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Food for Thought

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The need to see a bigger picture to understand the ups and downs of Pacific salmon abundances

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There are more Pacific salmon in the ocean recently than in recorded history. Increases are believed to be related to shifts in climate but specific, biologically based mechanisms linking climate to increases are not known. At the same time, Pacific salmon abundances in Japan and on Canada's west coast are at historic low levels with attempts to stop the decline unsuccessful. Most juvenile salmon that enter the ocean die, resulting in large abundance increases and decreases from small changes in the already very low ocean survival. Because of this sensitivity to changes in ocean ecosystems and because of the recent basin-scale fluctuations in trends in abundance, I propose that it is time to see a bigger picture and improve the understanding of the biological mechanisms that most influence ocean survival. I leave it to readers to decide if my example of Pacific salmon is part of a more general need in fisheries science to better understand the biological mechanisms linking survival to climate.

Keywords: climate, mechanisms, ocean survival, Pacific salmon, stewardship.

Introduction

I think there is some agreement that ecosystems supporting fishes are changing in a way that past population dynamics are a less reliable measure of future dynamics. I use the example of Pacific salmon to suggest that our changing climate requires that we better understand the biological mechanisms linking climate and survival of commercially important fishes.

The dynamics of Pacific salmon (*Oncorhynchus* spp.) populations in the past few decades is remarkable and almost hard to believe. Many people on the west coast of North America are shocked when they learn that commercial catches by all countries are at historic high abundances (Figure 1). There are more Pacific salmon in the ocean recently than in recorded history (Ruggerone and Irvine, 2018; Beamish, 2018a). People living in British Columbia, on Canada's Pacific Coast, think that stories of high abundances of salmon are "fake news" because commercial catches and abundances in British Columbia in recent years are at historic low levels (Figure 2). What should be alarming is that we do not understand the reasons for these recent high and low abundances. In a future of quickly changing ecosystems, it is time to understand the mechanisms that regulate production of populations we need to steward.

This is an opinion paper and not a review of the literature on mechanisms affecting the ocean survival of Pacific salmon. This also is not a commentary on current Pacific salmon research. It is my opinion, based on my west coast of Canada experience that the recent extreme changes in Pacific salmon abundances that I report here are clear examples of the urgent need for more information about the biological mechanisms that most affect their ocean survival. A mechanism is a process that allows something to happen. There will be many examples of mechanisms in the life history of Pacific salmon, but it is the mechanism or mechanisms that mostly affect ocean survival in the early marine period that I propose to be most relevant at this time of changing ocean ecosystems. I review the life histories of Pacific salmon and the importance of understanding mechanisms that regulate their production in the ocean. Readers can find some consideration of mechanisms related to Pacific salmon production in books and publications by Groot and Margolis (1991); Pearcy (1992); Shuntov and Temnykh (2011); Quinn (2018) and Beamish (2018a). I provide a summary of the recent state of Pacific salmon with a focus on alarming developments on the west coast of Canada. I propose and discuss a mechanism that could be a major regulator of production of Pacific salmon in the ocean. I conclude by proposing new research and suggesting that understanding mechanisms may have a broader relevance to understanding recruitment and stewardship of other exploited fishes.

Pacific salmon

There are 12 species in the genus *Oncorhynchus* and six that have a common name ending in the word salmon. One of the six, *O. masou* or cherry salmon is mostly found only from Japan to southeastern Kamchatka. It is not abundant with 99% of the commercial catch coming from Japan and averaging 1186 t annually over the past decade (2010–2019). Steelhead are the anadromous form of rainbow trout (*O. mykiss*) and not one of the six species with salmon as a common name. However, they are managed along with Pacific salmon and are a sought after species in the recreational fishery in North America. Steelhead are scarce in the commercial fishery averaging only 147 t annually over the past 10 years.

The five major salmon species are pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), coho (*O. kisutch*) and Chinook (*O. tshawytscha*). The most abundant species in the commercial catch is pink salmon, followed by the larger body size chum salmon. The smaller size and more abundant pink

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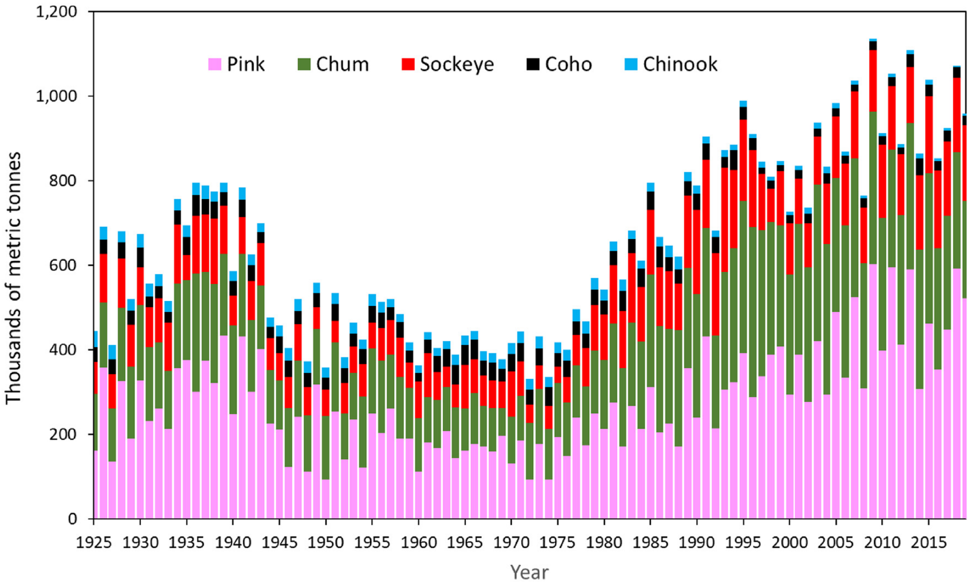

Figure 1. Total catch of pink, chum, sockeye, coho and Chinook salmon by all countries for all countries in thousands of metric tonnes from 1925 to 2019. Data Source: North Pacific Anadromous Fish Commission (NPAFC). 2020. NPAFC Pacific salmonid catch statistics (updated 21 July 2020). North Pacific Anadromous Fish Commission, Vancouver. Accessed Month, Year.. Available: https://npafc.org.

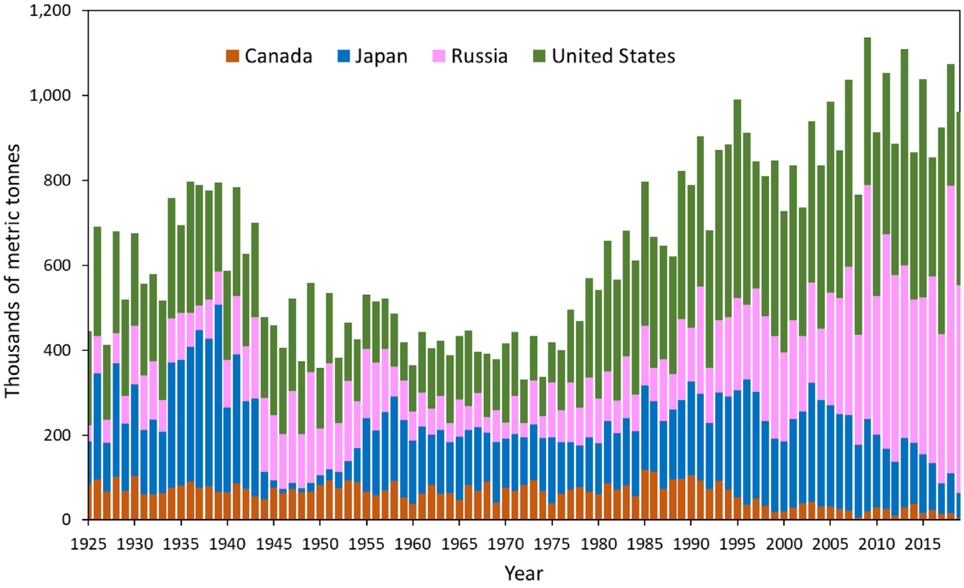

Figure 2. Total catch of Pacific salmon by Canada, Japan, Russia and United States in thousands of metric tonnes from 1925 to 2019. Data Source: North Pacific Anadromous Fish Commission (NPAFC). 2020. NPAFC Pacific salmonid catch statistics (updated 21 July 2020). North Pacific Anadromous Fish Commission, Vancouver. Accessed Month, Year. Available: https://npafc.org.

salmon produce the largest weight of catch, but occasionally, weight of the commercial catch of chum salmon will exceed pink salmon catch. Pink and chum salmon are less popular in North America, but valued commercially. Chum salmon are the most important species commercially and socially in Japan and pink and chum salmon are the most important in Russia. The recreational fishery in North America values Chinook salmon because of their large size and coho salmon because they are tasty and fun to catch. Sockeye salmon are esteemed because of their red flesh and taste.

All of these Pacific salmon die after spawning, with a normal life span ranging from two years for pink salmon to eight years for Chinook salmon. Pink and chum salmon spend only a short time in fresh water after emerging from gravel before they migrate to the ocean (Groot and Margolis, 1991; Quinn, 2018). Chinook, coho and sockeye salmon spend months to several years in fresh water depending on the specific life history. The life histories of Pacific salmon are reported in detail in a number of publications including Groot and Margolis (1991); Pearcy (1992); Quinn (2018); Beamish (2018a). Much of the management and research effort in North America is focussed on the freshwater life cycle of these three species.

All five species are produced in hatcheries by all countries. Hatchery releases from all countries have been almost constant since 1988 at about five billion fish, which are mostly pink and chum salmon (NPAFC, 2021a). The numbers of pink, chum, and sockeye from hatcheries in the total maturing ocean population in the recent years are estimated to total 28%, with 60% chum salmon, 15% pink salmon and 4% sockeye (Ruggerone and Irvine, 2018). Hatchery production of coho and Chinook salmon to catches off the west coast of North America varies among regions and among years with contributions being substantial in the southern areas of their distribution.

The issue

I like to tell audiences that we know a lot about Pacific salmon, but what we need to know most, we mostly do not know (Beamish, 2018b). This mostly means that we do not understand the natural processes that regulate salmon abundances. The consequences of natural processes fill the literature, but explanations of mechanisms responsible for abundance trends are rare. What are the causes of mortalities and how do they occur? There are arguments that understanding how ocean survival is regulated would be nice to know, but management historically has been possible without this information. My message is that the changing variability of climate means that past population dynamics are no longer a reliable indicator of future abundances. For example, there is now ample evidence of climate and ocean related trends in Pacific salmon abundances (Beamish, 2018a) which were not found by Ricker in 1958 (Ricker, 1958). There can be a number of factors influencing abundance trends but ultimately it is the mechanisms we need to discover. An understanding of these mechanisms will provide a professional stewardship that interprets how changing ecosystems will affect Pacific salmon production trends. A reliable forecast should be a goal of any science (Beamish and Rothschild, 2009). A forecast should provide more information than an expected return in the next year and should provide insight into future trends. Fisheries science needs to be steps ahead of impacts of climate related ecosystem changes and be able to use an understanding of the biological consequences of ocean and freshwater ecosystem changes to help forecast abundance trends. Providing reliable abundance forecasts can also be a test of a proposed mechanism.

The example of Pacific salmon

Pacific salmon are the dominant group of fishes in the daytime in the surface waters of about 15 000 000 km^2 of the subarctic Pacific (Shuntov *et al.*, 2010). They are important economically, culturally and an iconic indicator of health of the environment. Recent record high total catches started in 2007 with catches exceeding 1 000 000 t in six years from 2007 to 2019 and the record 1 137 689 t occurring in 2009 (Figure 1). The largest catch by any country was 676 200 t by Russia in 2018. Pink salmon and chum salmon make up 79.2% of the weight of the average total catch in the past 10 years (Figure 1). Sockeye salmon are the third largest catch, representing 17.3% of the recent 10-year average catch. Chinook and coho salmon combine to represent the remaining 3.4% of the past 10-year average catch. It is catches of pink, chum, and sockeye that are increasing in recent years (Figure 1).

Trends are mixed when catches are looked at by country (Figure 2). In the 1970s, average % of total catch by all countries in decreasing order (excluding Republic of South Korea that has minimal catches) was: USA 34.4%, Japan 28.6%, Russia 20.7%, and Canada 16.3%. In the past 10 years from 2010 to 2019, the percents are: Russia 44.9%, United States 40.3%, Japan 12.7% and Canada, 2.1%. The total catch has more than doubled between the 1970s and 2010s (Figure 2) with Russia increasing their total catch by 4.9 times. United States (mostly in Alaska) increased their total catch 2.6 times. As catches increased in Russia and USA, there were declining trends in Japan and British Columbia. Canadian catch in the 2010s decreased to 29.6% of its 1970s average. From 2019 to 2021, the preliminary Canadian catch estimates averaged only 6.1% of the 1970s average. There was a dramatic increase and then a dramatic decrease in Japanese catch that resulted in virtually no change in catch between the 1970s and the past 10 years. Salmon catches in Japan are almost all chum salmon that are virtually all produced in hatcheries (Urawa *et al.*, 2018). In the 1990s, average annual catch was 219 208 t representing 34.2% of total catch by all countries. Beginning in 2008, Japanese catches steadily declined to a low of 59 460 t in 2019 or only 27.1% of the average in the 1990s.

These increases and decreases in production and catch by all countries can be linked in a very general way to climate and ocean changes (Beamish and Bouillon, 1993; Mantua *et al.*, 1997; Beauchamp *et al.*, 2007; Kaeriyama *et al.*, 2012). Chinook salmon that are an iconic indicator of the general attempt to manage Pacific salmon are declining in abundance throughout most of their distribution on the west coast of North America (Riddell *et al.*, 2018; Welch *et al.*, 2021). Crozier *et al.* (2021) concluded that a dramatic increase in juvenile ocean survival was required to compensate for climate and ocean changes that were mostly responsible for the declines. However, these authors also concluded that there is no understanding of the mechanisms regulating Chinook salmon ocean survival. Wells *et al.* (2020) reported, in an excellent study, that there are a number of mechanisms in the ocean that affect the survival of Chinook salmon and they provided an example of predation. There is no doubt that predation can be a source of ocean mortality, but a basin-wide decrease in ocean survival of Chinook salmon is unlikely a result of a simultaneous basin-wide increase in abundance and diversity of predators. There needs to be a more basin-wide mechanism. It is early in the marine life of Chinook salmon that a reduced growth rate has been linked to declining ocean survival of Chinook salmon populations in Alaska (Graham *et al.*, 2019) and in Puget Sound (Duffy and Beauchamp, 2011). Thus, a mechanism fundamental to ocean survival appears related to growth in the early marine period. The need to discover the mechanisms becomes apparent in the predictions of a continued warming of the surface waters of the North Pacific Ocean with probability of frequent extreme states as realized in 2014 (DiLorenzo and Mantua, 2016).

There may be urgency

An unprecedented warming in the eastern North Pacific Ocean occurred from 2014 to 2016 (Bond *et al.*, 2015; DiLorenzo and Mantua, 2016) followed by a brief cooling and a return to warming late in 2018 that extended into the fall of 2019 (Cornwall, 2019). The persistent warming in the Gulf of Alaska occurred to at least 250 m (Suryan *et al.*, 2021). The urgency is that most Pacific salmon from British Columbia rear in or near to the Gulf of Alaska. One apparent consequence of the warming was a complete collapse of the Pacific

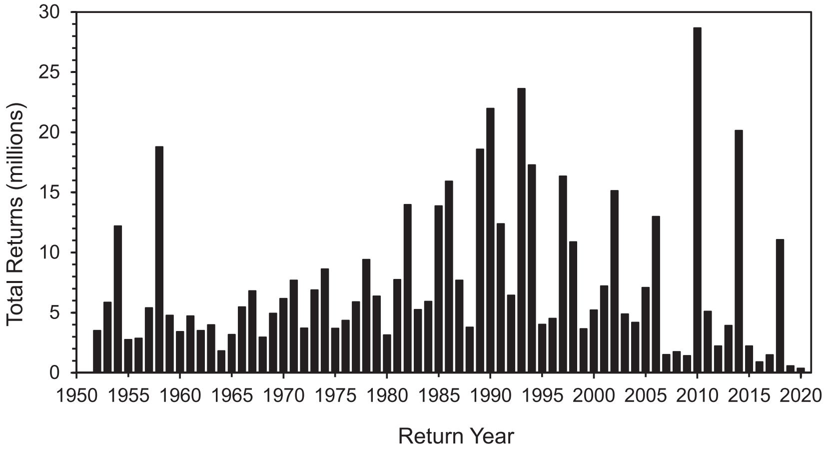

Figure 3. Total return (catch plus spawning adults) of sockeye salmon to the Fraser River in millions of fish 1952–2020. Fraser River sockeye salmon predominately live for 4 years and produce a series of distinct 4-year cycles (Ricker, 1997). One of these years is a persistent large dominant brood year as in 2018, 2014, 2010, 2006, 2002, 1998, 1994, 1990 etc. There is a second year with a smaller, subdominant abundance and two years of low abundance. There have been changes in the dominance within the pattern, but the 4-year pattern persists. There have been attempts to explain the biological basis for the pattern, but there is no consensus (Ricker, 1997). The total return in 2009 alarmed the Canadian government resulting in judicial enquiry. The returns in 2016, 2019, and 2020 were lower than 2009, with 2020 the lowest in the 65-year history.

cod (*Gadus microcephalus*) fishery in the Gulf of Alaska that had a commercial catch average of about 80 000 t from 2010 to 2015 (Barbeaux et al. 2020; Laurel *et al.*, 2021). The sudden collapse of Pacific cod population is shocking commercially and should be equally shocking scientifically. The cod collapse along with the warming is a warning that future fisheries management cannot rely on assumptions that past ocean survival relationships are a model of future relationships and that abundances can change quickly. There needs to be an ability to use mechanistic understandings of ocean survival to understand the impacts of a future of changing ocean ecosystems on Pacific salmon.

The surprise of 2020

The commercial catch of Pacific salmon by all countries in 2020 totaled 606 682 t (NPAFC, 2021b). This is the lowest commercial catch since 1982 and a shocking decrease without explanation. Even more alarming is that about one half of this total catch came from just two fishing regions, Bristol Bay (91 100 t) and the coast of Kamchatka (194 400 t). Russian catch was about 293 000 t, down from 676 200 t in 2018 and 499 207 t in 2019. An explanation for this alarming reduction is now a focus for researchers in Russia and hopefully may be a focus in the other Pacific salmon producing countries. I have little doubt that a common mechanism is responsible for the synchronous and precipitous decline in ocean survival that resulted in the surprise of 2020.

Preliminary Pacific salmon catches in 2021

The final Pacific salmon catches for 2021 are not available at the time of submitting this paper. However, the preliminary estimates are reliable. The poor commercial catches in Japan and Canada continued. Russian catches appear to be back to previous high levels with about 540 000 t of all species. Catches in Alaska improved with an historic high return of sockeye salmon. This sudden return to large catches in Russia and Alaska is another example of the need to improve the understanding of processes affecting ocean survival.

The example in British Columbia

I am using two examples from the recent history of Pacific salmon management in British Columbia to illustrate the need for an improved understanding of mechanisms. In the first example, researchers told the Canadian Government Treasury Board in the mid-1970s that the commercial catch of Pacific salmon in British Columbia could double from about 70 000 t to about 140 000 t by 2005 if more juveniles could be added to the ocean off the coast of British Columbia (DFO, 1979). This interpretation was based on an assumption that there was "unused" ocean capacity to produce salmon as evidenced by the much larger historic abundances (Larkin, 1974). The implied hypotheses were that adding more juveniles would produce more adult returns and that ocean and climate effects on the population dynamics were random (Ricker, 1958), the latter being a seldom recognized hypothesis. The assumptions in both scientifically defensible hypotheses were that the ocean capacity that produced much larger abundances in the past was still available, meaning that total adult returns were affected by the number of juveniles produced in fresh water (Ricker, 1954, 1958). According to the proposal to government, increases in juvenile production could occur by restricting fishing to allow more spawning and thus more juveniles or by building hatcheries. Beginning in 1977 more hatcheries were built with the establishment of the Salmon Enhancement Program because few people liked the idea of reducing fishing. Fast forward to 2005, the total commercial catch was 31 811 t or only 54.6% of the average before the hatchery program officially started. Alarmingly, in 2019 the total commercial catch was 3423 t or about 5% of the catch at the beginning of the enhancement program.

The second example of sockeye salmon returns to the Fraser River in British Columbia is equally alarming. Sockeye salmon produced in the Fraser River in British Columbia support what some consider the most important fishery on Canada's west coast. Certainly, it is Canada's most important Pacific salmon fishery. The commercial fishery goes back more than 100 years and the importance to First Nations goes back thousands of years. The complexity of management and stewardship of the fishery, that involved fisheries in Canada and United States, required international cooperation resulting in the creation of the International Pacific Salmon Commission between Canada and the USA that began operations in 1937. The population dynamics are dominated by persistent patterns of relatively high and low abundances in each successive group of four years (Ricker, 1997) as shown in Figure 3. In general, over the past 50 years there was an increasing trend in abundance that turned into a declining trend in the early 1990s (Figure 3). As the decline continued, there was an historic low return in 2009 that was sufficiently alarming to cause the Prime Minister of Canada to establish a commission of enquiry (Cohen, 2012). The judge listened to just about anyone with an explanation for the poor return and declining trend. The three volume report was published in October 2012 with 75 recommendations. There was no explanation for the declining trend or as the judge wrote, "there was no smoking gun." The judge reported that no one who testified before him presented a convincing explanation for the declining trend which is another way of saying that there was no understanding of the mechanism. The poor return in 2009 was identified as a consequence of extremely poor ocean and climate conditions when the juvenile sockeye salmon went to sea in 2007 (Cohen, 2012; Beamish *et al.*, 2012a; Thomson *et al.*, 2012). However, there was no comment on why more fish died when the ocean and climate conditions were so unsuitable. What was the exact reason the survival was so poor? Why were more fish more susceptible to the usual causes of death? The alarming low total return in 2009 was 900 000 fish (Figure 3). In 2019, the total return was 490 000 fish and the total return of 290 000 fish in 2020 was even worse (Figure 3). Preliminary estimates for 2021 indicate an improved return of several million sockeye salmon.

Summary

Pacific salmon catches are in a period of extremes. Up to 2020 there were historic high abundances in Russia and in parts of Alaska with historic low abundances in British Columbia and collapsing hatchery catch in Japan. Then there was the collapse of the commercial catch by all countries in 2020. This was followed by a return to larger catches in 2021 in Russia and Alaska. All extremes are reasons for a scientific community to move beyond correlating changes with events and work in harmony to identify the principal mechanisms that regulate abundances.

A clue to a mechanism

Coho salmon spend at least one winter in fresh water after they hatch and emerge from the gravel in the early spring (Sandercock, 1991; Pearcy, 1992). The number of winters in fresh water depends on condition of individual fish which is related to growth. Coho salmon at the southern limits of their range mostly spend one winter in fresh water after emerging from the gravel and at higher latitudes commonly take two winters or more to change their physiology to be able to adapt to a life in salt water (smoltify), presumably because of the shorter growing period farther north. The physiological decision to smoltify in preparation to be able to osmoregulate in the ocean is affected by a number of influences including photoperiod and growth rate (Mahnken *et al.*, 1982). Photoperiod is related to day length with the longest day at the summer solstice known to be closely associated with the onset of smoltification if growth rate was rapid and has exceeded a threshold (Brauer, 1982). Size is important as there appears to be a minimal size to smoltify (Mahnken *et al.*, 1982; Dickhoff *et al.*, 1997), but it is growth rate that is the determining factor. Growth-related hormones are known to be affected by photoperiod and nutritional status and would be cued to begin to direct physiological changes needed to become a smolt (Beckman *et al.*, 1998). In laboratory studies using a natural photoperiod, smolting can occur 4–5 months after first feeding (Clarke and Shelbourn, 1982, 1986). Thus, although mechanisms regulating the onset of smoltification need a better understanding, it appears that growth rate that exceeds a threshold at a peak in day length, cues the onset of a major change in the physiology, behaviour and morphology in preparation for the individual to migrate into salt water. Thus, coho salmon juveniles delay smoltifying to another year if growth rate does not exceed a threshold. This shows that there is an external cue at a critical time in development that stimulates a metabolic decision to prepare an individual for future survival in the ocean.

Connie Mahnken and I proposed that coho salmon in the early marine period follow a similar process that is mechanistically linked to their ocean survival (Beamish and Mahnken, 2001). We called the concept, the critical size, critical period hypothesis and the most recent versions are in Neville and Beamish (2018) and Beamish *et al.* (2018). According to the hypothesis, regulation of abundance in the ocean occurs in two stages. The first stage is predation-based starting immediately after fish enter the ocean and it is related to fish size, density of juveniles and the abundance and type of predators. The second mortality is a consequence of rate of growth in the early marine period and ability of a fish to survive the first ocean winter. Fish with reduced stored energy would be less able to survive in the winter when prey were less available. Predation may still be a cause of death, but ocean survival is related to internal physiology that becomes affected as food resources become limiting in the fall and winter of the first ocean year.

A possible mechanism and coastal ocean survival

Evidence is accumulating that adult abundance of pink, chum, sockeye, coho, and Chinook salmon is related to survival in the first months in the ocean (Karpenko, 1998; Wertheimer and Thrower, 2007; Pyper *et al.*, 2005; Graham *et al.*, 2019; Farley *et al.*, 2020; Duffy and Beauchamp, 2011; Beamish and Mahnken, 2001). I propose that a major mechanism affecting ocean survival for all salmon is that individuals that grow very quickly in the early marine period will have growth that exceeds a threshold at a time that a metabolic decision needs to be made about future use of energy. Individuals exceeding a threshold will change their metabolism to store lipids to better survive the first ocean winter. Those not exceeding a threshold will continue to direct most energy into growth.

The timing of the critical period and threshold decision needs to be cued and day length as early as the summer solstice may be involved. The process is essentially analogous to the events around smoltification of coho salmon in fresh water. The relevance of the hypothesis to all Pacific salmon is the importance of growth rate and the necessity to grow quickly in the first weeks in the ocean. "Grow faster and quicker to survive better" would be the rule. An explanation for the declining catch of Japanese chum salmon beginning in 2008 would be a declining trend in prey production at the time of ocean entry and an inability to reach a critical size. It would not be related to the abundance of juveniles because the hatchery releases have remained about the same (Urawa *et al*., 2018). It is unlikely related to an increasing predation, although predation could be a cause of death, just not a regulator of production. It is unlikely that the declining trend is mostly a result of processes after juveniles leave the coast of Japan because chum salmon from Russia occupy similar feeding areas and Russian chum are increasing in abundance (Urawa *et al*., 2018). A declining trend in coastal prey production at the time of ocean entry could also be an explanation for the declining trends of Pacific salmon in British Columbia. The opposite would be the explanation for the record large catches in Russia and Alaska. Early growth and related metabolic responses would be the main mechanism regulating survival up to the end of the first ocean winter.

Average ocean survival for Pacific salmon that was considered to be "normal" can range from about 3% to about 7%, depending on the species (Pearcy, 1992; Groot and Margolis, 1991; Beamish, 2018a). A good survival for Chinook salmon would be about 5%, meaning that 5% of all smolts that entered the ocean survived to be caught in a fishery or return to spawn (Riddell *et al*., 2018). In the Strait of Georgia on Canada's west coast, a survival of 5% historically provided enough individuals for fisheries and for spawning that there was little interest in understanding the reasons for the 95% mortality (Beamish *et al*., 1995). The hypothesis for production of adults was that the relationship between number of fish that spawned and numbers that returned or were caught was related to production of smolts in fresh water (Ricker, 1954). This relationship assumed that there was adequate carrying capacity in the ocean that varied randomly with environmental conditions. Ocean carrying capacity has been defined "as a measure of the biomass of a given population that can be supported by the ecosystem" (US GLOBEC, 1996). For Pacific salmon, carrying capacity is the mean biomass that can be supported in a particular ocean habitat. There was a generally accepted relationship that as the ocean carrying capacity became limiting, density-dependent processes would reduce survival which would reduce abundances. Fishing theory allowed for the fishing of individuals that were not needed to spawn and produce juveniles in fresh water to fill the ocean capacity. Fundamental to this thinking was that it was the number of juveniles produced in fresh water that was regulating return adult abundances. In the example of Chinook salmon, concern and controversy started in the mid-1980s as ocean survival started to decline to 1% (Beamish *et al*., 1995) or even as low as 0.1% (Beamish *et al*., 2012b). A decline in ocean survival rate from 5% to 1%results in an 80% decline in abundance and a 4.9% decline in survival results in a 99% decline in abundance. These declines in ocean survival are now occurring coast wide for Chinook salmon on the west coast of North America as recently reported (Graham *et al*., 2019; Welch et al.2021). There now is developing concern about reasons for increased ocean mortality but concerns tend to be local, such as seal predation (Thomas *et al*., 2017) and without a coordinated research effort to understand the mechanisms responsible for the large scale synchrony of the increasing mortality. Mechanisms that operated across small geographical scales would be a component of a much more comprehensive mechanism that would explain large-scale reductions in abundance. Equally fundamental, is the importance of working as international teams that might contribute different pieces of the mechanism puzzle to facilitate seeing the bigger picture.

What kills salmon in the ocean?

If I return to the example of Chinook salmon with a 5% ocean survival that produced the fish needed for fishing and conservation in the Strait of Georgia in the 1970s (Beamish *et al*., 1995) there is a question of what actually caused the mortality of the remaining 95%. It had been determined in the late 1940s by two of Canada's best scientists that it was increased vulnerability to predation (Ricker and Foerster, 1948). There now are more variations on the hypothesis. The major hypotheses are (1) that it is only the encounter with predators that affects survival; (2) it is the density of the individuals that affects growth through food limitation that results in reduced growth and increased risk of predation; and (3) it is not size or density, but the productivity of the ocean that results in more fish growing faster in the first months in the ocean (Peterman, 1978; Pearcy, 1992). There are, of course, some common aspects to all the hypotheses as all have predation as a cause of death. I find it hard to accept that other proximate causes such as disease and starvation are as important as predation. However, I propose that there is a difference between predation being a cause of death and a regulator of abundance. The ocean is full of potential predators and I suggest that there is a distinction between the predation on fish that have the potential to survive to return to spawn and fish that are compromised because of condition. In a study of coho salmon ocean survival, we estimated the early ocean survival from ocean entry in May until September, just prior to migrating to the open ocean, in comparison with the ocean survival after September and until they returned to spawn (Beamish *et al*., 2008). We estimated that the early ocean survival was 10.0% and the subsequent survival of these fish in the ocean was 13.1%. Predation or other mechanisms in this early marine period was reducing abundances, but there were still large abundances that would survive to migrate into the open ocean where survival to adult return averaged 13.1%. We proposed that a percentage of the fish surviving to September would be less able to survive the winter and essentially were moribund. The growth threshold that affected survival could be and probably is earlier than September. Thus, there would be predation that affects total returns by removing faster growing healthy fish and predation that is removing fish that eventually will not survive. Fish experiencing a reduced ability to grow quickly are unlikely to survive the first ocean winter and are equivalent to "dead fish swimming."

One problem with the hypothesis that the rate of early ocean growth is a major regulator of ocean survival is apparent from the preceding example of coho salmon. The survival after coho salmon left the nearshore area in the late fall was 13.1% and while some of the mortality could be from metabolically compromised fish, it is likely that sources of ocean mortality other than fishing occurred after the first ocean winter and before the fish returned to natal rivers. Predation is the traditional mechanism used to explain these open ocean mortalities. However, in two recently organized studies of the winter ecology of Pacific salmon in the Gulf of Alaska, we were unable to identify abundances of predators either from wounds or scars on salmon or from using eDNA (Proceedings of the virtual conference summarizing survey results are in preparation). More studies of the population dynamics of Pacific salmon in the open ocean are needed to understand the mechanisms regulating ocean survival during this period of their life history.

Carrying capacity and early ocean survival

Carrying capacity could be specific to ocean entry time, species and area specific if early ocean growth is a major regulator of abundance. However, large abundance changes such as seen for Japanese chum salmon must represent a large decrease in carrying capacity. A relationship with carrying capacity could be that with increasing carrying capacity, more fish are growing faster in the early marine period and will have better survival. In a period of decreasing carrying capacity, there simply are more fish that are not growing as fast in the early marine period and will eventually die apparently from predation. A principle in ecology is that the abundance of plants and animals that produce large numbers of seeds or babies is not regulated by the number of seeds or babies but by the available habitat. Salmon produce a large number of fry or smolts in fresh water that migrate into a coastal ocean habitat. If the coastal ocean habitat capacity for supporting salmon survival is declining because of reduced food supply, there should be no expectation that adding more fry or smolts to the coastal habitat along with all the wild juveniles will increase total abundance. In this case of a declining ocean carrying capacity, management efforts might experiment with finding ways of ensuring rapid early marine growth. For example, there is evidence that populations that are genetically programmed to enter the ocean later in the summer than other populations can survive better (Beamish and Neville, 2016; Beamish *et al*., 2016). This survival of the late ocean entering fish could indicate a more favourable carrying capacity later in the year for the current ecosystem dynamics. This observation that ocean entry time of some populations provides better ocean survival is evidence of the importance of maintaining and if possible, restoring resilience by restoring diversity to freshwater production systems and protecting wild salmon.

Relevance of hatchery programs

In British Columbia, and in the United States, hatchery programs in the late 1970s were based on the hypothesis that adding more juvenile salmon to the ocean would increase total abundances as it was believed that there was ocean capacity to produce more salmon. The end result, as reported previously for British Columbia, was that hatcheries produced salmon but have not produced hypothesized increases to populations. After over 40 years, hypotheses involving unused ocean carrying capacity can be rejected. But hatcheries do produce adults which mean that there is some capacity for hatchery fish. Are hatchery fish simply replacing wild fish by out competing them in the early marine period or is there another reason that some hatchery fish survive. If we understood more about the mechanisms that regulate carrying capacity in the early marine period we could answer this question and perhaps identify if hatchery fish can use ocean capacity differently and are not replicas of the wild species.

Try some different research and try doing some research differently

We need international research teams and we need to carry out complete life cycle studies to understand how ocean and climate variability affect Pacific salmon abundances. There are ample numbers of very qualified researchers in all salmon producing countries. These researchers mostly know each other and generally get along quite well internationally. There is a history of effective communications coordinated by organizations such as the five-country North Pacific Anadromous Fish Commission or the International Pacific salmon Commission representing Canada and the Unites States. These are examples of coordinated international organizations that study Pacific salmon, but almost all Pacific salmon research is national. I propose that there needs to be international agreements that identify research topics related to major issues regulating Pacific salmon production that will be funded and assigned to international teams of researchers. Existing organizations such as the North Pacific Anadromous Fish Commission could coordinate the administration of the research. A particular topic could be identified and offered to open competition. The international team with the best proposal would receive the financial support and members would receive national encouragement. My guess is that the costs would be a small fraction of what is currently spent by all countries on Pacific salmon research.

Complete life cycle research that I call stream-to-stream studies could be an extension of some existing research in each Pacific salmon producing country. Depending on the species and country, specific salmon research has more of a focus on either the ocean or freshwater stage of the life history. I do not know for sure, but I do not think there has ever been a complete life cycle study of a population of a particular species of Pacific salmon. Certainly, we did not report any in our recent publication of the ocean ecology of Pacific salmon and trout (Beamish, 2018a). My suggestion is that each Pacific salmon producing country agrees to study the factors affecting the abundance of a population of a particular species for a complete life cycle. This would include spawning, egg development, freshwater development and freshwater habitat, migration into the ocean, early marine ecology, migration into coastal areas, first winter in the ocean, ocean residence including the period of rapid ocean growth and return migration. We have that abilities and technologies to do this and most of these activities are already happening. We only need to focus them on one population.

A bigger picture and a harmony in identifying mechanisms

Rice and Browman (2014) found evidence of a fading interest in recruitment research for major species of fishes in the North Atlantic. For Pacific salmon, recruitment is readily estimated because adults obligingly return to their natal streams to spawn. Thus, there has been a focus on factors that regulate salmon recruitment during their residence in fresh water in North America. My opinion is that the changing trends in ocean ecosystems that can occur quickly means that it is now essential to understand the major biological mechanisms that regulate ocean survival of Pacific salmon.

One good that has come from COVID 19 is how quickly the international scientific effort worked to understand how the virus affects humans and how to combat the virus with vaccines. In the case of Pacific salmon, there is an international community that has demonstrated an ability to work well together in a coordinated effort to study Pacific salmon survival in the Bering Sea (NPAFC, 2005). The effort was short lived, but was a good beginning for possible future cooperation. An intent of this paper is to encourage international attempts to understand the mechanisms that are the biological basis for the mathematical relationships for salmon production originally proposed by Ricker (1954). It is necessary now because climate influences that were not apparent in the 1950s (Ricker, 1958) are now a well-recognized factor in the population dynamics of salmon and other commercially important species. The saying "everything is simple once it is discovered" is credited to Galileo. I have no doubt that when we see a bigger picture we will finally understand the simple mechanisms that regulate abundances and wonder why it took so long. I think the certainty of more rapidly changing ecosystems identifies the need to dig deeper into the biological basis of recruitment of other commercially important species but I leave this to readers to decide if my example for Pacific salmon is part of a bigger picture in fisheries science.

Data availability statement

No new data were generated or analyzed in support of this research.

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