Abundance Dynamics of Pink Salmon, *Oncorhynchus gorbuscha*, as a Structured Process Determined by Many Factors

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Despite the fact that pink salmon is a fish species with a short-cycle life span, its stock abundance dynamics exhibit features typical of common pelagic fish species with an average life-cycle duration. Interchanging periods of high and low pink salmon abundance levels relate to positive and negative stock abundance trends inherent for major regional groups, Asian and American parts of aggregate stocks, and for pink salmon species as a whole (Radchenko et al. 2007). This feature of pink salmon abundance dynamics is determined by structural organization of the species and its populations. Major regional groups of pink salmon are divided into temporally isolated even- and odd-year populations. The life cycle of pink salmon can be conditionally divided into two periods: freshwater (including spawning, embryonic, and downstream migration phases) and marine (including inshore, marine waters in marginal seas, and oceanic phases). The phases repeat in reverse order until fish return from the sea and reach their spawning grounds. Most stocks, in turn, are separated by paired seasonal races with distinct morphological characteristics and spawning areas within river basins.

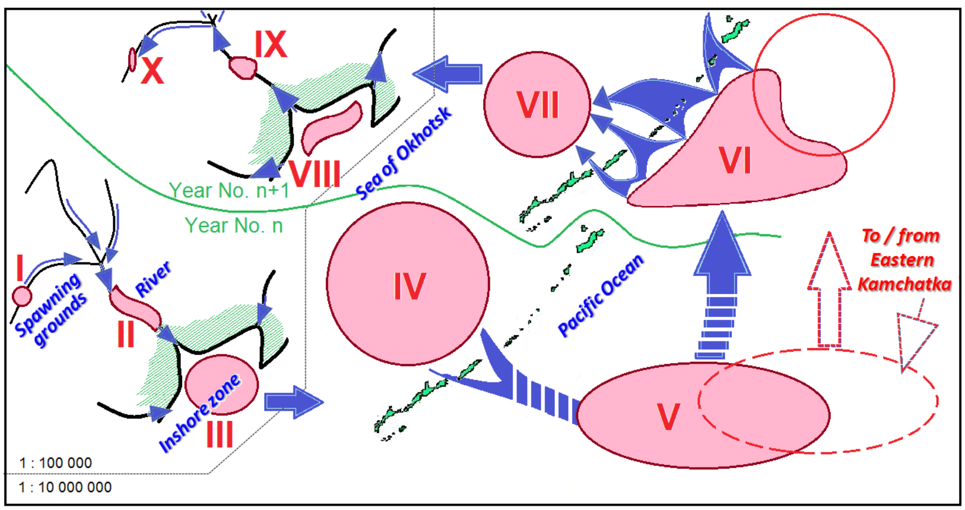

Fig. 1. Pattern of pink salmon migrations during the life-cycle phases of aggregate stocks of the Sea of Okhotsk. Selected life-cycle phases are indicated by Roman numerals.

For the purposes of assessing factors affecting mortality, abundance, and biomass losses on the basis of the pink salmon life cycle, I used typical data from an aggregated stock of Sea of Okhotsk pink salmon as an example (Fig. 1). The average abundance dynamics are based on data for 22 pink salmon generations spawning in 1989 to 2010 (Table 1). Average numbers and biomass estimates were calculated based on survey data, fishery statistics, and published literature.

Table 1. Abundance dynamics of an average pink salmon generation throughout the different life-cycle phases using the aggregate stocks of the Sea of Okhotsk. Data are shown for generations of fish spawning in the years 1989-2008.

Phases	I	II	III	IV	V	VI	VII	VIII	IX	X
Numbers, million fish*	21,448	3,860	1,136	1,020	730	418	300	176	65	52
Biomass, 1,000 mt	3.4	0.7	3.3	157.1	351.9	465.3	401.6	245.1	84.5	65
Number of cases	22	22	1	20	1	7	6	20	22	22

* including roe during first phase

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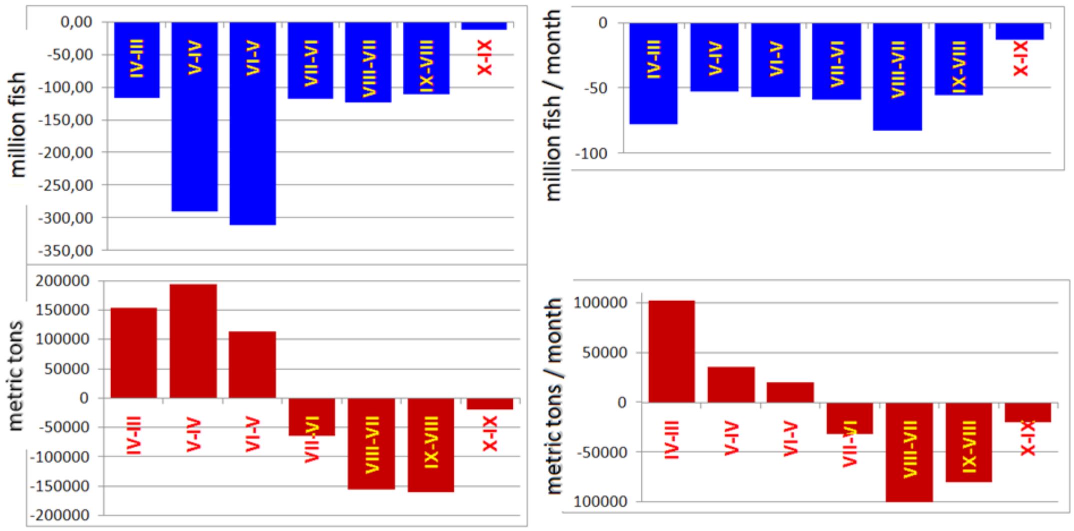

Fig. 2. Abundance and biomass losses of an average generation Sea of Okhotsk pink salmon between phases III and X. Total (left panels) and amount relative to one month (right panels). Data are shown for generations of fish spawning in 1989-2008.

Higher mortality rates occur in the first life-cycle phase and there is a gradual decrease in abundance observed during phases III to VIII (Fig. 2). Significant loss occurs in phases III and IV, which is explained by the critical size hypothesis, and occurs again during phases V and VI in the pre-anadromous migrations in the ocean. Total biomass increases until phase VI due to somatic growth. The surplus is then converted from somatic tissue into gonadal development as the fish begins to mature. Distinctions between the phases are more balanced, if estimated values are determined on the basis of the same time period (e.g., relative to one month). Based on monthly relative values, the most intensive growth of biomass occurs during phases III and IV (first marine summer). Relative biomass and abundance decrease most significantly during the prespawning migrations in the coastal zone (i.e., during phases VII and VIII). Fishery mortality notably contributes to total mortality during the prespawning migrations in the coastal zone, and natural mortality also increases during this period (Radchenko 2007).

The multiple factors effecting pink salmon abundance dynamics during the different life-cycle phases were summarized from the literature (Table 2; see reviews by Shuntov and Temnykh 2008, 2012). The strength of the factor's effect was roughly defined in the following manner: strong – if mass mortality was fixed under the factor's influence; moderate – if estimates suggest notable changes in fish abundance under the factor's influence; and low – if the exact calculation is unavailable or the factor's effect is evaluated as insignificant. The physiological alterations of fish during phases III, VII, and VIII are included due to the significant increase in salmon vulnerability to mortality at those stages. Phase III is divided into two parts (IIIa and IIIb) to emphasize the time period just after entering the sea, when pink salmon mortality is characterized by the highest rates.

All influencing factors are conditionally combined into three groups: (1) density dependent factors, (2) factors with an abundance/biomass level of fish to trigger the effect, and (3) density independent factors, with no abundance/biomass level to trigger the effect. Food supply conditions are usually regarded as a density dependent factor, whereby a portion of the fish population is supported by the supply and the unsupported portion is eliminated. The degree of population damage done by parasites and diseases is also density dependent. Environmental conditions are mainly formed by factors with a trigger level. For example, spawning ground conditions stabilize spawner abundance at some optimal level that corresponds to the hydrological conditions of a particular year. The predation effect is generally density independent because it is mostly determined by predator abundance and distribution. The first group of influencing factors forms the bulk of resources, the second group determines conditions. The second and third groups determine the so-called carrying capacity.

Regional factors affect pink salmon abundance during the first and last phases of the life span. These factors determine the regional peculiarities in abundance dynamics for distinct pink salmon groupings. Between life-cycle phases IV and VII, factors contribute to sea-basin scale dynamics. It is remarkable that density dependent factors are more significant during the second and third portions of the life span, while density independent factors predominate during the first portion. Factors during the initial life-cycle stages of approximately eight months duration form the basic level of the generation's abundance. Thus, juvenile pink salmon abundance during the fall trawl surveys in the southern Sea of Okhotsk was estimated at 250-450 million fish for the 1989-1991 generations. Such an amount of pink salmon could not ensure a powerful prespawning approach to inshore areas. For the subsequent 19 generations, juvenile pink salmon abundance did not fall below 800 million fish and averaged 1,184 million fish.

Table 2. Phases of the pink salmon life-cycle and factors affecting mortality rates using the aggregate stocks of the Sea of Okhotsk. Factors with a trigger level of fish abundance/biomass to start their effect are shown in italics; density dependent factors are shown in bold; density independent factors are shown in plain text.

Phase	Life stage	Factor affecting mortality rates	Strength of the factor
I	Embryonic	*Hydrological regime of spawning grounds (straight freezing danger);* Predators and scavengers;	Moderate Low
II	Freshwater	Hydrological regime of river (powerful flood danger)	Moderate
IIIa	Estuary	*Hydrological regime of estuary during fry entering in sea water (shock danger due to water temperature distinctions in rivers and inshore zone);* Predation by near-coastal piscivorous fish and bird species; Readiness to the exogenous feeding; Osmoregulatory system alteration in the salty environment	Strong locally Moderate Moderate Moderate
IIIb	Early marine	*Hydrological regime of inshore zone (seasonal sea surface layer heating rates);* **Food supply in the inshore zone;** Predation by near-coastal piscivorous fish and birds;	Low Moderate Low
IV	Marine	**Food supply in the open sea waters;** **Competitive relationships with other planktivorous fish and invertebrates;** Predation by pelagic piscivorous fish and marine mammals	Low Moderate Low
V	Oceanic (wintering)	*Hydrological regime of oceanic waters off Kurile Islands (water T^o, currents and hydrological fronts expression);* *Hydrological regime of wintering zone in Pacific Ocean (hydrological fronts expression and location);* **Food supply in the open ocean (related to subarctic waters transport);** **Competitive relationships with other planktivorous fish and invertebrates;** Predation by pelagic piscivorous fish and marine mammals; **Parasites and diseases**	Moderate Moderate Moderate Low Moderate Low
VI	Oceanic (pre-anadromous migrations)	*Hydrological regime of oceanic waters off Kurile Islands (water T^o, including gradients near the Kurile straits, currents and hydrological fronts expression);* **Food supply in the open ocean;** **Competitive relationships with other planktivorous fish and invertebrates;** Predation by pelagic piscivorous fish and marine mammals; **Parasites and diseases**	Moderate Low Low Moderate Low
VII	Marine	*Okhotsk Sea epipelagic layer hydrological regime (heated layer thickness);* **Food supply in the open sea;** Predation by pelagic piscivorous fish and marine mammals; **Parasites and diseases;** Availability of native region spawning rivers (complex of factors); **Metabolism alteration (linear growth cessation and intensive maturing)**	Low Moderate Low Moderate Moderate Moderate
VIII	Inshore	*Hydrological regime of inshore zone (water T^o, heated layer thickness);* Complex of factors determining maturity rates; **Anthropogenic factors (fishery);** Predation by marine mammals; **Parasites and diseases**	Moderate Moderate Moderate Moderate Moderate
IX	Freshwater	*Hydrological regime of rivers (spawning grounds availability);* **Anthropogenic factors (fishery; poaching);** Predation by terrestrial mammals and birds; **Parasites and diseases**	Moderate Moderate Lowering Strong
X	Spawn	*Hydrological regime of spawning grounds (spawning success);* **Anthropogenic factors (poaching);** **Parasites and diseases (pre-spawning die-offs)**	Strong Moderate Strong

Large-scale factors influence pink salmon aggregate stocks and smooth fluctuations in total abundance. For example, large-scale factors supported pink salmon returns to the Sea of Okhotsk basin of 152 million adult fish from an estimated 1570 million juveniles (as estimated in the fall survey) for brood year 1998, and 252 million adult fish from an estimated 1000 million juveniles for brood year 2007. Mortality rates totaled 90-91% from fall to the next year's prespawning approach for fish spawning in 1998-2002, and mortality rates decreased to 75-77% for two generations of pink salmon spawning in 2007 or 2008. Effects of large-scale factors with harmonics generated from multiple years of variability are not enough to induce immediate salmon mortality. However, for future reproductive success pink salmon sacrifice about 82.7% of the total abundance in one marine year, as compared to mature herring losses of 20-27% in year classes aged 5-8 including fishery mortality, and walleye pollock annual mortality in the northern Sea of Okhotsk of about 26-30% for year classes aged 4-6. The distinctions among these species are determined by their different life strategies.

According to the critical size hypothesis, smaller individuals in the salmon cohort may not have sufficient energy reserves to survive late fall and winter in the ocean (Farley et al. 2007). Linear size is used as a proxy for estimation of accumulated energy resources. In my opinion, this point of view does not lose validity for the subsequent phases of the life cycle. Salmon need large energy resources to cover the enormous distances of the oceanic migration route and to overcome opposing water flow and rapids in spawning rivers. According to Shuntov and Temnykh (2012), the main features of the salmon life-history strategy were shaped in the historical period, when the near-coastal zone was densely populated by common fish species. Consequently, salmon were forced to choose a remote area in the open ocean for feeding migrations. This marathon life strategy is expressed most strongly in the features of pink salmon because it has the shortest life span.

Several studies consider salmon starvation in the ocean as a cause of enhanced mortality during winter (Nomura et al. 2000; Nomura and Kaga 2007). What does "starvation" really mean for salmon? Dwelling in conditions with an absolute absence of food? Insufficient amount or nutritional quality of food organisms? These conditions are not likely what starvation means for salmon. It is likely that starvation for salmon means a bigger energy expenditure for feeding (including searching for and capture of prey) than the caloric and nutritional content of the food. Some rare organic compounds and micro-elements also can be important for growth and development. Several facts support this hypothesis: no exhausted salmon specimens were caught over the many years of ecosystem surveys by TINRO; consumption by salmon does not exceed 3-5% of plankton biomass and 0.1-0.3% of plankton production; salmon usually consume preferred diet items, like hyperiids; and their diurnal feeding dynamics usually follows a one-peak pattern (Shuntov and Temnykh 2012). Salmon are flexible and react to poor food conditions by changing their body content and postponing gonadal development. Under laboratory conditions, chum salmon exhibited a 40% decline in body energy content and a 9% increase in moisture content after 45 days of starvation, but the fish remained alive and demonstrated slow linear growth (Fergusson et al. 2010).

Salmon at sea are active visual feeders with individual (not schooling) behaviors. Their preferred prey is not evenly distributed in the epipelagic layer. Most likely, forage organisms aggregate in thin lenses, on the surface of bacterial films, at the border between different water masses, etc. In relation to these types of prey aggregations, the inter-specific competition between salmon and abundant pelagic planktivorous fish can exhibit an aspect other than food supply exhaustion. Abundant pollock, herring, or sardine aggregations can destroy the fine structure of forage fields that would otherwise be suitable for energetically-beneficial salmon feeding. That is a reason why areas of high Pacific salmon catches do not overlap the areas of high catches of other pelagic fish during trawl surveys. Intra-specific competition can also act in this manner. In the last two odd-numbered years and the highest pink salmon abundance of adults approaching the coast, the southern Kuril stock, which is a late seasonal race and is the last to return, was notably lower in abundance than expected: in 2009 – lower by 44% and in 2011 – lower by 86%. Furthermore, Fulton's condition factor was low for the less mature cohort of pink salmon during the migration flow to the coastline. It would be useful to estimate the caloric content of pink salmon sampled from the later part of the migration in years of high total abundance to determine if body condition decreases over the duration of the migration.

Salmon are susceptible to relatively high mortality during catch-and-release fisheries in fresh waters (Reiss et al. 2011). This is surprising, considering their viability after wounds caused by predatory fish and marine mammals at sea. Unexpected energy loss related to salmon fighting the fishing line can be critically important for spawning success. Most salmon species do not feed in rivers, so their "batteries" cannot be "charged" there. It must be noted that mortality estimates do not include fish that are released soon after capture and are flushed downstream by the flow and may die sometime thereafter.

Analysis of the salmon life strategy has brought us to reconsideration of the carrying capacity term for this group of fish. While theoretical reasoning uses total fish biomass as the measure of carrying capacity, biomass consists of individual fish, and, in reality, salmon explore their surroundings individually. The individual characteristics of each fish determine whether it will attain the subsequent stage in its life span. This is one of the differences between salmon and common schooling pelagic fish species like sardine, anchovy, herring, etc. If a salmon population includes a significant portion of fish with sub-optimal physiological characteristics for further development, then notable abundance fluctuations become possible if variations of environmental conditions predominate at a critical juncture for these fish. Even a small enhancement of conditions can support a notable portion of the salmon population, but the same degree of worsening conditions could eliminate most of them.

Since the 1980s, pink salmon abundance trends for large regional groupings have been characterized by increased positive and negative deviations from average values. Thus, pink salmon catch in Aniva Bay has exceeded the expected value by 50,000 tons and exceeded the historical maximum for the even-year broodline by 5.5 times in 2006. This year (2011), the negative deviation was 25,100 tons in Aniva Bay. Expected excess catch on Iturup Island (positive deviation) was 23,900 tons in 2007, and negative deviations of the same magnitude (23,800 tons) was observed for four consecutive years.

Observed fluctuations in pink salmon abundance has coincided with intensification of pink salmon hatchery programs around the Pacific Rim (Beamish et al. 1997; Ruggerone et al. 2010), and both the western and eastern North Pacific are characterized by a notable portion of total pink salmon abundance comprising hatchery fish. It is possible to consider the genetic and physiological diversity of young salmon as a source of the observed deviations from expected returns. However, large deviations in abundance have likewise been observed on the coast of eastern and western Kamchatka, which are without notable pink salmon hatchery enhancement. Perhaps some factors of hatchery enhancement are so widespread as to influence pink salmon stocks that do not originate from regions of intense artificial production.

Relevant scientific directions in the study of pink salmon dynamics include research in the following areas: (1) establish a data series on salmon energy contents in the ocean and coastal areas, (2) develop simple indices of optimal physiological condition for different stages of the pink salmon life cycle, (3) conduct comparative studies for different periods of the migration flow to benefit natural mortality forecasts and spatial differentiation of seasonal races and regional groupings, and (4) develop new information on wild/hatchery salmon relationships. Studies of the quantitative distribution of juvenile Pacific salmon in the inshore zone and in the wintering areas of North Pacific Ocean must also be continued.

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