington, British Columbia, southeast Alaska, and up through the Yakutat peninsula, Alaska, but not in central and western Alaska (Peterman and Dorner 2012). In the Fraser River, the total returns of sockeye salmon in 2009 were the lowest recorded since quantitative records began in the late 1940s, but one of the strongest sockeye returns was recorded in 2010 (Irvine and Akenhead 2013, McKinnell et al. 2014).

Contrary to pink, chum, and sockeye salmon, many populations of coho, Chinook, and cherry (masu) salmon have been decreasing in abundance. At a NPAFC workshop on pink and chum salmon in 2011, although explanations for the high production of pink and chum salmon were not precisely determined, it was recognized that pink and chum salmon have been able to benefit more than other species as a result of (i) changing environmental factors, (ii) biological and life history characteristics of pink and chum salmon allowing these species to benefit from changing conditions, and (iii) human activities including such as stock enhancement and responsible fisheries management (Davis and Beamish 2012).

3) Annual regional production of hatchery and wild salmon

From 1993-2013, NPAFC generated hard-copy and on-line versions of its Statistical

Yearbooks containing annual salmonid catches and hatchery releases. In 2014, updated time series of these datasets, including statistics for years prior to 1993, were made publicly available for download from the NPAFC webpage. These have replaced the hard-copy and on-line versions of the NPAFC Statistical Yearbooks. There are two data files: (1) catch statistics (commercial, sport, and subsistence) and (2) hatchery release statistics. In addition, the NPAFC Statistics Metadata Report provides information on data file organization, data sources, and limitations for users.

Provisional estimates of hatchery and wild abundances in the North Pacific were provided by Ruggerone and Irvine (2015). Based on the data from this report, the proportion of hatchery-origin chum salmon in the North Pacific peaked in the late 1990's at ~70%, and is currently ~45%. Hatchery-origin pink and sockeye salmon currently constitute ~19% and ~4% of the total returns for these species respectively. These estimates are similar to those of Kaeriyama et al. (2012) who estimated that the biomass contributed by hatcheries amounted to 50% for chum salmon, more than 10% for pink salmon, and less than 10% for sockeye salmon.

Summary

This research component is concerned with monitoring key salmon populations and important biological characteristics of them and making datasets available for easy access. These time series (e.g. catch, hatchery release) are a primary means to assess the biological status of stocks of salmon in the North Pacific Ocean. During 2011-2015, summaries of monitoring programs were published by each country and major datasets were posted on the NPAFC publicly accessible website. Provisional estimates of hatchery and wild abundances were published. A framework for enhanced scientific cooperation with PICES needs to be more fully implemented to evaluate the utility of using key populations as ecosystem indicators. An NPAFC status assessment updated in 2012 has been supplemented by numerous publications and reports but should be repeated with a focus on biological traits of key salmon populations.

Recommendations for the new Science Plan

Time series information gathered on regional salmon production (wild and hatchery) and biological and physical characteristics of salmon and their ocean habitat can provide the broad scale perspectives necessary for examining the underpinnings of ocean salmonid production, biological characteristics, and marine ecosystem conditions.

We recommend:

- The maintenance of important ongoing monitoring programs and the identification of new sampling opportunities;
- Additional collaborations with PICES scientists to evaluate the utility of using key populations and their biological traits as ecosystem indicators;
- The quantification of uncertainty associated with existing and new data time series;
- Increased collaboration among members to investigate scales of variation in productivity;
- Increased collaborations with climate modellers;
- The expansion of accessible databases to store important time series datasets including associated metadata;
- Better separation between wild and hatchery salmon in datasets; and
- Updated status assessment with a focus on biological traits of key populations.

Research Component 5: Development and Applications of Stock Identification Methods and Models for Management of Pacific Salmon

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Background and Aim

Consensus on genetic baselines for sockeye, Chinook, coho and chum salmon and the development of genetic baselines for pink salmon are necessary to monitor stock specific ocean distributions and abundance. This information is needed to produce more accurate estimates of the timing and abundance of adults that are returning to coastal rivers. High-seas tagging and otolith mark programs, in addition to those provided by genetic analysis, are also important to examine migration behavior of specific populations. Finally we need models to explain how Pacific salmon production will change in ocean ecosystems affected by changing climate.

Cooperative research focused on the following issues:

1) Improve genetic baselines for chum, sockeye, coho and Chinook salmon and steelhead
2) Develop genetic baselines for even-year and add-year pink salmon
3) Integrate the database of tag recoveries
4) Develop the database of otolith mark recoveries
5) Improve forecast models for estimating abundance of specific salmon populations

Research Review

1) Improve genetic baselines for chum, sockeye, coho, Chinook salmon, and steelhead

Coastwide genetic baselines have been developed for chum (Beacham et al. 2009; Seeb et al. 2011), sockeye (Habicht et al. 2010; Beacham et al. 2011, 2014a, b), and Chinook salmon (Templin et al. 2011). Regional baselines exist for all species with examples including chum salmon in Japan (Sato et al. 2014; Sato and Urawa 2015; Tsukagoshi et al. in press), sockeye salmon in Kamchatka (Khrustaleva et al. 2014), coho salmon in British Columbia (BC) (Beacham et al. 2012a), Chinook salmon in western Alaska (Larson et al. 2014), and steelhead trout in the Skeena River, BC (Beacham et al. 2012c). Genetic baselines continue to improve stock composition analyses through the addition of genetic markers, many of which are now being discovered using next generation DNA sequencing methods capable of assaying thousands of single nucleotide polymporphisms (Campbell et al. 2014).

2) Develop genetic baselines for even-year and odd-year pink salmon

Regional and species-wide allozyme baselines have been developed in the past for odd-year (i.e. Shaklee et al. 1991; Varnavskaya and Beacham 1992; Hawkins et al. 2002; Kondzela et al. 2002) and even-year pink salmon (i.e. Noll et al. 2001; Hawkins et al. 2002). More recently, genetic baselines for pink salmon have also been developed using mitochondrial DNA sequence analysis (Yamada et al. 2012; Shpigalskaya et al. in press), microsatellite markers (Beacham et al. 2012b), and single nucleotide polymorphisms (Seeb et al. 2014).

3) Integrate the database of tag recoveries

The NPAFC database of tag recoveries has been summarized (NPAFC Secretariat 2014) and made electronically available either through the NPAFC web site for members or by request. The

High Seas Salmon Research Program (HSSRP) of the University of Washington conducted their data storage tag (DST) tagging experiments on high seas salmon and steelhead from the late 1990s to the late 2000s. Recently, the HSSRP provided their DST data files to NPAFC, and these files are available for downloading. A total of 92 DSTs was recovered from 38 chum, 21 sockeye, 15 coho, 10 pink, 7 Chinook salmon and one steelhead trout.

4) Develop the database of otolith mark recoveries

The current version of the NPAFC Otolith Mark Release Database was launched in October 2006 and now includes data from all member countries. Since 1988, there have been 4,775 release records created representing a significant coordination effort by the Working Group on Salmon Marking. The release database is available through the NPAFC web portal (http://wgosm.npafc.org/) to identify marked salmon and trout recovered in the ocean as well as in rivers. Otolith recovery data is currently being coordinated by individual countries with reports of recoveries from high-seas salmon sampled from the Bering Sea, North Pacific Ocean, and Gulf of Alaska (e.g., Sato et al. 2009; Urawa et al. 2009).

5) Improve forecast models for estimating abundance of specific salmon populations

In general, there are two main approaches used to model salmon populations. The first approach uses a statistic model (e.g., Sethi and Tanner 2013; Satterthwaite et al. 2015) which can also include the effects of climate change. The other approach uses a coupled physical (temperature and salinity) and ecosystem model (e.g., Kishi et al. 2012; Yoon et al. 2015) which can also incorporate results from a three dimensional physical migration model to account for horizontal and vertical movement. These models have been used to predict how salmon ocean distributions may be impacted in the future and are critical to evaluating stock production in a changing environment (Yoon et al. 2015).

Summary

Stock and fish identification methods including genetic analysis, otolith marking, and tag recoveries continue to develop and are integral to the formulation of models predicting the migration and abundance of salmon populations.

Recommendations for the new Science Plan

The following recommendations are provided for the 2016-2020 NPAFC Science Plan:

- Continue research into the development of genetic baselines encompassing the species range of Chinook salmon, coho salmon, chum salmon, sockeye salmon, pink salmon (odd- and even-year), and steelhead trout. This should support high-quality marker development and regional stock representation to enable accurate delineation of important stocks. Such baselines are critical to inform our understanding regarding the stock composition of mixtures collected on the high-seas.
- Continue to report the stock compositions of salmon and trout encountered in ocean fisheries, helping to inform migration models for salmon and trout.
- Continue to support the development of parental based tagging methods for identifying hatchery stocks.
- Support the development of higher throughput genotyping methods for stock composition analysis, potentially taking advantage of next generation DNA sequencing methodologies.
- Support the development of additional statistical protocols for the analysis of fisheries stock composition data.
- Support the genetic stock composition analysis of samples seized through Illegal,

Unreported and Unregulated (IUU) fisheries. Provide scientific information to support the activities of the NPAFC Committee on Enforcement (ENFO).

- Ask the Working Group on Salmon Marking to assess the interest and/or feasibility of establishing a mark recovery database and data standards group. Such a database may be useful to assess returns across each species range to infer broad geographic and climatic changes and make inferences on population dynamics between salmon and other species.
- Encourage modelers to continue developing statistic models as well as ecosystem models coupled with physical models to estimate the impact of climate change on salmonid populations.

Conclusive Remarks: Forecast of Pacific Salmon Production in the Ocean Ecosystems under Changing Climate

The vision of the NPAFC Convention is to promote the conservation of anadromous populations in the North Pacific Ocean. Pacific salmon producing countries need the best available scientific information to make appropriate decisions for sustainable fisheries management that optimize economic opportunities and consider the capacity for Pacific salmon production in changing environments. Accurate forecasting of salmon abundances is of great importance to management and for anticipating future variations in production affected by a changing climate. In addition, precise pre-season forecasts increases economic efficiency of the salmon industry, enable managers and resource stakeholders to predict harvest with more certainty, and help promote resource sustainability.

Sibling models, which compare adult salmon returns from a brood year’s younger age class to the subsequent age class, are frequently used for the forecast of chum and sockeye salmon returns (Peterman 1982; Bocking and Peterman 1988; Haeseker et al. 2007). For example, current abundance forecast methods include Bayesian approaches to capture uncertainty in Fraser River sockeye survival and resulting returns (Grant et al. 2015). The forecast probability distributions are wide, given uncertainty in the specific mechanisms influencing Fraser sockeye survival and the very dramatic changes in survival in recent years (McKinnell 2016). Standard sibling models assume constant parameters over time, but many sockeye salmon populations show temporal changes in age-at-maturity, which cause forecasting errors (Holt and Peterman 2004). The accurate forecast requires considering the ecological mechanisms that regulate salmon production in the ocean.

Forecasting pink salmon returns is also challenging under conditions of a changing ocean climate, because pink salmon only spend a single winter in the ocean before returning to spawn (Heard 1991). Thus, they lack any leading indicator information generated from younger siblings. Early marine mortality of pink salmon can be highly variable and affects year class strength (Parker 1968; Pearcy 1992; Bradford 1995; Karpenko 1998; Mortensen et al. 2000). Conducting surveys assessing seaward migrating juveniles after this critical period can usually predict year class strength. In addition, subsequent ocean conditions during some years may impact pink salmon productivity. Of the ecosystem metrics considered, important variables for forecasting the adult pink salmon return are juvenile pink salmon CPUE, timing, the percentage of pink salmon in the catch, a predator index, and the North Pacific Index (Orsi et al. in press). Among available methods to forecast salmon returns, this may be the most reliable model including parameters of juvenile mortality and climate impact.

There is, however, still a limitation on explaining and forecasting the annual variation in Pacific salmon production. The trends in production and catches of Pacific salmon around the North Pacific Ocean are a history of unexpected changes with global regime shifts (Beamish 2012b). The total commercial catch of all Pacific salmon placed historic high records in 2009, 2011 and 2013. The historic high catches might result mainly from the improved marine survival of pink and chum salmon. However, the reasons for the improved marine survival remain to be explained in a way that can be used to manage salmon production (Beamish 2012b). It is important for all countries to understand how to optimize the early marine survival of salmon by designing cooperative research programs throughout the distribution of juvenile salmon. The marine survivals vary as a result of the conditions in the early marine coastal environment and possibly as a consequence of the summer and winter rearing areas in the open ocean.

Global warming may decrease the carrying capacity and distribution area of Pacific salmon in the North Pacific Ocean and expand their distribution to the Arctic Sea (Kaeriyama et al. 2009). In general, however, there is a lack of detailed knowledge about stock-specific ocean distribution. It is necessary to identify the stock-specific seasonal distribution of Pacific salmon from all countries in the open ocean to better understand the ocean capacity to produce Pacific salmon, and how climate change affects the future distribution and production of each population. International fisheries science has now the ability with new technologies to identify stock-specific ocean migration and distribution of major salmon populations.

Ecological risk management consisting of adaptive management and the use of precautionary principles is a necessity for sustainable protection of Pacific salmon under conditions of a changing climate. For successful long-term risk management of Pacific salmon, the following items need to be considered: (1) limited and fluctuating ocean carrying capacity, (2) a paradigm shift in aquatic sciences from traditional population level ecology to ecosystem level ecology, and (3) education on sustainability sciences of Pacific salmon for future generations (Kaeriyama et al. 2015).

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Appendix 1. Panel and editorial members for the review of 2011-2015 NPAFC Science Plan. Note: Asterisks (*) indicate panel leaders (= session conveners at 2015 NPAFC Symposium).

2011-2015 NPAFC Science Plan Research Components	Panel members				
	Canada	Japan	Korea	Russia	USA
1. Migration and survival mechanisms of juvenile salmon in ocean ecosystems	*M. Trudel A. Tompkins	T. Saito	*J.K. Kim D.-H. Lee	O. Temnykh M. Koval	D. Oxman
2. Climate impacts on Pacific salmon production in the Bering Sea and adjacent waters	M. Trudel	T. Azumaya S. Sato	NA	*O. Temnykh A. Zavolokin	*E. Farley
3. Winter survival of Pacific salmon in North Pacific Ocean ecosystems	*M. Trudel J. Irvine	S. Urawa	NA	*S. Naydenko	E. Fraley
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