

Forecasting Pacific Salmon Production in a Changing Climate: A Review of the 2011–2015 NPAFC Science Plan

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Abstract: In recent decades, the marine production of Asian and North American Pacific salmon and steelhead populations has undergone significant variability linked to climate change. Improved forecasts of the abundance and distribution of salmon are needed that will benefit stock management in all salmon producing countries around the North Pacific Rim. The North Pacific Anadromous Fish Commission (NPAFC) Science Plan is a long-term comprehensive strategy for international cooperative research. The primary goal of the 2011–2015 Science Plan was to explain and forecast annual variations in Pacific salmon production. The plan was developed with an overarching research theme “Forecast of Pacific Salmon Production in the Ocean Ecosystems under Changing Climate” and five research topics. This paper describes progress made on each research topic and the overarching theme, much of which was assessed at an international symposium in Kobe, Japan, on May 17–19, 2015. In summary, the reliability of stock identification methods including genetic and otolith mark analyses has improved, enabling better monitoring of stock-specific ocean distribution and abundance. Salmon marine survival depends on early marine coastal environments but also on conditions later in life, including winter. Models incorporating fish mortality and various environmental factors improve our ability to forecast returns of specific salmon stocks. However, limitations on our ability to accurately explain and forecast annual variations in Pacific salmon production remain, in part because of uncertainty in the factors responsible for salmon mortality and from the effects of climate warming on the marine distribution and abundance of salmon. It is more important than ever to promote cooperative and innovative international research to identify and better understand the ecological mechanisms regulating the distribution and abundance of salmon populations for sustainable salmon and steelhead management.

Keywords: NPAFC Science Plan, review, Pacific salmon, distribution, marine production, survival, biological monitoring, stock identification, models, climate change, forecast

INTRODUCTION

Over the past several decades, there have been significant variations in the marine production of Asian and North American anadromous salmon populations that are linked to climate change (Beamish et al. 2009). There is a strong need for international cooperative research that provides better scientific information on the ecological mechanisms regulating production of anadromous populations, climate impacts on Pacific salmon populations, and the utility of using salmon populations as indicators of conditions in North Pacific marine ecosystems.

Accurate forecasts of returning salmon abundance are of great importance for stock management in North Pacific Rim countries. Long-term monitoring of abundance and biomass

in the ocean may be the most reliable method for predicting changes in production of anadromous populations. Reliable stock identification methods such as genetic and otolith mark analyses are necessary to monitor stock-specific ocean distribution and abundance.

The North Pacific Anadromous Fish Commission (NPAFC) Science Plan is a long-term comprehensive strategy for international cooperative research that can be used by Pacific salmon producing countries to design national research. The plan has been revised every five or eight years (1993–2000, 2001–2005, and 2006–2010) after review of research progress. In 2010, the NPAFC adopted a five-year (2011–2015) Science Plan to explain and forecast the annual variation in Pacific salmon production (Anonymous 2010). The plan identified the overarching research

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theme “Forecast of Pacific Salmon Production in the Ocean Ecosystems under Changing Climate” and five research topics: (1) migration and survival mechanisms of juvenile salmon in ocean ecosystems; (2) climate impacts on Pacific salmon production in the Bering Sea and adjacent waters; (3) winter survival of Pacific salmon in 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.

This summary reports progress on each research topic and the overarching theme of the 2011–2015 NPAFC Science Plan, much of which was assessed during the *International Symposium on Pacific Salmon and Steelhead Production in a Changing Climate: Past, Present, and Future*, held in Kobe, Japan, on May 17–19, 2015.

MIGRATION AND SURVIVAL MECHANISMS OF SALMONIDS DURING CRITICAL PERIODS IN THEIR MARINE LIFE HISTORY

Application of Hjort’s (1914) critical period hypothesis to anadromous salmon populations suggests that the initial period after migration to sea is the most critical phase with respect to ocean survival. More recently, Beamish and Mahnken (2001) hypothesized that brood-year strength of Pacific salmon was determined during two stages when fish were in their first year in the ocean. There is an early natural mortality that is mostly related to predation, which is followed by physiologically-based mortality. Juvenile salmon that fail to reach a critical size by the end of their first marine summer do not survive the following winter (critical-period and critical-size hypothesis).

Long-term cooperative and national research suggests considerable inter-annual variation in abundance, growth, and survival rates of juvenile salmon in the ocean (e.g., Orsi and Davis 2013). These variations may be related to climate-induced changes in habitats 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 the conservation and sustainable management of anadromous populations.

There has been an explosion of research on the early marine life of Pacific salmon during the last five years (Radchenko et al. 2013; Trudel and Hertz 2013; Hertz and Trudel 2014, 2015). This research has benefited from long-term epipelagic monitoring 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.

Western Subarctic Gyre and Gulf of Alaska ecosystems provide major wintering habitats for various anadromous salmon populations (Myers et al. 2007, 2016). While previous research suggested this as a critical period that defines

the biological characteristics and biomass of anadromous populations, winter open-ocean field research and monitoring programs have been too limited to test it directly. Better information on the status and trends in production and condition of Pacific salmon during the late fall to early spring period and knowledge of the variation in the characteristics of winter marine production in the Western Subarctic Gyre and Gulf of Alaska ecosystems is needed to conserve salmon populations.

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 largely to the challenges associated with conducting field work at this time of the year. The knowledge gained during the last five years on the winter ecology of Pacific salmon is based primarily on surveys conducted by Russia in central and western parts of Subarctic Frontal Zone in the winter and spring 2009–2011, a synthesis of surveys conducted by Russia in 1982–1992, and cruises by Canada on the continental shelf from west of Vancouver Island to Southeast Alaska in the fall and winter 2000–2014, much of which was reviewed in Myers et al. (2016).

Initial Period of Marine Life

Seasonal Distribution and Migration Route/Timing of Juvenile Salmon

The first step required to understand the interactions between Pacific salmon and marine ecosystems is to determine when salmon smolts enter the ocean, where juveniles migrate, and how long they reside in different regions of the ocean. Research indicates that their downstream migration timing 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 (Volobuev and Marchenko 2011; Kaev et al. 2012; Kolpakov et al. 2012; Kasugai et al. 2013). Sea-entry timing of juvenile salmon has also been linked to body size, life-history, migration distance in fresh water (Weitkamp et al. 2012, 2015), and release date (Kasugai et al. 2013). Climatic effects on the timing of juvenile migration are also apparent from long-term data sets, 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 fry and smolts will require an increase in the number of systems that are monitored to encompass the diversity of conditions experienced by juveniles (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 Kolomeytssev 2011), otolith marking (Kasugai et al. 2011, 2016; Chistyakova and Bugaev 2013, 2016; Chistyakova et al. 2013; Saito et al. 2013; Sasaki et al. 2013; Nagata

et al. 2016a, b; Shubin and Akinicheva 2016), 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. 2011, 2012a, b; Sato et al. 2013; Shpigalskaya et al. 2013, 2016; Beacham et al. 2014a; Teel et al. 2015; Kondzela et al. 2016a, b). 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 physiological condition such as body size (Hasegawa et al. 2013; Saito et al. 2013; Beacham et al. 2014b; Freshwater et al. 2016) and environmental cues such as water temperature (Kasugai et al. 2011; Urawa 2015; Nagata et al. 2016b), ocean currents (Burke et al. 2013a; Chistyakova and Bugaev 2016), phytoplankton biomass (Bi et al. 2008; Peterson et al. 2010), location of river mouths (Burke et al. 2014), and magnetic cues (Putman et al. 2014). Furthermore, migration behavior of hatchery and wild fish appears to be different at small scales during 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).

Hydrological Characteristics, Primary Production and Prey Resources in Juvenile Salmon Habitats

Our understanding of the dynamics of zooplankton communities in Russia's far-eastern seas and adjacent waters has been 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 have generally larger biomass in the western North Pacific Ocean compared to the eastern North Pacific Ocean and exhibit different trends between basins (Shuntov and Temnykh 2011a). Zooplankton biomass appeared to have varied inversely between the Bering Sea and Okhotsk Sea from 1980 to the early 2000s (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 2012a, b, c). The diet of juvenile salmon is also reflected in the variability in zooplankton communities. For instance, the hyperiid amphipod (*Themisto libellula*) dominated the diet of juvenile salmon and other nekton species following their demographic explosion in the western and eastern Bering Sea (Volkov 2012a, c, 2013; Pinchuk et al. 2013).

In the California Current System, salmon survival has been linked to changes in wind direction and intensi-

ty through their effects on upwelling, nutrient availability, and phytoplankton and zooplankton production (Wells et al. 2012), and on zooplankton community composition and nutritional quality (Bi et al. 2011; Keister et al. 2011; Peterson et al. 2014). In addition to winds, the hydrology of marine ecosystems may be affected by winter precipitation 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, and result in poor feeding and growth conditions for juvenile salmon (Ferriss et al. 2014; McKinnell et al. 2014).

Trophic Linkages, Growth Rates, and Predation Rates of Juvenile Salmon

Bioenergetic 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 because 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. 2009a; but see Daly and Brodeur 2015). As diet is 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 2012a, c, 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 long-term research may improve understanding of how changes in diet affect the survival of salmon.

Better measurements are needed to improve the usefulness of bioenergetics models for Pacific salmon (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 fresh water, 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 bioenergetic 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 for freshwater environments. Consequently, further effort is needed to parameterize these models for juvenile salmon in the marine environment.

Ecological Interactions of Juvenile Salmon

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 feed 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). 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 western Bering Sea, juvenile salmon growth was not negatively affected by increased biomass. Instead, size and growth of juvenile salmon in these waters were generally higher in years of high salmon biomass and synchronized between pink and chum salmon (Shuntov and Temnykh 2011a; Zavolokin 2013). Hence, the impact of competitive interactions for juvenile salmon growth may vary among ocean basins, depending on prey availability.

Predation by Pacific salmon on other salmon species has rarely been documented, but it occasionally occurs 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 populations (Krkošek et al. 2011a). This hypothesis, however, is not supported by empirical data (Sturdevant et al. 2013). Simulation models suggest that the differential impacts of sea lice (*Lepeophtheirus salmonis*) infection on juvenile pink and chum salmon may be mediated by the preference of juvenile coho salmon for juvenile pink salmon (Peacock et al. 2013). As prey become parasitized, they may be easier for predators to identify and/or catch. Predation on juvenile pink salmon by juvenile coho salmon may also affect the dynamics of the sea lice population, increasing adult and pre-adult louse abundance on coho salmon by trophic transmission (Connors et al. 2008, 2010).

Survival Rate and Survival Mechanisms 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 cost-effectively estimate mortality rates of juvenile salmon along their migration corridor, provided that fish are sufficiently large to carry the burden of these tags without affecting their behavior (Anglea et al. 2004), and that migration corridors are narrow enough to allow for adequate tag detection. However, most applications to date have been performed on the large smolts of a cohort, which may not be representative of the population (Freshwater et al. 2016). 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 (Melnichuk 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 for sea water or to differences in foraging behaviour. In particular, hatchery fish may be more surface-oriented during their early marine life, and thus more vulnerable to both avian and fish predators than wild fish.

Predation is thought to be a main source of mortality for juvenile salmon. Fish predators have been documented on both sides of the North Pacific Ocean (Nagasawa 1998b; Duffy and Beauchamp 2008; Emmett and Krutzikowsky 2008; Sturdevant et al. 2009, 2012a, b; Miyakoshi et al. 2013). Bird predation (Nagasawa 1998b; Toge et al. 2011; Osterback et al. 2014; Hostetter et al. 2015; Tucker et al. 2016) and marine mammal predation on juvenile salmon (Thomas 2015) 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 in the dynamics of juvenile salmon (Krkošek et al. 2006, 2007, 2011b). Field studies suggest that juvenile growth may 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 from farmed salmon on the dynamics of wild salmon populations has been frequently 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). Infection experiments and field observations have indicated that the ectoparasitic flagellate *Ichthyobodo salmonis* causes high mortality in

juvenile chum salmon when they migrate into the coastal ocean because the heavy parasite infection disturbs the osmoregulation of juveniles (Urawa 1993, 1996, 2013).

It is generally thought 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., in winter) for longer periods of time (Beamish and Mahnken 2001). However, 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; Woodson et al. 2013; Zavolokin and Strezhneva 2013; Miller et al. 2014b), size-selective mortality has not always been apparent during either summer or winter in juvenile salmon (Welch et al. 2011; Trudel et al. 2012). Furthermore, a negative relationship between adult returns and juvenile salmon growth has also been observed (Miller et al. 2013), indicating that other factors may override the effects of large size and fast 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 Belief Network (Araujo et al. 2013; Malick et al. 2015a; Hertz et al. 2016a), and state-space models (Ye et al. 2015). It should be remembered though, that no matter how sophisticated the analysis, correlation does not mean causation (Peters 1991), and correlations often break down over time (Skud 1983; Walters and Collie 1988). Nevertheless, correlation analyses 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 Temnykh 2011a, b; Radchenko et al. 2013), the timing of prey availability (Malick et al. 2015b; Satterthwaite et al. 2015), prey quality (Peterson et al. 2014; Tucker et al. 2015b), and climate (Killduff et al. 2015; Hertz et al. 2016a). If correlations break down over time, it may simply indicate that other factors not initially considered may contribute to the dynamics of salmon populations, and thereby lead 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.

Population Size and Carrying Capacity of Juvenile Salmon

The number of salmon that can be sustained in the North Pacific Ocean has long been a component of NPAFC-related research. Estimation of this number requires knowledge of the abundance of juvenile salmon in the marine environment, their feeding rates, the availability and production of their

prey, and 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 large when their abundance is high and small when their abundance is low, which is contrary to expectations from density-dependent interactions when food is limiting (Shuntov and Temnykh 2011a; Zavolokin 2013). Bioenergetic model calculations indicate that juvenile salmon consume only a small proportion of the available zooplankton biomass, suggesting that salmon 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). The intensity of competitive interactions may also 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 salmon biomass (PICES 2005; Shuntov and Temnykh 2011a).

Winter Period

Winter Distribution of Salmon

Myers et al. (2016) reviewed winter salmon research on 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 the 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” (Myers et al. 2016). 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 the position of the 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 temperatures 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 FL) are distributed in the Subarctic Front Zone between 3°C and 8°C, while larger chum salmon shift to cooler water with a peak at 4.5°C (Naydenko et al. 2016). Urawa et al. (2016) summarized that the SST of pink and chum salmon winter habitats was almost 2°C higher in the Gulf of Alaska than in

the western subarctic water during the winters of 1996, 1998 and 2006, while the SST of the winter habitat in each area was stable across the three years. These observations suggest that salmon select similar temperature regimes each winter, despite variable SST in the western subarctic waters.

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), although one population of sockeye salmon remains 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 programmed (Tucker et al. 2012a, 2015a). Unlike in the open ocean, juvenile/immature salmon tend to be caught deeper in the water column during wintertime (Orsi and Wertheimer 1995; Trudel and Tucker 2013). 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; X. Minobe, minobe@mail.sci.hokudai.ac.jp, pers. comm.). They concluded that salmon would migrate farther north and west as a result 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). 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 our understanding of potential climate change effects (Myers et al. 2016).

Hydrological Characteristics, Primary Production, and Prey Resources in Winter Salmon Habitats

The biomass of zooplankton prey resources in the Pacific Ocean has been observed 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 western North 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 western North Pacific Ocean indicate that the feeding intensity of Pacific salmon is lower in winter than in summer and fall. Feeding intensity differs among species within the same location, and high feeding intensities are occasionally observed during winter. Thus the reduction in the feeding intensity that occurs during winter period may be because salmon require less food at lower temperatures to sustain metabolic function (Ueno et al. 1997; Nagasawa 2000) rather than to a reduction in food availability during this period (Naydenko and Kuznetsova 2011, 2013). Naydenko et al. (2016) have suggested that changes in feeding, growth, and

lipids during winter may be due to seasonal changes in physiological processes of salmon.

Comparison of winter and summer stomach contents of immature and maturing Chinook salmon in the eastern Bering Sea showed that the proportion of empty stomachs was higher in winter samples, suggesting a longer duration between prey capture in winter (Davis et al. 2009). The winter diet was characterized by a high diversity of squid with all age groups (ocean-1 to -4) consuming fish offal, presumably originating from fishery processors (Davis et al. 2009).

On the continental shelf off the west coast of Vancouver Island, stomach contents and stable isotope 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. 2016b). On the continental shelf, zooplankton biomass decreased 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 temperatures, these results suggest that food supply may be sufficient to maintain growth during winter.

Winter Survival of Salmon

Winter mortality is expected to be high and variable in juvenile salmon, and higher in smaller fish than in larger fish because 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 that salmon reside in the ocean, from smolts leaving fresh water 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 scarce. Other published estimates include mortality that occurred after the 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 after the first summer at sea, and thus covered two years of their marine life. Hence estimates of mortality rates specific to the winter period are generally lacking.

Evidence for the overwinter size-selective mortality hypothesis is also equivocal, with some results being consistent (e.g. Farley et al. 2011; Zavolokin and Strezhneva 2013) and other results 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 to survive winter (Zavolokin and Strezhneva 2013). 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 was extremely low, suggesting fish malnutrition during winter (Kaga et al. 2006). The lipid content of pink salmon caught in the Gulf of Alaska was significantly lower than in fish caught in the western North Pacific Ocean during winter (Nomura et al. 2000; Kaga et al. 2006). Survival after 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). This relationship, however, was not significant, indicating that further work is required to test the critical-size and critical-period hypothesis.

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 walleye pollock (Hunt et al. 2011; Heintz et al. 2013), which are prey of salmon. As a result, juvenile sockeye salmon would get smaller (Farley and Trudel 2009), accumulate less lipid, and potentially experience higher size-selective mortality.

Summary and Future Directions

Our understanding of early marine migration and survival of particular stocks has increased tremendously during the last five years, in large part due to the application of genetic stock identification and mass otolith marking methods, and to the miniaturization of acoustic and smart tags. Linkages between ocean physics (i.e., currents), lower trophic levels, salmon diet and growth, predation, and ultimately survival have been examined. However, much remains to be done to understand the causes of ocean mortality of juvenile salmon and the relative importance of these causes of mortality for driving recruitment variability.

Most anadromous salmon stay in the cool waters of the North Pacific from December to May, for almost a half of their ocean life period. 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 attain a certain critical size are expected to be eliminated from the population. In the last five years, some progress has been made toward testing this hypothesis. There is, however, 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 difficult to determine the primary 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.

Testing the critical-period and critical-size hypothesis will require an assessment of how winter mortality contributes to the overall recruitment of salmon and an understand-

ing of the factors affecting the variability associated with winter mortality. This will require estimates of winter mortality (as opposed to combined winter and spring mortality), 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, winter, and spring (e.g., Trudel et al. 2012).

The body size and lipid concentrations reached prior to winter are expected to affect winter survival through size-selective mortality processes. A better understanding of the conditions that affect marine growth and lipid dynamics in juvenile salmon from their ocean entry to the end of the first winter at sea is needed. For example, Klimov et al. (2013) examined seasonal changes in the lipid content of juvenile chum, pink, and sockeye salmon. The mean lipid content of juvenile chum salmon was 1.3–1.6% in the western coastal water of Kamchatka in July, peaked at 5.5% in the Okhotsk Sea in October, and then declined to 1.7% in the western subarctic water during winter. Pink salmon showed a similar seasonal lipid content change, while sockeye salmon showed few changes in the lipid content. Under an experimental condition with no feeding, the total lipid content of juvenile chum salmon decreased rapidly from 4.2% to 2.2% ten days after the start of experiment, and it was then maintained at a low level (1.8–2.0%) until their death by starvation (Ban et al. 1996). This kind of laboratory experiment may also help us to understand the salmon mortality process during winter.

It is important to consider that non size-selective mortality processes may also be operating during winter (Middleton 2011; Trudel et al. 2012) such as predation by salmon sharks (Nagasawa 1998a), 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. 2016), it is certainly worth identifying the factors that may contribute to this mortality.

Salmon prey resources encountered in different oceanic habitats (e.g., community composition of zooplankton, monthly dynamics of zooplankton biomass, caloric content of oceanic zooplankton species in different seasons) and salmon feeding intensity need to be investigated throughout the seasons.

The main objectives of future studies should be focused on the following areas:

- linkage between marine survival of salmon and changes in climate and in the ocean, such as primary production and prey resources in salmon ocean habitats;
- effect of natural environmental variability on stock-specific distribution and abundance of salmon;
- predicting the potential impacts of climate change on marine salmon habitats; and
- understanding causes of salmon ocean mortality.

CLIMATE CHANGE IMPACTS ON SALMONID PRODUCTION AND THE MARINE ECOSYSTEM

Climate change and its impact on salmon carrying capacity in the Bering Sea have been investigated through the Bering-Aleutian Salmon International Survey (BASIS) program initiated by NPAFC in 2001. Evidence has linked increased levels of atmospheric carbon dioxide 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); and it has been suggested 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). However, there are mixed opinions regarding the effects of climate change on Bering Sea ecosystems, with some studies indicating no direct effect on the ecosystem (e.g., Shuntov and Temnykh 2009), and others suggesting reduced ecosystem productivity with increasing sea surface temperatures (Coyle et al. 2008, 2011).

Climate-ocean and Biological Factors Related to Salmon and Ecologically Related Species

The extent and duration of winter and spring sea ice along the eastern Bering Sea shelf plays a key role in structuring the ecosystem. Interannual variability in spring sea ice extent over the shelf has recently given way to “stanzas” of warm and cold events (Overland 2011). These stanzas have had profound effects on the ecosystem by restructuring the types and abundances of zooplankton and fish communities, and fitness of fishes along the shelf (Stabeno et al. 2012a, b). For example, 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 (Stabeno et al. 2012b). During the cold period, the portion of large-sized zooplankton (euphausiids, hyperiids, copepods, and chaetognaths) significantly increased. These changes in zooplankton communities were reflected in Pacific salmon diets (Farley et al. 2007). During the warm period, 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. In the cold period after 2006, euphausiids, hyperiids, and pteropods became the dominant salmon prey items in their diet. Interestingly, cooling of the Bering Sea during 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 (Pinchuk et al. 2013; Volkov 2014). During 2008–2010, the importance of *T. libellula* in salmon diets subsequently increased with increasing biomass of this amphipod.

The stanzas of warm and cold years on the eastern Bering Sea shelf also had an effect on the relative abundance of

the nekton community. During warm years, juvenile salmon and age-0 walleye pollock were generally more abundant on the eastern Bering Sea shelf (Farley et al. 2009; Moss et al. 2009b); however, capelin and adult walleye pollock declined (Ianelli et al. 2011; Andrews et al. 2016). The variability in relative abundance of these species was linked to sea ice extent during spring and the impact of warm or cool ocean temperatures during spring and summer has on the ecosystem (Hunt et al. 2011). Stanzas of warm years reduced the amount of energy that juvenile and young-of-the-year fish received, thereby negatively impacting their fitness. Over-winter mortality was high for age-0 walleye pollock during those years leading to low recruitment success (Heintz et al. 2013).

Changes in the composition and trophic structure of the nekton community in the western Bering Sea and the role of Pacific salmon on the dynamics of energy flow related to their abundance have been assessed for the last several decades using the Ecopath ecosystem model (Zavolokin et al. 2014, 2016). A significant decrease in walleye pollock abundance between the 1980s and 2000s caused a two-fold reduction in the total food consumption by nekton species; increased consumption by salmon and squid in the 2000s compensated for only a small portion of the decreased consumption from reduced walleye pollock abundance. At present, salmon are the only abundant upper trophic level predators in the upper pelagic layer of the offshore waters in the western Bering Sea. In the simulation model, when salmon biomass was expanded 1.5 times relative to the 2000s estimate, the abundance of forage species was sufficient to maintain higher salmon consumption. The ability of Pacific salmon to access a variety of prey species at several trophic levels appears to give them the capacity to satisfy their food requirements even during periods of extremely high salmon biomass (Zavolokin et al. 2014, 2016).

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. A shift in water circulation occurred in 2007 with the cyclonic gyre becoming smaller and restricted by the Commander Basin (Zavolokin and Khen 2012; Khen et al. 2013; Khen and Zavolokin 2015). A longitudinal current from Near Strait northwards intensified, while a latitudinal current from the Aleutian Basin to the west became substantially weaker. The latitudinal current limited the flow of the dichothermal layer to the east, and as a result, a hydrodynamic front occurred near the border of the Russian Exclusive Economic Zone. The change in water circulation in the Bering Sea in 2007–2011 affected the intensity of feeding migrations of immature salmon to the western Bering Sea. The abundance of immature chum, sockeye, and Chinook salmon decreased, and their distribution changed. In 2012, the water circulation returned to a “normal” regime, with salmon abundance going back to its former state.

Influence of Climate-ocean Conditions on Biological Parameters of Salmon

The body size of most Russian chum salmon stocks, particularly Anadyr chum salmon, decreased significantly from 1960 to the 2000s (Zavolokin et al. 2011; Temnykh et al. 2012). As estimated from scale measurements, first-year growth increased, but third and fourth year growth decreased, like other chum salmon stocks in Russia, Japan and Korea (Ishida et al. 1993; Kaev 2003; Kaeriyama et al. 2007; Seo et al. 2009). Hence, some large-scale factors have influenced these stocks across vast areas of the North Pacific and its marginal seas. Negative correlations between some climatic indices (ocean surface temperature, ground air temperature, and heat content of the North Pacific Ocean) and scale increments of Anadyr chum salmon in the second, third, and fourth year growth zones suggest that warming of the North Pacific Ocean may have an adverse impact on chum salmon growth after the first year of life (Zavolokin et al. 2011; Temnykh et al. 2012). The authors suggested that the chum salmon growth reduction after the early marine period may have resulted from increasing abundance of Pacific salmon combined with warming ocean conditions.

The energetic status of juvenile Bristol Bay sockeye salmon during warm years was significantly lower than those captured during cold years, and low fat reserves prior to winter were believed to lead to higher overwinter mortality for juvenile sockeye salmon (Farley et al. 2011). Based on the results of integrated ecosystem research in the eastern Bering Sea, Farley et al. (2011, 2013) hypothesized that winter survival of Bristol Bay sockeye salmon would decrease as a result of continued warming conditions on the eastern Bering Sea shelf, as extended periods of warming are expected to decrease the availability of lipid-rich zooplankton and the recruitment of young-of-the-year walleye pollock (Hunt et al. 2011; Heintz et al. 2013), both of which are important prey items for juvenile salmon on the shelf. Recent warming of the southeastern Bering Sea was accompanied by increased returns of Bristol Bay sockeye salmon. Relative abundance and growth rates of juvenile Bristol Bay sockeye salmon were shown to be high during warm years (Farley and Trudel 2009; Yasumiishi et al. 2016). Yasumiishi et al. (2016) reported that the total length of juvenile sockeye salmon during the first ocean year increased with summer SST in the eastern Bering Sea, suggesting a possible mechanism for increased abundance of Bristol Bay sockeye salmon. They hypothesize that there is a trade-off between increased length and reduced energetic status of sockeye salmon in warming climate regimes, which may affect their survival.

A recent investigation into changing size trends for Canadian Pacific salmon over six decades (Jeffrey et al. 2016) found that declines in size at maturity of up to 3 kg in Chinook and 1 kg in coho salmon during the 1950s and 1960s were later reversed to match or exceed earlier siz-

es. Pink and chum salmon initially declined in body size with little change over the past two decades. There was relatively little change in the body size of sockeye salmon. Although abrupt climatic regime shifts do not appear to have had any consistent or substantial effect on salmon body size, continuous indicators of oceanic conditions (North Pacific Gyre Oscillation and Multivariate ENSO (El Niño – Southern Oscillation)) contribute to explaining size variation in all species except for chum salmon (Jeffrey et al. 2016).

Potential for Climate Change Impacts on Salmon Habitats

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 spawning 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), and BASIS surveys conducted in the Arctic that year documented relatively high abundance of juvenile pink and chum salmon in the Chukchi Sea (Moss et al. 2009c). Abundant juvenile salmon returned as adults to subsistence users in coastal communities of the Pacific Arctic region in relatively high numbers during 2008 (pink salmon) and 2009–10 (chum salmon; Carothers et al. 2013; T. Hepa, taqulik.hepa@north-slope.org, pers. comm.). These events (anomalously warm summer sea temperatures, historic summer sea ice minima, and highly abundant juvenile pink and chum salmon in the Chukchi Sea) surprised researchers due to the deviation from predicted anthropogenic effects on temperatures and sea ice loss from climate models (Overland 2011). While salmon caught in the Chukchi Sea are likely seasonal migrants from further south, natal populations of chum salmon have been documented ~1800 km east within Canada's Mackenzie River watershed (Irvine et al. 2009; Dunmall et al. 2013). Continued warming in marine, terrestrial, and riverine environments may enable additional salmon populations to become permanently established in the Arctic.

Although effects of climate change on Bering Sea habitats requires further clarification, recent anecdotal observations have pointed to biological changes in marine habitats, particularly in the Gulf of Alaska. For example, since 2013, sea temperatures have been anomalously warm and the manifestations of warming in the Gulf of Alaska have included the warm "Blob" (Bond et al. 2015) and strongest 2015–2016 El Niño in recent history (Becker 2016). Agencies and observers in the popular press have discussed recent shifts to late run timing for sockeye, coho, and chum salmon in the eastern Bering Sea and Gulf of Alaska (Brenner and Munro 2016), one of the lowest Fraser River sockeye returns ever (Hoekstra 2016), toxic algal blooms of *Pseudo-nitzschia* stretching from central California to the Alaska Peninsula resulting in fishery closures (NOS 2016), the

unusual mortality event of large whales in the western Gulf of Alaska (NOAA 2016), and population losses of gulls, puffins, and auklets in the Gulf of Alaska and northeast Bering Sea (Joling 2015). Northward shifts in the distribution of temperate and sub-tropical fish species have been observed in the collection of *Mola mola*, market squid, and a thresher shark (*Alopias* spp.) off the coast of Southeast Alaska during summer salmon surveys (J. Orsi, Joe.Orsi@noaa.gov, pers. comm.). These anecdotal observations highlight the strong need for research and monitoring of North Pacific marine ecosystems in order to register early signs of changes in biota and marine habitats based in changing climate-ocean conditions.

Summary and Future Directions

The Bering Sea has experienced large changes in the extent of sea ice, hydrology, and zooplankton community composition and quality during the last decade, especially in the eastern Bering Sea. These changes have been reflected in the diet and survival of juvenile salmon, as well as in their distribution. Although the limit to the carrying capacity of the Bering Sea is unknown, prey productivity, particularly in the western Bering Sea, appears to be sufficiently large to sustain an abundance of juvenile salmon. With 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. In addition, salmon distribution at the southern end of their present range in Asia and North America will likely be jeopardized by loss of cool water zones where salmon have historically been distributed.

The issue of climate change and its relationship with salmon and ocean ecosystems will continue to be a major concern for ocean salmon research, fisheries, and conservation. The impact of climate changes on salmon distribution and the role of salmon in the marine ecosystems will continue to be of increasing importance in the coming decade. Studies investigating the future of salmon in areas particularly affected by climate change may mean a change in the dominant species composition and could affect the location and timing of marine salmon fisheries. Summer surface waters in the northeastern Bering Sea will continue to warm and be a source of heat advected to the Pacific Arctic Region, providing new marine habitat for juvenile salmon. With changing marine environments, modifications to release timing and the size of juvenile fish at release will likely be required to optimize hatchery production.

Developing models like 20-year climate forecasts for salmonid marine ecology, namely integrated ecosystem modeling—IPCC Scenarios, physical oceanography, nutrient-phytoplankton-zooplankton, fish bioenergetics, distribution at several spatial scales—will help managers make informed decisions in allocating scarce resources to hatchery production, fisheries management, and ocean salmon surveys.

BIOLOGICAL MONITORING OF KEY SALMONID POPULATIONS

To assess 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 use by Pacific Rim salmonid populations at varying levels of abundance is increasingly important. This is accomplished, in part, by monitoring the status and important biological characteristics (e.g., fish size, age composition, survival) for key (important) salmonid populations. Time series information on catches, spawner escapements, and regional salmon production trends for hatchery and wild stocks are also important. Quantifying estimates enables researchers to better examine the effects of ocean salmon biomass and climate change on subsequent survival, size and age at return for key population groups. Maintaining and expanding long-time data series are crucial to understanding linkages between climate and Pacific salmon production.

To support research efforts in the NPAFC Science Plan (Anonymous 2010), the time series of Pacific Rim salmon and steelhead catches and hatchery enhancement statistics are now publicly available at www.npafc.org/new/science_statistics.html. In addition, biological monitoring programs, which generally include the identification of key populations and streams, have been documented by each member country: 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), and salmon escapement (i.e., the number of salmon that escape fisheries) monitoring activities were recently described (www.npafc.org/new/science_escapement.html). Gathering these data and making them available is an important step in understanding trends in salmon abundance and/or productivity.

Biological Status of Key Salmon Populations

The last major overview assessment of stock status was conducted in 2012 by NPAFC (Irvine et al. 2012a). The abundance of Pacific salmon in the North Pacific Ocean, as indexed by aggregate commercial catches, remains near all-time high levels. Since 2007, the largest catches on record exceeded one million metric tonnes, (2007, 2009, 2011, 2013, and 2015) usually in odd-numbered years (Fig. 1). Even-year catches are somewhat less than those of odd-years because even-numbered year returning pink salmon are less abundant than genetically distinct odd-year fish; nevertheless, since the 1990s even-year catches have typically exceeded 800 thousand tonnes. 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 greatly among regions.

Over the long term (1926–2010), odd-year pink salmon have become increasingly dominant over even-year returning fish, particularly in the southeastern 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), Sakhalin-Kuril region (Kaev 2012; Kaev and Irvine 2016), and the northwestern coast of the Okhotsk Sea, including the Amur River basin (Klovach et al. 2014, 2015). In contrast, there are relatively few pink salmon in Japan, which is near the southern extent of their distribution in the western North Pacific Ocean. Their adult returns have declined dramatically since 2011, which may be associated with increasing negative coastal SST anomalies in spring (Saito et al. 2016). In the Sakhalin-Kuril region, changing marine survival indices and adult returns were consistent with what one would expect if early marine conditions were responsible for discrepancies among stocks in terms of abundance and survival, while final fish sizes appeared to be chiefly the result of conditions later, when fish were further offshore (Kaev and Irvine 2016). This study demonstrates the importance of long-term monitoring of abundance data at the fry (smolt) and adult life-history stages, which enable the partitioning of survival patterns between freshwater and marine habitats.

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 gener-

ally catches have remained at high levels in recent years with some years of poor runs (Piston and Heintz 2012). In British Columbia and Puget Sound, near the southern portion of pink salmon distribution, odd-year runs are more abundant than even-year runs in the same watershed, and they show increasing trends as do populations farther 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 North Pacific Ocean increased following the late 1970s and amounted to 250–300 thousand metric tonnes annually in the 2000s (Nagasawa 2015). Anadyr River chum salmon increased in the 1930s–1940s, and again in the 1980s, showing 40- to 50-year fluctuations in abundance (Khokhlov 2012). During 2001–2010, chum salmon catches along both coasts of Kamchatka were three times the catches of the previous decade (Zavarina 2012). In Russia, a sharp increase in chum salmon catch occurred in the mid-2000s, and historically the highest catch was recorded in 2015 (Klovach et al. 2016). 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 Russian Far East, 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 region, relatively low in the Sea of Japan region, and highly variable in the Pacific Ocean region (Miyakoshi and Nagata 2012). Regional differences in return rates of chum salmon are also found in

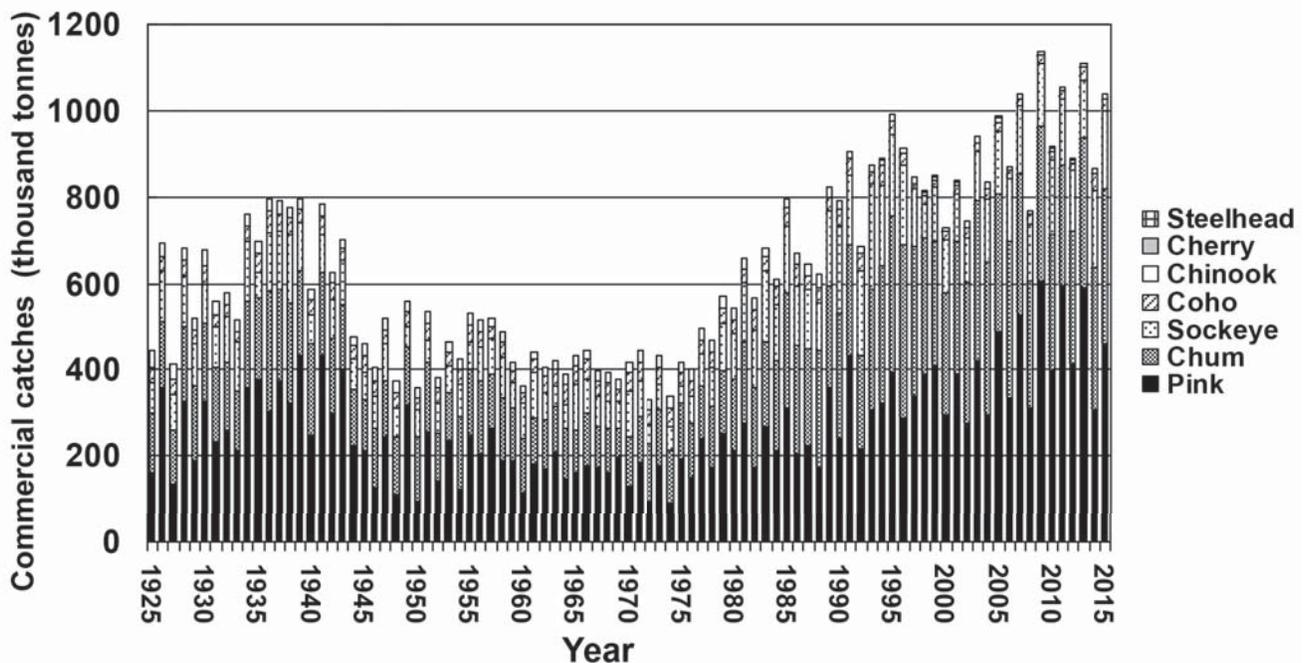


Fig. 1. Annual North Pacific commercial catches (thousand tonnes) of Pacific salmon and steelhead trout from 1925 to 2015. Data source: NPAFC (2016a).

northern Honshu (Saito and Nagasawa 2009). To clarify regional differences in biological characteristics of chum salmon in Japan, Saito et al. (2015) reviewed adult returns (coastal and river catches), peak timing of upriver migration (PUM), coastal sea surface temperature at the PUM, fork length of age-4 adults, age at maturity, egg diameter, and fecundity of age-4 females for seven regional populations monitored between 1994 and 2008. All biological characteristics showed clear differences among the regions or between some pairs of regions, and some characteristics appeared to change along latitudinal gradients. In particular, the values for PUM, fork length, age at maturity, and egg diameter in river stocks along the Sea of Japan coast exhibited an abrupt change at the boundary of the Tsugaru Strait. In Hokkaido, the PUM was earlier than before the 1960s, probably resulting from artificial alterations of the run timing in many stocks. Consequently, the advanced PUM resulted in fish experiencing higher sea temperatures during their spawning migration. Standardized egg diameters decreased over the study period, although a problem in the dataset might have influenced the apparent trend. Takahashi (2015) also reviewed trends in artificial enhancement activities (timing of spawning operations, effective population size, timing of fry releases, and body size of released fry) among seven regional populations of chum salmon. Monitoring programs such as these have proved indispensable to identify future directions to maintain Japanese chum salmon populations: (1) better understand the features of each regional population, (2) conserve the diversity of each population, and (3) identify optimal timing of fry releases and body sizes to maximize their survival in the changing ocean environments.

Commercial chum salmon catches increased after 1990 in 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, commercial catches of chum salmon have comprised primarily hatchery fish, and estimated catches of wild chum salmon have recently declined to levels similar to those of the 1970s (Piston and Heintz 2012). Population abundance of chum salmon originating in the Columbia River and southward 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 increased in west and east Kamchatka (Karpenko and Koval 2012). In 2013, Russian sockeye catches exceeded 50 thousand metric tonnes, which was almost a historic high (NPAFC 2016a). 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 Fra-

ser River, the total returns of sockeye salmon in 2009 were the lowest recorded since quantitative records began in the late 1940s (Beamish et al. 2012), but one of the strongest sockeye returns was recorded in 2010 (Irvine and Akenhead 2013; McKinnell et al. 2014).

Contrary to the upward trends in pink, chum, and sockeye salmon abundance, many populations of coho, Chinook, and cherry (masu) salmon have been declining. Although reasons for the high production of pink and chum salmon are not fully understood, these species appear to have benefited more than other species from favorable conditions: (1) changing environmental factors; (2) biological and life-history characteristics of pink and chum salmon allowing these species to benefit from changing conditions; and (3) human activities including stock enhancement and responsible fisheries management (Davis and Beamish 2012).

Annual Regional Production of Hatchery and Wild Salmon

Total North Pacific salmon hatchery releases have been fairly stable during the last 28 years at approximately 5 billion fish (Fig. 2). Asian hatchery production has generally been > 2.5 billion releases since 1981, with the exception of reduced chum salmon releases that was linked to the Great East Japan earthquake in 2011. Asian hatchery releases are predominately chum salmon.

North American hatchery production has exceeded 2 billion releases since 1988. Pink and chum salmon are the primary species released from North American hatcheries, mainly from Alaska. The relatively large numbers of enhanced Canadian sockeye salmon are produced in spawning channels, not hatcheries. Hatcheries in Washington, Oregon, California, and Idaho produce mostly Chinook salmon.

Provisional abundance of pink, chum, and sockeye salmon in major regions of the North Pacific from 1952 through 2015 were recently estimated (Irvine and Ruggerone 2016). Estimates included numbers and biomass of natural-origin and hatchery-origin salmon returns (i.e., catch plus escapement) by species, as well as total biomass that included immature salmon. Temporal abundance patterns generally followed commercial catch patterns. The proportion of hatchery-origin chum salmon abundance peaked in the late 1990s 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 (Irvine and Ruggerone 2016). These values are similar to ones provided in earlier estimates by Kaeriyama et al. (2012) who estimated hatcheries contributed 50% of the biomass of chum salmon, more than 10% for pink salmon, and less than 10% for sockeye salmon. Total abundance and biomass of adult pink, chum, and sockeye salmon peaked in 2009 (910 million fish; 1.7 million metric tonnes), while the total biomass including immature fish exceeded 5 million metric tonnes in 2009 and again in 2013 (Irvine and Ruggerone 2016).

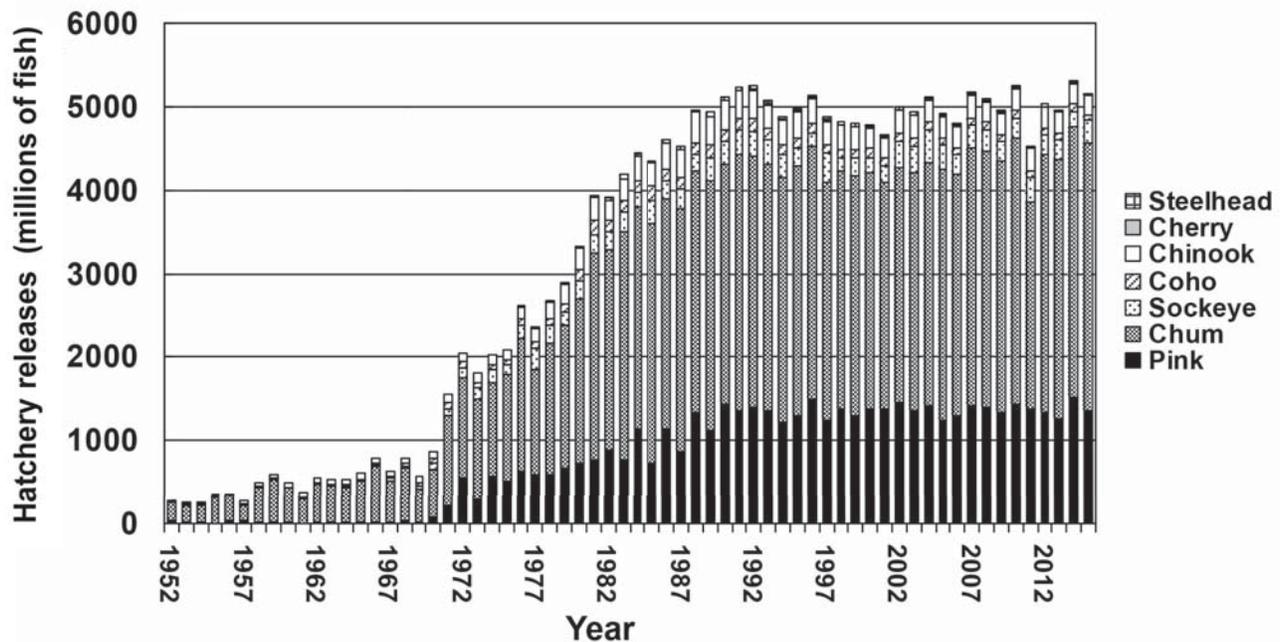


Fig. 2. Annual North Pacific hatchery releases (millions of fish) of Pacific salmon and steelhead trout from 1952 to 2015. Data source: NPAFC (2016b).

Summary and Future Directions

Monitoring key salmon populations is required for sustainable management of salmon stocks and to obtain the information needed to understand the status of salmonid populations as well as their ecosystems. Creation of easily accessible datasets containing important biological characteristics, such as genetics, distribution, catch and hatchery statistics, and salmon marking information is crucial to observe changes in the biological status of stocks, especially during periods of climate-change related variability in salmon habitats. During 2011–2016, summaries of monitoring programs were published by each country, major datasets were posted on the NPAFC publicly accessible website (www.npafc.org/new/science_statistics.html), and provisional estimates of hatchery and wild abundances were published. These need to be updated regularly.

To evaluate whether biological traits of key populations were reasonable ecosystem indicators, collaboration with scientists from outside NPAFC was encouraged. 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 (NPAFC-PICES Study Group 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 associated with the growth and survival of Pacific salmon. Several joint papers from this collaborative effort were presented at the 2015 NPAFC *International Symposium on Pacific Salmon and Steelhead Production in a Changing Climate: Past, Present, and Fu-*

ture, and they are published in NPAFC Bulletin 6. 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 and study are needed to more fully explore the utility of using salmon biological traits as ecosystem indicators.

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 to examine the underpinnings of ocean salmonid production, biological characteristics, and marine ecosystem conditions.

To increase the effectiveness of monitoring anadromous stocks and improve assessment of salmon and steelhead stock status, we recommend future studies in the following areas:

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

DEVELOPMENT AND APPLICATIONS OF STOCK IDENTIFICATION FOR SALMONID POPULATION MANAGEMENT

Genetic baselines for salmon are needed to monitor stock-specific ocean distributions and abundance as well as to produce more accurate estimates of the timing and abundance of adults 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.

Development of Genetic Baselines

Genetic baselines for salmon throughout the Pacific Rim have been developed for chum salmon using microsatellites (Beacham et al. 2009a) and single nucleotide polymorphisms (SNPs; Seeb et al. 2011) to assess population structure. Beacham et al. (2009a, b) reported that the most genetically diverse chum salmon were observed from Asia, particularly Japan, whereas chum salmon from the Skeena River and Queen Charlotte Islands in northern British Columbia and those from Washington State displayed the least genetic variation compared with chum salmon in other regions. Seeb et al. (2011) reported that variable linkage relationships between SNPs were associated with ancestral groupings and that outlier loci displayed alleles associated with latitude. The population structure of chum salmon has been investigated in Japan using allozyme (Sato and Urawa 2015), mitochondrial DNA (Tsukagoshi et al. 2016), and SNPs (Sato et al. 2014), and in Washington using SNPs (Small et al. 2015). Sato et al. (2014) reported the presence of eight regional groups of chum salmon in Japan, with six groups in Hokkaido and two groups in Honshu. Using 10 microsatellite loci, Chen et al. (2005) detected two groups of chum salmon in northwest China. Small et al. (2015) reported that similar to the genetic patterns detected with microsatellites and allozymes, genetic variation with SNPs followed a regional structure along geographic distance, with genetic diversity being highest in the north and decreasing southward, then increasing in and near the Columbia River. Within Puget Sound, Washington, genetic variation was structured further according to run timing (fall, summer, and winter) and shared ancestry.

Asian and North American chum salmon stocks mix frequently in offshore waters especially after the first year of ocean life. Pacific Rim genetic baselines have been used to estimate the stock composition of chum salmon caught in the Bering Sea and North Pacific during summer and fall (Kondzela et al. 2009, 2016a, b; Moriya et al. 2009; Sato et al. 2009a; Urawa et al. 2009), and in subarctic waters and the Gulf of Alaska during winter (Sato et al. 2006, 2007; Beacham et al. 2009b; McCraney et al. 2012; Urawa et al. 2016). These genetic analyses have contributed to estimating the stock-specific distribution and abundance of chum salmon in the ocean and to developing ocean migration models.

Geographically diverse genetic baselines have also been developed for sockeye salmon with both microsatellites (Habicht et al. 2007; Beacham et al. 2011a, 2014a, b) and SNPs (Doctor et al. 2010; Habicht et al. 2010) to assess population structure and stock identification. Habicht et al. (2007) reported that genetic differentiation among spawning populations in Bristol Bay, Alaska, was shallower than in other regions of comparable size around the Pacific Rim. Beacham et al. (2014a) reported that during July, larger juveniles from the same Fraser River stock were observed in more northerly locations compared with those in the Strait of Georgia in southern British Columbia. There was a relationship between timing of northward migration from the Strait of Georgia and juvenile body size with individuals from larger-sized populations or stocks migrating earlier than individuals from smaller-sized stocks, which remained resident for longer. Tucker et al. (2009) and Beacham et al. (2014b) reported that the primary migration route of Columbia River and Washington stocks was northward along the west coast of Vancouver Island, with a majority of the juveniles subsequently migrating through Queen Charlotte Sound and Dixon Entrance. Fraser River stocks migrated principally through the Strait of Georgia and Johnstone Strait. For British Columbia central coast and Owikeno Lake stocks, not all individuals migrated northward in the summer, as some individuals remained in local areas in the fall and winter after spring entry into the marine environment.

Beacham et al. (2014c) assessed population structure and run timing of sockeye salmon in the Skeena River drainage, British Columbia, and reported that genetic mixed-stock analysis, coupled with a test fishery in the lower river, can assist managers in regulating fisheries directed at Skeena River sockeye salmon. For SNPs, Doctor et al. (2010) reported that stream-spawning populations migrated onto the spawning grounds before river-spawning populations. However, beach-spawning populations were among the earliest to migrate but spawned as late as river-spawning populations.

The first application of DNA-based genetic markers to estimation of sockeye salmon stock composition in the Bering Sea was reported by Habicht et al. (2010). By using a set of 45 SNPs, they defined eight regional stocks of sockeye salmon in the baseline, with a single eastern Gulf of Alaska stock comprised of sockeye salmon from southeast Alaska, British Columbia, and Washington. A regional sockeye salmon baseline was reported for Kamchatka populations that included analysis of both microsatellite and SNP variation (Khrustaleva et al. 2014). McClelland et al. (2013) reported on variation at major histocompatibility (MHC) loci across the species range of sockeye salmon and concluded that there was no correlation in heterozygosity between MHC and microsatellite loci. They also suggested that fluctuating selection has resulted in divergence in MHC loci in contemporary populations.

Since 2011, significant advances have been made developing information on the regional genetic variation in

Chinook salmon by microsatellite analysis (Van Doornik et al. 2011; Moran et al. 2013; Teel et al. 2015). Teel et al. (2015) developed a coast-wide microsatellite baseline to investigate stock-specific distributions of juveniles occupying coastal habitats extending from coastal Oregon to northern Washington. Weitkamp et al. (2015) applied this baseline to evaluate stock-specific size and timing of ocean entry of juvenile Columbia River Chinook salmon and reported that yearlings from the lower Columbia and Willamette rivers migrated farther north than other yearlings, likely due to the early spring timing of their releases from hatcheries and subsequent out-migration from the Columbia River. Hess et al. (2011) compared microsatellites and SNPs for fine-scale identification of Chinook salmon originating within the Columbia River Basin, and they reported that between 100 and 200 informative SNPs are required to meet management standards for resolving stocks in fine-scale genetic stock identification applications. Beacham et al. (2012d) outlined a similar genetic analysis for Chinook salmon in British Columbia and reached similar conclusions. The species-wide SNP baselines including Russian and North American stocks were developed by Templin et al. (2011) and Larson et al. (2014). Larson et al. (2013) applied a SNP baseline and reported that stocks from Western Alaska and the Yukon River overwinter on the Alaska continental shelf and then travel to the middle and western Bering Sea during the summer and fall.

The genetic baseline of coho salmon in North America and Russia, based upon analysis of microsatellite variation, was developed by Beacham et al. (2011b), who reported that the least genetically diverse coho salmon were observed from Russia, the Porcupine River in the Yukon River drainage, and the middle Fraser and Thompson rivers in southern British Columbia. However, coho salmon originating from Vancouver Island in British Columbia; from Puget Sound, Hood Canal, and Juan de Fuca Strait in northern Washington; and from Oregon displayed the greatest genetic variation as compared with coho salmon in other regions. Beacham et al. (2011b) suggested that genetic variation likely reflected the origins of salmon radiating from refuges after the last glaciation period.

Applications of genetic stock identification to coho salmon were outlined by Beacham et al. (2012a), who reported that estimated stock compositions of five mixed-fishery samples collected in British Columbia and the San Juan Islands in Washington reflected the presence and timing of migration of local populations. Beacham et al. (2016) examined variation in juvenile size and migration timing in British Columbia. They reported that during June, larger individuals within a stock were observed in more northerly locations compared with those in more southern sampling regions. There was a relationship between timing of northward migration and juvenile body size, with larger individuals from stocks migrating earlier than individuals from the same stocks that remain resident longer. Stock composition was more diverse in the northern sampling re-

gions compared with those in southern British Columbia. There was only a modest change in stock composition between fall and winter sampling in both the Strait of Georgia and the west coast of Vancouver Island sampling regions, indicating that the extent of juvenile migration had largely been completed by the fall.

Population structure of steelhead trout in the Skeena River, British Columbia, was outlined by Beacham et al. (2012c). They reported that the results of analysis of lower Skeena River test fishery samples indicated that upper drainage populations generally migrated through the lower river earlier than lower river populations.

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 SNPs (Campbell et al. 2014). With panels using hundreds of SNPs, it is possible to utilize a parentage-based tagging method for stock identification, with an application to Columbia River steelhead trout outlined by Steele et al. (2013). They showed that results provided by coded-wire tags and parentage-based tagging were equivalent. Hinrichsen et al. (2016) reported that parentage-based tagging and mixed-stock analysis for Columbia River steelhead trout revealed important stock-specific differences in migration timing and relative abundance and provided critical information for management of mixed-stock fisheries. They outlined how parentage-based tagging can be used to estimate the proportion of hatchery-origin Chinook salmon in escapements in the Columbia River. They reported that in some cases, there were 340% more parentage-based tagging recoveries than with coded-wire tags, leading to greater precision in estimating the proportion of hatchery fish in the escapement.

Regional and species-wide allozyme baselines have been developed for odd-year (i.e., Shaklee et al. 1991; Varnavskaya and Beacham 1992; Hawkins et al. 2002; Kondzela et al. 2002) and even-year broodline 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; Torao and Yanagimoto 2015; Shpigalskaya et al. 2016), microsatellite markers (Beacham et al. 2012b), and SNPs (Seeb et al. 2014). All studies incorporating different classes of genetic markers showed that genetic differentiation between odd-year and even-year broodlines was greater than population differentiation within broodlines. Beacham et al. (2012b) and Seeb et al. (2014) reported that, in North American populations, differentiation among populations was greater in the odd-year broodline compared with the even-year broodline. In Asian populations, however, the genetic diversity of the even-year broodline was higher than that of the odd-year broodline (Golovanov et al. 2009). There have been few genetic stock identification studies on high-seas pink salmon. Shpigalskaya et al. (2013, 2016) applied a mitochondrial DNA baseline of Russian stocks to identify the origin of juvenile pink salmon in the Okhotsk Sea, and they

reported that the southern population, including Sakhalin stock, was dominant (58%), followed by the northern population (24%; west Kamchatka and north Okhotsk Sea stocks) and the Amur/Primorye population (17%).

Disk Tag and Data Storage Tag Recoveries

The NPAFC database of disk tag recoveries has been summarized (NPAFC Secretariat 2012) and will be publically available at the NPAFC web site. These data on known ocean distributions of juvenile, immature, and maturing salmon and steelhead are a valuable resource to examine changes in ocean distributions.

Data storage tag (DST) tagging experiments on high seas salmon and steelhead trout from the late 1990s to the late 2000s were conducted by the High Seas Salmon Research Program of the University of Washington. Various electronic tags recorded information such as water temperature, depth, and conductivity experienced by the salmon during its movements and migrations at sea. The High Seas Research Program provided the DST data files to NPAFC, and these files are available for download (NPAFC Secretariat 2014). Although some tags did not successfully complete their data mission, a total of 92 DSTs was recovered from 38 chum, 21 sockeye, 15 coho, 10 pink, 7 Chinook salmon and one steelhead trout.

Recent migration models have suggested that salmon use the Earth's magnetic forces to find their way back to their birthplace after migrating across thousands of miles of open ocean (Bracis and Anderson 2012; Putman et al. 2013, 2014). According to the geomagnetic imprinting hypothesis, the difference between the imprinted geomagnetic value and that at a salmon's ocean location can potentially guide the fish's homeward migration. Salmon navigate homeward from oceanic habitats by comparing properties of the Earth's magnetic field at their immediate location to those imprinted as juveniles entering the ocean. DST magnetic tags attached to two maturing chum salmon in the central Bering Sea were recovered at the Okhotsk Sea coast of Hokkaido, Japan (Azumaya et al. 2016). The recorded data (temperatures, depth, magnetic field strength, and tilt of the fish's body) showed that the estimated homing migration routes of chum salmon were consistent with the isoline of the magnetic intensity rather than the magnetic inclination. Thus, recent tagging experiments support the geomagnetic imprinting hypothesis and demonstrate that the magnetic intensity plays an important role for homeward migrating chum salmon in the open ocean.

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. The release database is avail-

able 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 salmon sampled from the Bering Sea, North Pacific Ocean, Okhotsk Sea, and Gulf of Alaska (e.g., Sato et al. 2009b; Urawa et al. 2009, 2012, 2016; Chistyakova and Bugaev 2013, 2016; Chistyakova et al. 2013; Shubin and Akinicheva 2016).

With increasing number of otolith-marked fish releases from hatcheries, the recovery of marked fish in surveys in the ocean has been increasing. Chistyakova and Bugaev (2013) reported 211 otolith-marked juvenile chum salmon caught in the Okhotsk Sea during October and early November 2012. Among them, 169 fish (79%) originated from hatcheries in Honshu and Hokkaido, including all regional stocks in Japan. Their data confirmed all regional chum salmon stocks in Japan migrate into the Okhotsk Sea in the first autumn of ocean life. The recovery rate of otolith-marked fish was different among regional stocks, the highest being from the Okhotsk Sea coast of Hokkaido, the Pacific side of Hokkaido, and the Japan Sea side of Honshu. The body size of otolith-marked fish showed an increasing trend with distance from the originating region to capture in the Okhotsk Sea. This suggests larger fish have more of a chance to survive when they migrate a long distance along the coast before they reach the Okhotsk Sea (Urawa 2015). Chistyakova and Bugaev (2016) summarized otolith mark recoveries of pink and chum salmon in the Okhotsk Sea in the fall of 2011–2014, which indicated that their offshore migration routes were affected by the Okhotsk Sea Gyre.

In the Bering Sea, 372 otolith-marked chum salmon were recaptured, of which 352 (94.6%) fish were released from 11 hatcheries in northern Japan (Urawa et al. 2012). The Japanese marked fish showed no hatchery-specific distribution, and most fish were distributed north of 55°N in the Bering Sea during July and early August. Distribution patterns were slightly different between young fish (ocean age-1) and older fish and between immature and maturing fish that may reflect their specific migration routes (Urawa et al. 2009). Comparisons of the recovery rate of chum salmon otolith-marks in the Bering Sea during 2006–2010 summer surveys with the return rate of adults to natal rivers in Japan from 2004–2006 brood years suggested that high-seas otolith-mark recovery data could be useful in forecasting chum salmon runs of specific populations (Urawa et al. 2012).

Summary and Future Directions

Stock and fish identification methods including genetic analysis, otolith marking, and tag recoveries continue to be developed and are integral to the formulation of models predicting the migration and abundance of salmon populations. It is important to continue research into the develop-

ment of genetic baselines encompassing the species range of Chinook, coho, chum, sockeye, pink salmon (odd- and even-year), and steelhead trout. High-quality marker development will continue to be important for accurate delineation of stocks. Such baselines are critical to inform our understanding of stock composition collected on the high seas and to improve migration models. Refinements in models will come from future studies that include development of the following: (1) higher throughput genotyping methods for stock composition analysis, potentially taking advantage of next generation DNA sequencing methodologies; (2) parental-based tagging methods for identifying hatchery stocks; and (3) additional statistical protocols for the analysis of fisheries stock composition data.

FORECASTING SALMONID PRODUCTION AND LINKED ECOSYSTEMS IN A CHANGING CLIMATE

In general, there are two main approaches used to model salmon populations. The first approach uses a statistical model (e.g., Sethi and Tanner 2013; Satterthwaite et al. 2015), which can include the effects of climate change. The second 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 the ocean distribution of salmon may be impacted in the future and are critical to evaluating stock production in a changing environment (Yoon et al. 2015).

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 the 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. Ye et al. (2015) used empirical dynamic modeling (EDM) as an alternative to imposed model equations. Using time series from nine stocks of sockeye salmon from the Fraser River system, they performed a real-data comparison of contemporary fisheries models with equivalent EDM formulations that explicitly used spawning stock and environmental

variables to forecast recruitment. Their EDM models produced more accurate and precise forecasts compared with contemporary fisheries models, and they showed significant improvements when environmental factors (river discharge, sea surface temperature, and the Pacific Decadal Oscillation) were included.

Forecasting pink salmon returns is 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 variable and affects year-class strength (Parker 1968; Percy 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. Long-term annual monitoring of juvenile pink and chum salmon abundance in the Okhotsk Sea conducted by Russian scientists each fall provides a useful tool for forecasting adult returns in the Russian Far East (Radchenko et al. 2013). Japan has also annually conducted a long-term monitoring of immature and maturing salmon in the central Bering Sea. Recent increases of otolith-marked salmon recoveries in the ocean provide a potential to forecast stock or hatchery-specific adult returns (Urawa et al. 2012; Chistyakova and Bugaev 2016).

In addition, subsequent ocean conditions may impact pink salmon productivity. Since 1997, the Southeast Alaska Coastal Monitoring project has collected biophysical data associated with seaward migrating juvenile salmon from May to August and has used these data along with larger basin-scale indices to forecast Southeast Alaska pink salmon returns using regression and ecosystem metric models (Orsi and Fergusson 2015). In nine of the past eleven years (2004–2014), predictions from linear regression models ranged 0–17% of actual harvests, an average absolute forecast deviation of 10% (Orsi et al. 2016). Of the ecosystem metrics considered, important variables for forecasting adult pink salmon returns are juvenile pink salmon CPUE, ocean entry timing, percentage of pink salmon in the catch, a predator index, and the North Pacific Index (NPI). The higher NPI may contribute to a broadening of the Alaska Coastal Current, presumably through relaxed coastal downwelling, thus enabling fish to be transported farther offshore along the productive continental shelf (Orsi et al. 2016). Among available methods to forecast salmon returns, this may be one of the most reliable models that includes parameters of juvenile mortality and climate impact.

Other forecasts that include ecosystem and ocean survey data have been produced for Yukon River Chinook salmon. For instance, the timing of the adult Chinook salmon migration from marine waters of the northern Bering Sea to the Yukon River can vary substantially from year to year. Because of the "mixed stock" nature of Yukon River Chinook salmon (US and Canada), run timing information is critical to the success of the management of the fishery (Mundy 1982).

Annual timing of adult Yukon River Chinook salmon exiting the marine environment and entering the Yukon River was related to modelled sea surface temperature, air temperature, and sea-ice cover within the north-eastern Bering Sea where the best linear model explained 59% of the annual variability in migratory timing (Mundy and Evenson 2011). The model suggests that changes in phenology of high-latitude Chinook salmon could occur in response to global warming. The 13-year time series of late summer integrated ecosystem surveys in the northern Bering Sea (BASIS) have also provided a wealth of information on juvenile Yukon River Chinook salmon ecology (Murphy et al. in press). Foremost, the surface trawl catch data, mixed layer depth adjustments, and genetic stock mixtures have been used to estimate juvenile abundance of Canadian-origin Yukon River Chinook salmon in the northern Bering Sea. This combination of information (survey data and genetic analyses) was found to be significantly correlated ($r = 0.87$, $p = 0.05$) with adult returns of Canadian-origin Yukon River Chinook salmon and offers a dramatic improvement in forecast ability for management of Yukon River Chinook salmon stocks.

CONCLUSIONS

The goal 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 abundance is of great importance to management and for anticipating future variations in production affected by a changing climate. In addition, precise pre-season forecasts increase the economic efficiency of the salmon industry, enable managers and resource stakeholders to predict harvest with more certainty, and help promote resource sustainability.

The marine survival of specific salmon populations will 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. Several models coupled with parameters of fish mortality and environmental factors are useful to forecast returns of specific salmon stocks. There are, however, still limitations on explaining and forecasting the annual variation in Pacific salmon production because many factors remain to be identified as causes of salmon mortality. The trends in production and catches of Pacific salmon around the North Pacific Ocean have a history of exhibiting unexpected changes associated with global regime shifts (Beamish 2012b). The reasons for historic high catches of some populations by improved marine survival requires explanation and may be used to improve management of salmon populations (Beamish 2012b). All salmon-producing countries will benefit from learning

to optimize early marine survival of salmon by designing cooperative research programs.

Global warming may decrease the carrying capacity and distribution area of Pacific salmon in the North Pacific Ocean and result in an expansion of their distribution to the Arctic Sea (Kaeriyama et al. 2009). Farley et al. (2011) hypothesized that winter survival of Bristol Bay sockeye salmon would decrease as a result of continued warming conditions on the eastern Bering Sea shelf, as extended periods of warming are expected to decrease the availability of lipid-rich prey items. However, recent warming of the southeastern Bering Sea was accompanied by increased growth and returns of Bristol Bay sockeye salmon. The response of salmon to climate-driven environmental changes is variable and will likely differ by species, stock of origin, life stage, geographical distribution, and seasonal timing. Future trends of particular salmon stocks remain uncertain under the various scenarios of climate change. Model developments using statistical models as well as ecosystem models coupled with physical models will improve estimates on the impact of climate change on salmonid populations. For sustainable fisheries management, it is more important than ever to promote new cooperative and innovative international research to identify the ecological mechanisms regulating the distribution and abundance of anadromous populations and to anticipate climate impacts on salmon in North Pacific marine ecosystems.

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