Trends in Run Size and Carrying Capacity of Pacific Salmon in the North Pacific Ocean

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Abstract: Pacific salmon (*Oncorhynchus* spp.) play an important role as keystone species and as ecosystem services in the North Pacific ecosystem. Our objective is to evaluate the trends in and causes of variation in run size and carrying capacity of Pacific salmon, and to predict their future production dynamics. Salmon catch data indicate that the abundance of Pacific salmon has declined since the end of the twentieth century, despite the healthy condition of stocks. At the beginning of the 21st century, chum (*O. keta*) and pink salmon (*O. gorbuscha*) maintained high abundance commensurate with a sharp increase in hatchery-released populations. However, sockeye salmon (*O. nerka*) have shown a reduction trend since the late 1990s. The abundance of coho (*O. kisutch*), Chinook (*O. tshawytscha*), and masu (*O. masou*) salmon, which spend more than one year in fresh water, has declined sharply since the 1980s due to degraded environmental conditions in freshwater habitats (e.g., habitat loss, urbanization, and river channelization). The significant positive correlation between the carrying capacity (K) of three species (sockeye, chum, and pink salmon), defined as the replacement level of Ricker's recruitment curve, and the Aleutian Low Pressure Index (ALPI) indicate that their carrying capacity is synchronous with long-term trends in climate change. The carrying capacity of the three species is expected to continue the downward trend seen since the 1998/99 regime shift.

Keywords: carrying capacity, long-term climate change, Pacific salmon, run size

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) play an important role as keystone species and ecosystem services in the North Pacific ecosystem. They are important not only as fisheries resources but also as a keystone species in these ecosystems. Pacific salmon are also a key species for sustaining the biodiversity and productivity of riparian ecosystems because they supply marine-derived nutrients to rivers (e.g., Kaeriyama and Minagawa 2008).

Since the 1976/77 regime shift, catches of Pacific salmon have been increasing throughout the North Pacific Ocean, coinciding with favorable oceanic conditions and a successful artificial enhancement program (Beamish and Bouillon 1993; Kaeriyama 1998). The most abundant species caught is pink salmon (*O. gorbuscha*), followed by chum (*O. keta*) and sockeye salmon (*O. nerka*). Catches have been increasing almost steadily in coastal Japan, Russia, and central and southeast Alaska. Catches in western Alaska increased through the mid-1990s but have been decreasing recently. Salmon catches in British Columbia and the western United States (Washington, Oregon, and California) have been decreasing since the late 1980s (Eggers 2004). We estimated the carrying capacity of Pacific salmon from catch and/or abundance data which are based on the expansion rate of the terminal run in each regional population (D. E. Eggers, Alaska Department of Fish and Game, Douglas.Eggers@alaska.gov, unpublished data), using the equilibrium level on the Ricker recruitment curve (e.g., Kaeriyama and Edpalina 2004; Yatsu and Kaeriyama 2005). However, this expansion rate did not always accurately reflect the run size (catch and escapement, millions of individuals) when based on catch data, with the result that the run size of chum salmon was overestimated.

Since 1999, the North Pacific has been characterized by consistent spatial patterns in the sea level pressure anomaly (SLPA), sea surface temperature (SST), and the reversed Pacific Decadal Oscillation (PDO) (Bond et al. 2003: Chavez et al. 2003; Peterson and Schwing 2003; Rodionov and Overland 2005). These persistent changes in the North Pacific resulted in a new climate regime shift in 1998/99 (Minobe 2002; Chavez et al. 2003; Rodionov and Overland 2005).

The purpose of this paper is to update and extend the estimated run size and carrying capacity values of Pacific salmon proposed by Kaeriyama and Edpalina (2004) in order to assess near-future fluctuation(s) in carrying capacity in relation to long-term climate change and the biological interaction between wild and hatchery salmon.

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MATERIALS AND METHODS

We used INPFC (1979), Fredin (1980), Kaeriyama and Edpalina (2004), Eggers (2004), White (2008), and URLs: www.cf.adfg.state.ak.us and http://salmon.fra.affrc.go.jp/ to obtain catch data for Pacific salmon. Also, we used the Aleutian low-pressure index (ALPI) derived from Beamish and Bouillion (1993), the Pacific decadal oscillation (PDO) derived from Mantua et al. (1987) and URLs: http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/climate/clm_indx_alpi.htm and http://jisao.washington.edu/pdo/, as indices of long-term climate change. We estimated run size of sockeye, chum, and pink salmon from catch data using the expansion rate, which indicates the exploitation rate (catch per run size of three species) (D. E. Eggers, Alaska Department of Fish and Game, Douglas.Eggers@alaska.gov, unpublished data).

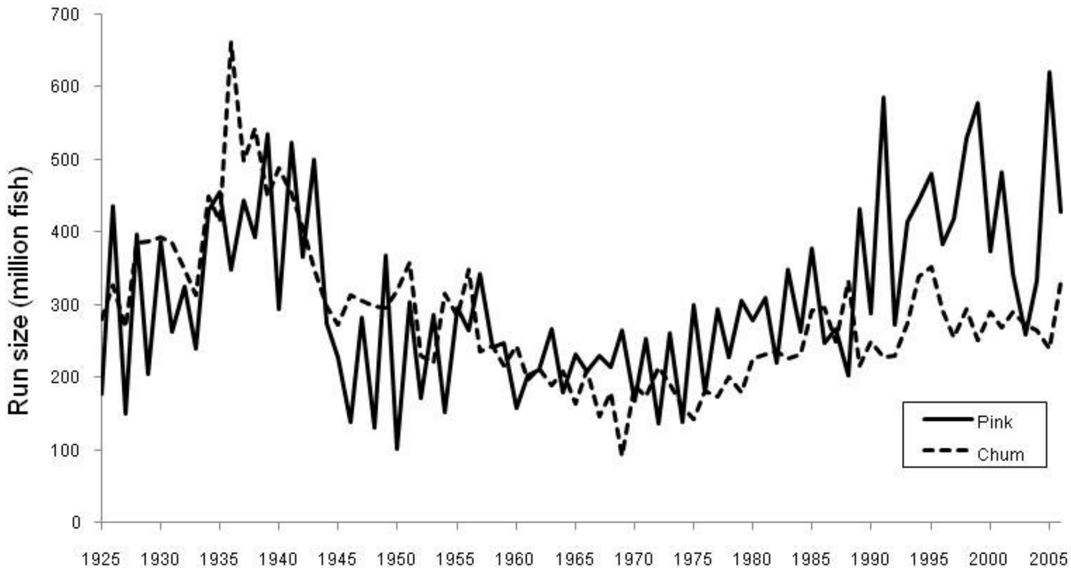

Fig. 1. Annual changes in run sizes estimated by Eggers' expansion rate of pink (solid line) and chum salmon (broken line). The expansion rate of chum salmon was 43% on the high seas, 11% in coastal Russia, 10% in western Alaska, 10% in central Alaska, 10% in southeast Alaska, and 10% in BC/Washington/Oregon (D.E. Eggers, Douglas.Eggers@alaska.gov, unpublished data).

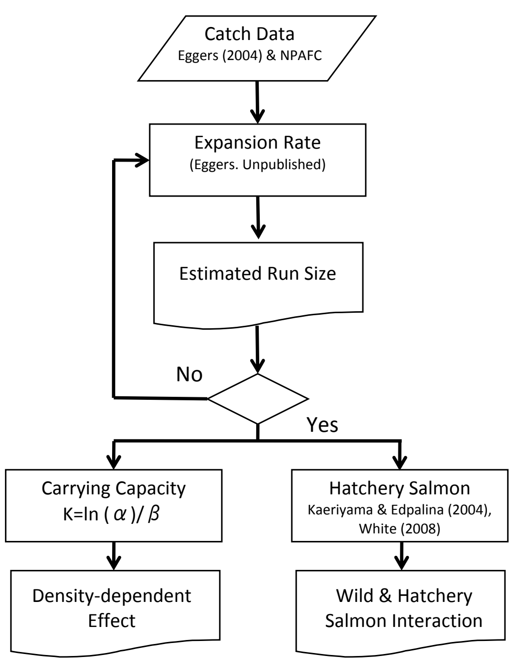

Fig. 2. Flow chart for estimating run size and carrying capacity of Pacific salmon.

However, the run sizes using Eggers' expansion rate were overestimated. For instance, the run size of chum salmon exceeded the run size of pink salmon (Fig. 1). As the result of trial and error using random exploitation rates (Fig. 2), we decided on a new expansion rate (Table 1).

Parameters for the Ricker recruitment curve ($R = \alpha P e^{-\beta P}$) were estimated for each of the three species by the Levenberg-Marquardt method (Marquardt 1963). Parameters were calculated by regression analysis and the index of carrying capacity (K) for salmon was defined as the unfished equilibrium level ($\ln(\alpha)/\beta$) (Ricker 1975). The time span of data used to estimate the parameters (α, β, K) for year-class, t, was 10 generations of odd- and even-year groups for pink salmon, and 20 brood years for sockeye and chum salmon from year-class t to t + 20 (Fig. 3). The choice of 10 generations or 20 brood years was based on the appearance of bidecadal cycles of climate conditions (Minobe 2000). The run size of salmon released from hatcheries was based on Kaeriyama and Edpalina (2004) and White (2008) in order to compare run sizes between wild and hatchery salmon.

Table. 1. Catch rate per run size of pink, chum, and sockeye salmon in the North Pacific Ocean. The expansion rate shows exploitation rate (catch per run size).

Area	Pink salmon	Sockeye salmon	Chum salmon
Japan; Coastal	49%	None	0%
Japanese: Japan Sea	57%	None	None
Japanese: High Seas Immature	None	46%	43%
Japanese: High Seas Maturing	56%	32%	22%
Russian: Coastal	50%	30%	20%
Western Alaska	None	30%	20%
Central Alaska	62%	30%	20%
PWS Hatchery	White (2008)	None	None
Southeast Alaska	55%	40%	20%
Southeast Alaska Hatchery	White (2008)	None	White (2008)
B.C./Washington/Oregon	55%	40%	20%

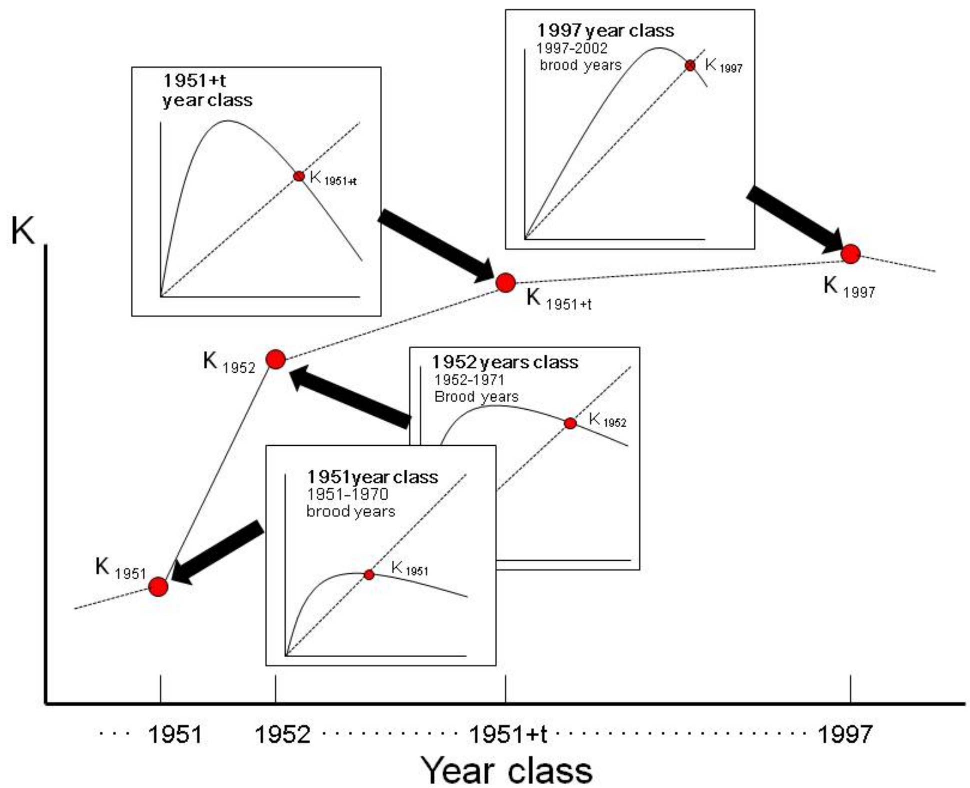

Fig. 3. Schematic diagram of temporal changes in carrying capacity of Pacific salmon.

RESULTS AND DISCUSSION

The catch of sockeye, chum, and pink salmon comprised more than 90% of the total catch of Pacific salmon. Temporal changes in the catch had roughly a 30- or 40-year periodicity, corresponding to long-term climate change indicators such as the PDO and the regime shift (Fig. 4). The general trend in Pacific salmon production was similar for both North American and Asian populations. Increased production began in the late 1970s, reaching historic levels in 1995. Catches declined slightly thereafter but were the second highest in history in 2003. In both the eastern and western Pacific, the catches of salmon generally increased substantially after the regime shift in 1977 (Beamish 2008). Recent trends in catch show increases in pink and chum, steadiness in Chinook (*O. tshawytscha*), and decreases in sockeye, coho (*O. kisutch*), and masu (*O. masou*) salmon (Fig. 5). In particular, masu and coho salmon which spend a long time in fresh water have shown significant decreasing trends since the 1980s. Japanese masu salmon decreased from more than 2000 tons in the 1960s to about 500 tons by 2000. This decreasing trend is attributed to losses of suitable habitat in fresh water (Kaeriyama and Edpalina 2004).

The run sizes of the three major species (sockeye, chum,

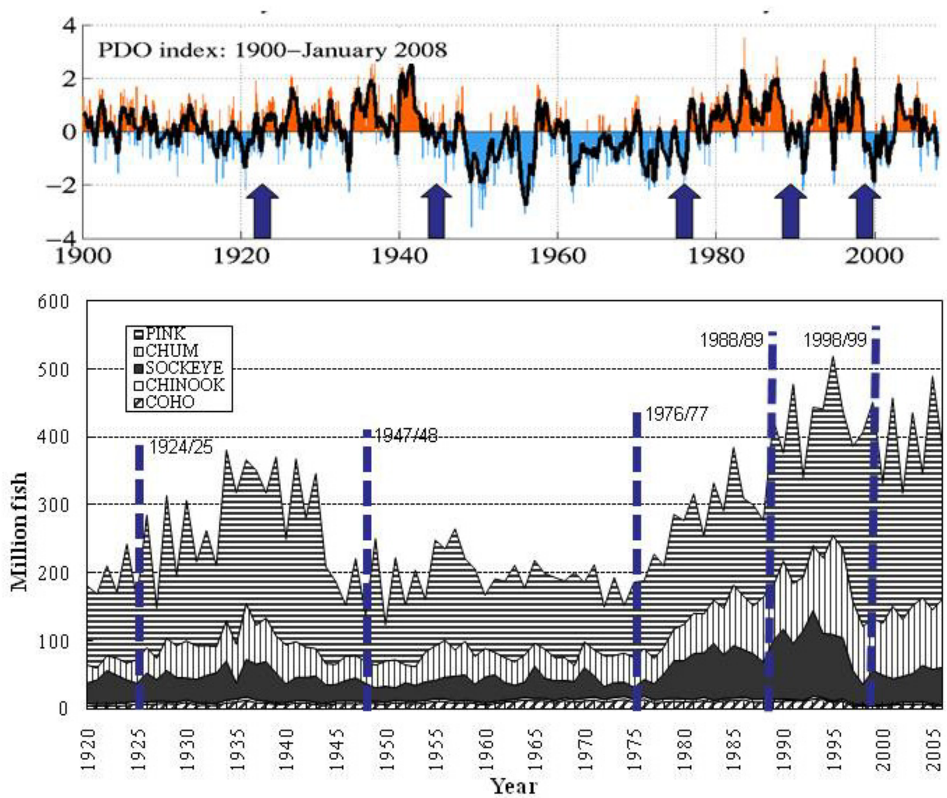

Fig. 4. Annual changes in catches of Pacific salmon (1920–2006) and the Pacific Decadal Oscillation (PDO; 1900–2008). Bars and arrows show regime shift years.

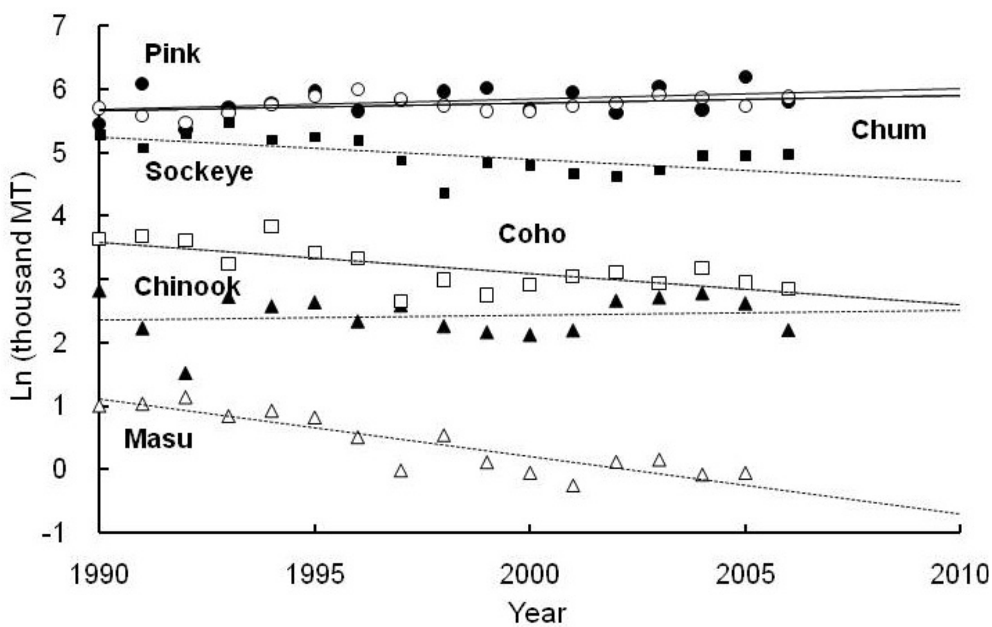

Fig. 5. Recent trends in catches of Pacific salmon since 1990. Lines indicate the results of a simple linear regression analysis between time (year) and natural logarithm of catch by species.

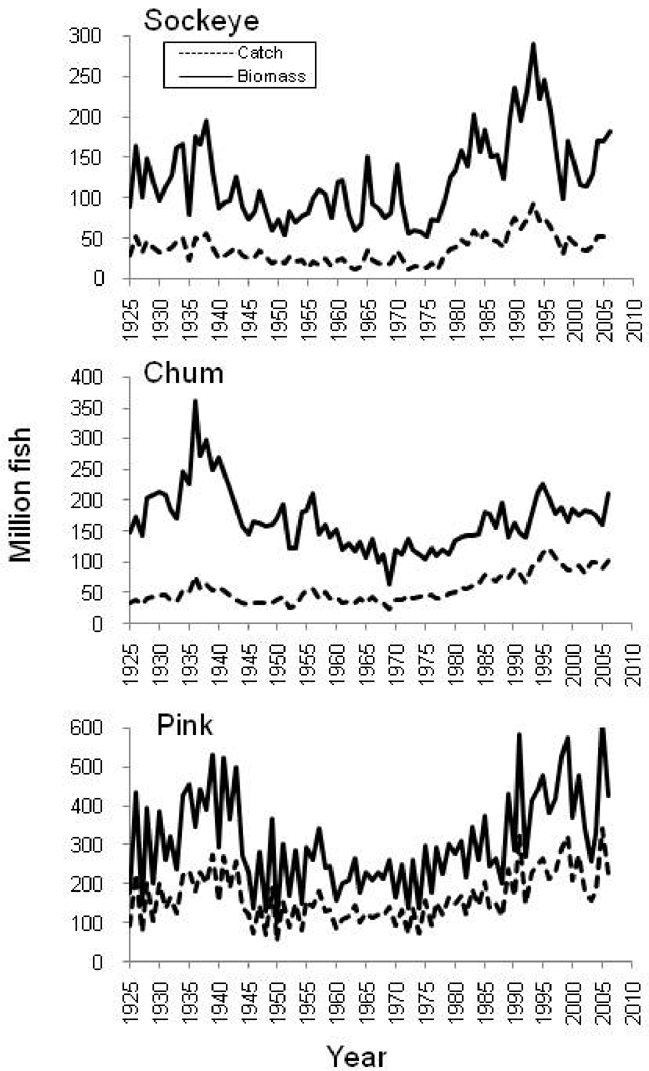

Fig. 6. Annual changes in catch and run sizes of sockeye, chum, and pink salmon in the North Pacific Ocean during 1925–2006.

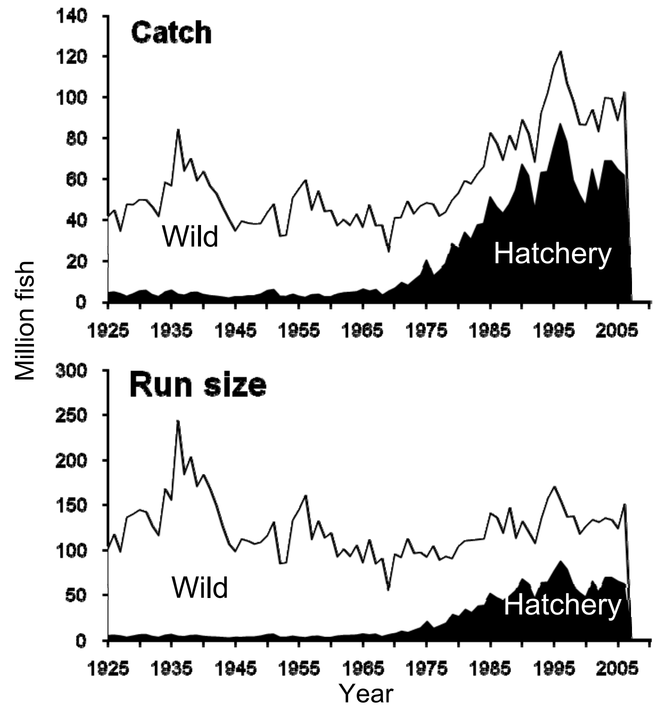

Fig. 7. Annual changes in catch and run size of wild and hatchery chum salmon during 1925–2006.

and pink salmon) were 1.9–3.7 times more than catch values (sockeye: 3.7 ± 0.82, chum: 3.3 ± 1.09, pink salmon: 1.85 ± 0.06), and showed increases in the late 1970s and the early 1990s (Fig. 6). Although catch and run sizes of chum salmon have increased since the late 1970s, wild chum salmon showed a decreasing trend. In contrast, hatchery chum salmon are increasing exponentially in Japan and southeast Alaska, comprising more than 80% of catch and more than 40% of run size (Fig. 7). Means (± SD) of the rate of change in hatchery salmon run size since the 1990s were 2.1 (± 2.83) % in sockeye, 46.9 (± 6.06) % in chum, and 9.3 (± 4.28) % in pink salmon (Table 2, Fig. 8).

Results for chum salmon showed that increases in run size might lead to a reduction in body size and increases in the average age at maturity of the population suggesting a population density-dependent effect (Kaeriyama 1998). Data for Alaskan sockeye salmon also showed that greater marine growth contributed to greater survival and abundance, which in turn led to density-dependent growth (Ruggerone et al. 2007). The biomass of wild chum salmon in the 1990s decreased to 50% below that of the 1930s, despite significant increases in hatchery populations. The density-dependent growth resulting from increases in hatchery salmon might affect wild chum salmon populations. This indicates that biological interaction between wild and hatchery populations is an important issue in the sustainable management of Pacific salmon production at the ecosystem level.

The carrying capacity of three species (sockeye, chum, and pink salmon) has decreased since the 1925 year-class, was minimal during 1945–1955 year-classes, increased during 1956–1975 year-classes, and remained constant during 1976–1997 year-classes (Fig. 9). Relationships between the carrying capacity of three species was significantly correlated with the Aleutian Low Pressure Index (ALPI) (Fig. 9; $R^2 = 0.868$, F = 462, $P < 0.001$, n = 72). Therefore, we predict that their carrying capacity will be significantly synchronized with the long-term trends in climate change. The carrying capacity of sockeye, chum, and pink salmon achieved peaks in 1985, 1993, and 1994 year-classes (Fig. 7). The total catch of Pacific salmon has declined slightly since the late 1990s (Fig. 4). Following a strong El Niño in 1997, the climate of the North Pacific underwent a rapid transition in late 1998. The PDO reversed direction and remained negative. These persistent changes in the atmosphere, upper ocean fields and ecosystem structure show that a new climate regime shift occurred in 1998/99 (Chavez et al. 2003; Peterson and Schwing 2003; Rodionov and Overland 2005).

Table. 2. Annual changes in run size (millions of fish) of sockeye, chum, and pink salmon in the North Pacific Ocean. Wild = salmon derived by natural spawning; Hatchery = salmon released from hatcheries.

Year	Sockeye salmon			Chum salmon			Pink salmon		
	Wild	Hatchery	Total	Wild	Hatchery	Total	Wild	Hatchery	Total
1925	89.3	-	89.3	95.3	4.3	99.6	177.8	-	177.8
1926	165.3	-	165.3	112.0	4.7	116.7	436.3	-	436.3
1927	100.0	-	100.0	93.3	3.9	97.2	150.7	-	150.7
1928	148.9	-	148.9	133.3	2.4	135.7	396.8	-	396.8
1929	120.3	-	120.3	135.7	3.8	139.5	203.6	-	203.6
1930	97.5	-	97.5	138.8	5.2	144.0	387.2	-	387.2
1931	114.1	-	114.1	136.3	5.5	141.8	262.3	-	262.3
1932	128.8	-	128.8	122.6	3.3	125.9	324.9	-	324.9
1933	162.6	-	162.6	113.2	2.3	115.5	239.4	-	239.4
1934	167.4	-	167.4	162.4	4.7	167.1	429.4	-	429.4
1935	80.2	-	80.2	149.4	5.6	155.0	454.6	-	454.6
1936	176.5	-	176.5	239.6	3.6	243.2	347.9	-	347.9
1937	167.2	-	167.2	180.5	3.0	183.5	442.8	-	442.8
1938	195.3	-	195.3	198.4	4.4	202.8	392.7	-	392.7
1939	134.6	-	134.6	165.5	4.6	170.1	534.0	-	534.0
1940	87.7	-	87.7	179.7	3.4	183.1	293.0	-	293.0
1941	94.4	-	94.4	165.1	2.8	167.9	522.9	-	522.9
1942	96.7	-	96.7	146.6	2.5	149.1	366.4	-	366.4
1943	125.8	-	125.8	123.3	2.1	125.4	500.1	-	500.1
1944	89.9	-	89.9	104.3	1.6	105.9	275.2	-	275.2
1945	74.3	-	74.3	95.3	2.3	97.6	228.7	-	228.7
1946	82.8	-	82.8	109.3	2.2	111.5	138.1	-	138.1
1947	108.4	-	108.4	106.7	2.7	109.4	281.3	-	281.3
1948	82.6	-	82.6	103.3	2.7	106.0	131.2	-	131.2
1949	60.0	-	60.0	104.3	3.7	108.0	368.2	-	368.2
1950	72.9	-	72.9	109.7	5.4	115.1	101.7	-	101.7
1951	54.3	-	54.3	124.3	5.9	130.2	303.2	-	303.2
1952	84.0	-	84.0	81.8	2.5	84.3	171.5	-	171.5
1953	69.5	-	69.5	82.9	2.4	85.3	286.5	-	286.5
1954	76.8	-	76.8	128.8	3.6	132.4	151.6	-	151.6
1955	81.2	-	81.2	142.0	2.5	144.5	295.8	-	295.8
1956	98.4	-	98.4	158.3	1.9	160.2	263.9	-	263.9
1957	110.9	-	110.9	107.9	3.3	111.2	343.1	-	343.1
1958	104.9	-	104.9	128.0	3.6	131.6	241.2	-	241.2
1959	74.8	-	74.8	110.8	2.2	113.0	248.0	-	248.0
1960	119.3	-	119.3	115.9	2.2	118.1	157.5	-	157.5
1961	121.7	-	121.7	88.1	3.7	91.8	202.8	-	202.8
1962	79.5	-	79.5	95.8	4.3	100.1	211.1	-	211.1
1963	60.6	-	60.6	87.7	4.5	92.2	265.8	-	265.8
1964	68.6	-	68.6	99.6	4.8	104.4	179.6	-	179.6
1965	151.8	-	151.8	79.0	6.1	85.1	232.3	-	232.3

Table. 2 (continued).

Year	Sockeye salmon			Chum salmon			Pink salmon		
	Wild	Hatchery	Total	Wild	Hatchery	Total	Wild	Hatchery	Total
1966	92.3	-	92.3	105.5	5.1	110.6	209.2	-	209.2
1967	87.1	-	87.1	78.1	5.9	84.0	229.1	-	229.1
1968	76.0	-	76.0	86.9	3.1	90.0	215.1	-	215.1
1969	80.6	-	80.6	49.7	5.1	54.8	264.2	-	264.2
1970	141.4	-	141.4	88.1	6.6	94.7	166.6	-	166.6
1971	93.5	-	93.5	81.7	9.3	91.0	252.4	-	252.4
1972	56.4	-	56.4	104.1	7.9	112.0	137.3	-	137.3
1973	60.4	-	60.4	85.2	10.5	95.7	261.7	-	261.7
1974	58.2	-	58.2	83.7	13.0	96.7	138.6	0.0	138.6
1975	52.4	-	52.4	71.5	20.0	91.5	299.6	0.0	299.6
1976	73.5	-	73.5	91.2	12.4	103.6	178.7	0.0	178.7
1977	72.3	-	72.3	73.0	15.2	88.2	293.9	0.2	294.0
1978	95.2	0.0	95.2	74.0	18.2	92.2	226.6	0.3	226.9
1979	125.9	0.3	126.2	61.8	28.0	89.8	303.2	1.6	304.8
1980	133.8	0.7	134.5	77.9	25.7	103.6	275.8	2.3	278.1
1981	158.6	0.4	159.0	76.2	33.5	109.7	305.6	4.4	310.0
1982	138.7	0.1	138.7	80.4	29.9	110.3	213.4	6.6	220.1
1983	202.4	0.2	202.6	73.9	37.1	111.0	341.7	5.9	347.6
1984	157.2	0.4	157.6	74.1	37.8	111.9	258.1	5.3	263.4
1985	182.7	0.8	183.5	89.2	50.9	140.1	362.6	14.2	376.7
1986	150.2	1.3	151.5	89.5	46.0	135.5	239.1	9.0	248.1
1987	151.2	1.0	152.2	75.4	42.7	118.1	244.7	22.0	266.7
1988	121.9	1.7	123.5	99.4	47.2	146.6	189.0	13.9	202.8
1989	195.7	2.0	197.8	58.3	54.1	112.4	399.3	31.8	431.0
1990	231.9	4.2	236.1	64.2	66.9	131.1	247.4	41.2	288.6
1991	190.3	5.4	195.7	57.6	61.4	119.0	546.1	39.8	585.9
1992	228.6	4.2	232.8	62.4	44.3	106.7	256.9	14.7	271.6
1993	285.3	5.1	290.3	71.9	62.8	134.7	393.5	20.7	414.2
1994	218.7	4.2	222.8	93.5	63.3	156.8	402.1	41.3	443.4
1995	244.9	1.5	246.4	94.3	75.6	169.9	455.7	24.8	480.4
1996	204.4	2.8	207.2	67.1	86.8	153.9	353.3	29.6	382.8
1997	148.9	3.0	151.9	58.5	77.9	136.4	384.3	34.0	418.3
1998	95.8	2.5	98.3	77.8	59.1	136.9	490.1	38.7	528.7
1999	166.8	3.6	170.4	65.1	52.0	117.1	524.7	52.0	576.7
2000	140.7	2.1	142.8	79.8	46.4	126.2	332.7	40.4	373.1
2001	112.9	3.3	116.3	68.6	64.5	133.1	434.2	47.2	481.5
2002	109.8	3.6	113.4	78.3	52.0	130.3	311.7	30.8	342.5
2003	126.0	4.8	130.7	66.4	68.5	134.9	199.8	59.8	259.6
2004	167.5	3.6	171.0	64.3	68.6	132.9	301.5	30.6	332.1
2005	168.3	2.8	171.0	58.8	64.3	123.2	551.9	69.1	621.0
2006	179.2	2.6	181.8	88.9	61.5	150.4	401.8	26.7	428.5

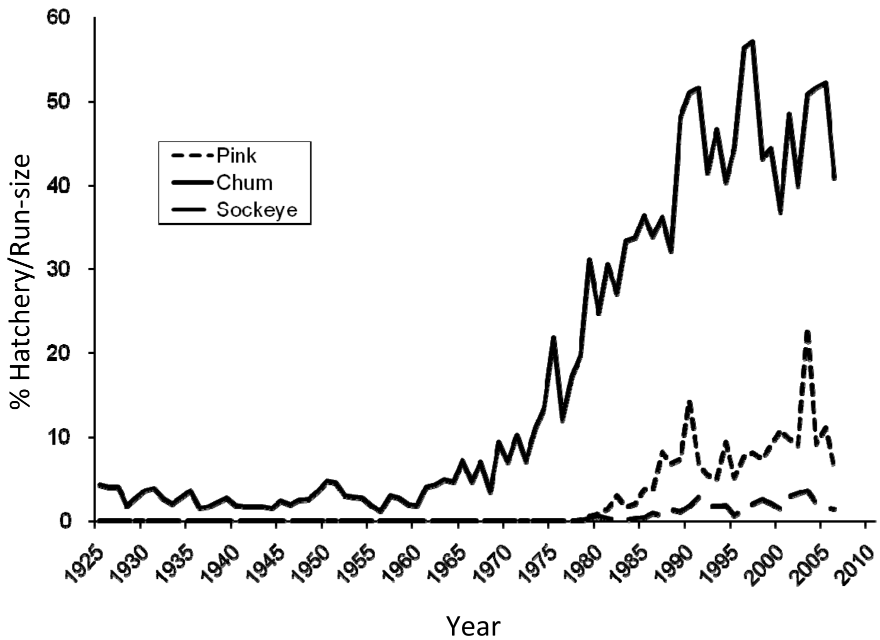

Fig. 8. Annual change in the percentage of hatchery salmon in Pacific salmon runs during 1925–2006.

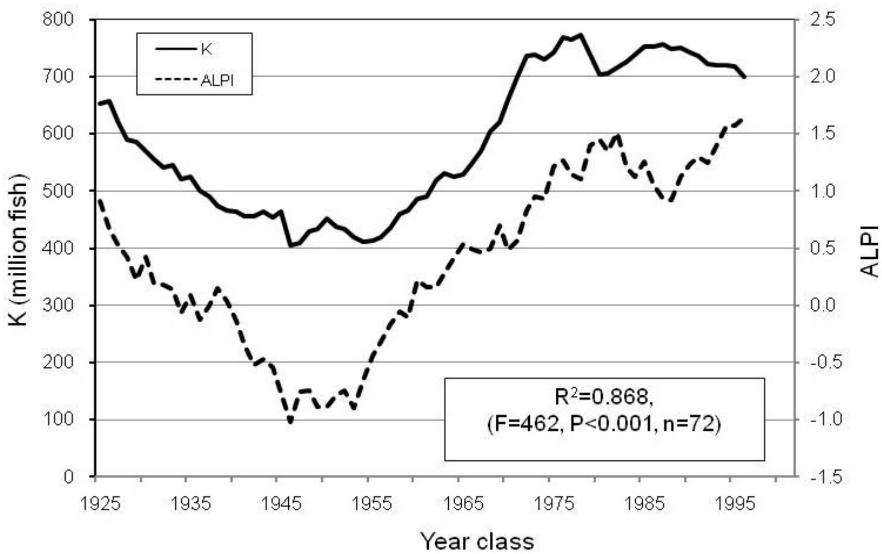

Fig. 9. Temporal changes in the Aleutian low pressure index (ALPI) and carrying capacity (K) of three species of Pacific salmon (sockeye, chum, and pink) for 1925-1997 year-classes.

In the 1998/99 change over the North Pacific, sea-surface temperatures and the upper water heat storage increased abruptly both in the Kuroshio/Oyashio Extension region in the western subarctic ocean and the central North Pacific, accompanied by cooling in the eastern North Pacific (Minobe 2002). These suggest that carrying capacities would have gradually changed to a downward trend since the 1998/99 regime shift.

REFERENCES

Beamish, R.J. (ed.). 2008. Impacts of climate and climate change on the key species in the fisheries in the North Pacific. PICES Sci. Rep. No. 35. 218 pp.

Beamish, R.J., and D. Bouillion. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. 50: 1002–1016.

Bond, N.A., J.E. Overland, M. Spillane and P. Stabeno. 2003. Recent shifts in the state of the North Pacific. Geophys.

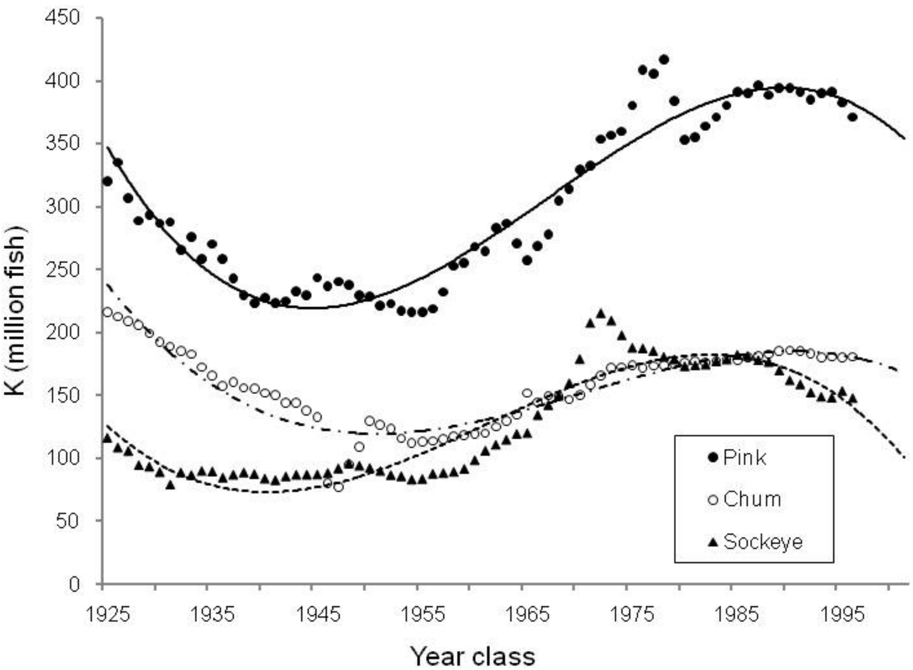

Fig. 10. Temporal changes in carrying capacity of sockeye, chum, and pink salmon for 1925-1997 year-classes.

Res. Lett. 30: doi:10.1029/2003GL018597.

Chavez, F.P., J. Ryan, S.E. Lluch-Cota, and M. Ñiquen C. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299: 217–221.

Eggers, D. E. 2004. Pacific salmon. *In* Marine ecosystems of the North Pacific. *Edited by* the PICES North Pacific Ecosystem Status Report Working Group. PICES, Sidney, B.C. pp. 227–261.

Fredin, R.A. 1980. Trends in North Pacific salmon fisheries. *In* Salmonid ecosystems of the North Pacific. *Edited by* W.J. McNeil and D.C. Himsworth. Oregon State University Press, Portland. pp. 50–119.

INPFC. 1979. Historical catch statistics for salmon of the North Pacific Ocean. Int. N. Pac. Fish. Comm. Bull. 39: 1–166.

Kaeriyama, M. 1998. Dynamics of chum salmon, *Oncorhynchus keta*, populations released from Hokkaido, Japan. N. Pac. Anadr. Fish Comm. Bull. 1: 90–102. (Available at www.npafc.org).

Kaeriyama, M. 2004. Evaluation of carrying capacity of Pacific salmon in the North Pacific Ocean for ecosystem-based sustainable conservation management. N. Pac. Anadr. Fish Comm. Tech. Rep. 5: 1–4. (Available at www.npafc.org).

Kaeriyama, M., and R.R. Edpalina. 2004. Evaluation of the biological interaction between wild and hatchery populations for sustainable fisheries management of Pacific salmon. *In* Stock enhancement and sea ranching, Second Edition. Developments, pitfalls and opportunities. *Edited by* K.M. Leber, S. Kitada, H.L. Blankenship, and T. Svasand. Blackwell Publishing, Oxford. pp. 247–259.

Kaeriyama, M., and M. Minagawa. 2008. Effects of anadromous fish on material transportations to the terrestrial ecosystem. *In* Discoveries in aquatic animal ecology presented by stable isotope scope - bivalve to whale. *Edited by* O. Tominaga and N. Takai. Koseisha-Koseikaku, Tokyo. pp. 110–123.

Mantua, N.J., S.R. Hare, Y. Zhang, J. M. Wallace, and R.C. Francis. 1987. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. 78: 1069–1079.

Marquardt, D.W. 1963. An algorithm for least-squares estimation of non-linear parameters. J. Soc. Ind. Appl. Math. 11: 431–441.

Minobe, S. 2000. Spatio-temporal structure of the pentadecadal variability over the North Pacific. Prog. Oceanogr. 47: 99–102.

Minobe, S. 2002. Interannual to interdecadal changes in the Bering Sea and concurrent 1998/99 changes over the North Pacific. Prog. Oceanogr. 55: 45–64.

Peterson, W.T., and F.B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. Geophys. Res. Lett. 30 (17), 1896, doi: 10.1029/2003GL017528.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191. 382 pp.

Rodionov, S., and J.E. Overland. 2005. Application of a sequential regime shift detection method to the Bering Sea ecosystem. ICES J. Mar. Sci. 62: 328–332.

Ruggerone, G.T., J.L. Nielsen, and J. Bumgarner. 2007.

Linkages between Alaskan sockeye salmon abundance, growth at sea, and climate, 1955–2002. Deep-Sea Res. II 54: 2776–2793.

White, B. 2008. Alaska salmon enhancement program 2007 annual report. Alaska Department of Fish and Game Fishery Management Report No. 08-03. 48 pp.

Yatsu, A., and M. Kaeriyama. 2005. Linkages between coastal and open-ocean habitats and dynamics of Japanese stocks of chum salmon and Japanese sardine. Deep-Sea Res. II 52: 727–737.