

Do Sea Surface Temperatures Influence Catch Rates in the June South Peninsula, Alaska, Salmon Fishery?

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Abstract: The influence of sea surface temperature (SST) on sockeye salmon catch per unit effort (CPUE) for the June south Alaska Peninsula fishery and on the run size of the western Alaska sockeye salmon was investigated for the period 1975–2008. CPUE was positively related to the size of the western Alaska sockeye salmon run but not to SST over the pooled time period. Time-stratified analysis before and after 1994/1993 revealed significant negative relations between the June fishery CPUE and winter and spring SST in the area to the east of the fishery. There were positive relations between the size of the western Alaska run and SST for temperature time series in the central Bering Sea, eastern Aleutian Islands, and between Kodiak and the Shumagin islands for one- and two-year lags prior to the adult return. Time-stratified analysis showed that there were significant changes in the influence of temperature on the June fishery CPUE and in the size of the western Alaska run. Combined the results suggest that warming temperatures in the Bering Sea have shifted regions of importance to the west for all ocean ages.

Keywords: sockeye salmon, sea surface temperature, ocean distribution, migration, western Alaska, Bering Sea, Alaska Peninsula, CPUE

INTRODUCTION

During June a coastal net fishery takes place on the Pacific Ocean side of the Alaska Peninsula and eastern Aleutian Islands targeting maturing sockeye salmon (*Oncorhynchus nerka*) with an incidental harvest of maturing chum salmon (Rogers 1986). Annual catches are typically between one and two million sockeye salmon and about one quarter that number for chum salmon (*O. keta*). Tagging studies have identified the majority of the sockeye salmon catch as of Bristol Bay origin (Eggers et al. 1991). Results of genetic stock identification show that the majority of the chum salmon catch is of western Alaska origin with one-quarter to one-third of Asian origin (Seeb and Crane 1999).

Most of the variance in June fishery sockeye salmon catches can be explained by a positive linear relation between catches and the total western Alaska sockeye salmon abundance alone ($P = 5.8 \times 10^{-7}$, $R^2 = 0.55$). Catch per unit effort (CPUE) in the fishery has been highly variable over time but is not closely related to changes in the management of the fishery (Fig. 1). For example, the depth of nets allowed in the fishery was reduced and restricted for the first time in 1990 following the year with the highest CPUE on record. Following modest CPUE in 1990 and 1991, the sockeye salmon CPUE in 1992 and 1993 were the third and fourth highest on record. Since 1994 the average June south Peninsula fishery sockeye salmon CPUE has dropped by about 30% while western Alaska sockeye salmon abundance has been above average. Years such as 1996 with near record re-

turns of sockeye salmon to Bristol Bay but unexpectedly low CPUE in the June fishery have prompted speculation that the availability of salmon to the fishery is influenced by environmental conditions along the migratory path of salmon at sea (Poetter 2009).

The freshwater reproductive and early life history of salmon is relatively attractive for study, but salmon populations experience most of their mortality at sea (Groot and Margolis 1991). Variability in marine survival is thus closely related to the abundance of returns. There has been considerable work aimed at understanding the influence of climatic variables such as sea surface temperature (SST) on growth, distribution and production of salmon (Beamish and Boullion 1992; Francis and Hare 1994; Adkison et al. 1996). These studies have focused on large-scale effects frequently related to the regime shift in about 1977 that marked the beginning of the present period of high production. Both Rogers (1987) and Isakov et al. (2000) studied the effects of temperature on growth of Bristol Bay sockeye salmon and found the greatest effects in the early marine life history stages. Francis and Hare (1994) have shown that the abundance of western Alaska sockeye salmon adult returns is correlated with winter temperatures on Kodiak Island two years prior. Welch et al. (1995, 1998) have shown that salmon distributions at sea have sharp thermal limits that vary by area during different months of the year.

Nagasawa et al. (2005) found a strong positive relation between sea surface temperature trends along the dateline in the Bering Sea in July and trends in CPUE of immature

sockeye and chum salmon in Bering Sea research gillnet surveys ($P = 8.15 \times 10^{-7}$, $R^2 = 0.586$). Greater abundance of immature fish with warmer temperatures would be consistent with a greater proportion of western Alaska sockeye salmon using a larger area in the Bering Sea for a longer period in the summer. This would correspond to a reduced distribution in the North Pacific during the following winter and spring. Perry et al. (2005) relate distribution shifts for marine fishes to SST changes in the North Sea using CPUE data and suggest “profound impacts on commercial fisheries through continued shifts in distribution and alteration of community interactions”. They also found that species with rapid generational turnover were more likely to show changes in marine distribution.

Because the June fishery is restricted to a relatively small nearshore area, changes in the migratory path of maturing salmon could have a large impact on availability to the fishery. Thus previous research suggests that SST might influence June CPUE both via changes in western Alaska sockeye salmon abundance and changes in ocean distribution and migration patterns (Beamish and Bouillon 1993; Francis and Hare 1994; Welch et al. 1995, 1998; Nagasawa et al. 2005; Perry et al. 2005). For example, later departure from the Bering Sea after summer feeding would limit the extent of eastward migration in the Subarctic Current in the winter. Reduced eastward distribution in winter would result in a westward migration farther offshore in the Alaskan Stream in spring with lower availability to the June fishery. The purpose of this study is to evaluate the potential importance of SST at specific ocean areas and times on the June fishery CPUE and to determine whether the importance of those locations has changed in concert with changes in the June fishery CPUE.

First I hypothesize that the June fishery CPUE is positively related to western Alaska sockeye salmon abundance and to SST in five regions of the North Pacific and Bering Sea from 1975–2008 and that there are significant changes

in those relations before and after 1994/1993. Second, I hypothesize that the abundance of western Alaska sockeye salmon has been positively related to SST in those five regions from 1975–2008 and that those relations also changed before and after 1994/1993.

MATERIALS AND METHODS

Sea Surface Temperature

Five locations were chosen to evaluate the influence of temperature by region on the June south Peninsula fishery catch rates (Fig. 2). T. Nagasawa (nagasat@affrc.go.jp, unpublished data) provided time series of SST for the Bering Sea and for an area near the eastern Aleutian Islands which includes the location of the June south Peninsula fishery. He has identified these areas as particularly important for immature sockeye salmon at sea. A Kodiak winter air temperature time series was constructed from the Alaska Climate Research Center (<http://climate.gi.alaska.edu/Climate/Location/Time-Series/Data/adqT>) to serve as a surrogate for SST, according to Francis and Hare (1994). An average for each year was computed by averaging the monthly average air temperatures for the period November through March, where March is the identified year. Time series of direct observation of SST are lacking for the winter and spring from the Gulf of Alaska and North Pacific Ocean in the vicinity of the Alaska Peninsula. However a global time series of average monthly SSTs (Smith-Reynolds Optimum Interpolation SSTs) is available for sub-sampling online at the NOAA site (http://nomads.ncdc.noaa.gov/cgi-bin/ncdc-ui/define-collection.pl?model_sys=sst&model_name=ersst&grid_name=999). For the Gulf of Alaska area between 55°N–60°N, 140°W–150°W, I extracted the minimum monthly average SST for each year, usually occurring in February or March in order to test whether the degree of extreme cold might keep fish

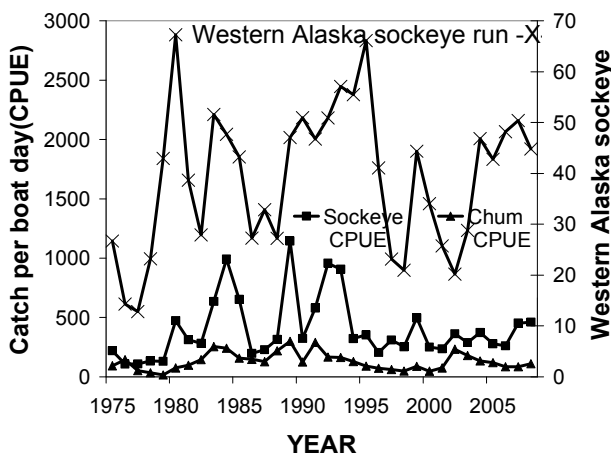
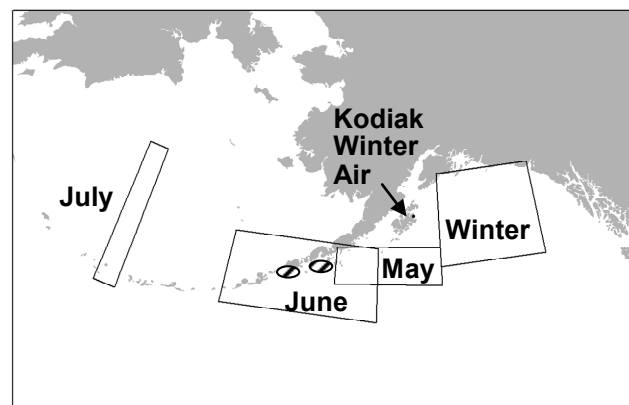


Fig. 1. Western Alaska sockeye run size and June south Peninsula fishery catch per boat per day for sockeye and chum salmon, 1975–2008.



○ - Locations of June South Peninsula Fishery
 □ - Boundaries of Sea Surface Temperature Areas

Fig. 2. Location of the June south Peninsula fishery and areas of temperature time series.

farther offshore. For the area offshore and between Kodiak and the Shumagin islands bounded by 54°N–56°N, 150°W–160°W, I extracted the May average SST. Maturing adult salmon migrate through this area in the period immediately preceding the fishery. The four time series of SST and one SST surrogate are shown in Table 1.

Catch per Unit Effort

Catch and effort information for the June south Penin-

sula fishery were obtained from the Alaska Department of Fish and Game (ADF&G) (Poetter 2009). The abundance of the western Alaska sockeye salmon run was computed from ADF&G data files as the sum of catch plus escapement for Chignik, the north Alaska Peninsula and Bristol Bay. Abundance, catch, effort and CPUE data are shown in Table 2.

Catches may not be simply dependent on availability of sockeye salmon during June along the south Peninsula. Throughout most of the period of this study, 1975–2008, fishing time in the June fishery was regulated based on fore-

Table 1. Temperature by time and area for the North Pacific Ocean and Bering Sea.

Year	July Bering Sea ¹	June Eastern Aleutian ¹	May Kodiak-Shumagin ²	Kodiak winter Air ³	Gulf winter monthly minimum ²
1972	7.28	5.22	5.06	-2.51	2.87
1973	7.03	5.53	5.09	-1.78	4.06
1974	8.10	6.21	5.62	-1.29	3.83
1975	6.63	5.23	4.84	-2.53	4.53
1976	6.85	5.65	4.85	-2.42	4.07
1977	7.95	7.13	5.59	1.68	5.46
1978	7.43	6.55	5.84	0.23	4.77
1979	7.55	7.39	5.88	1.97	4.47
1980	7.98	6.29	5.35	0.63	4.29
1981	8.58	7.69	6.38	1.99	4.84
1982	6.85	5.96	4.96	0.42	4.07
1983	7.60	7.31	6.19	2.41	4.79
1984	8.10	7.73	6.05	1.43	5.28
1985	7.30	5.91	5.12	1.62	4.77
1986	7.95	6.24	5.64	0.58	4.84
1987	7.20	6.34	5.64	1.92	5.12
1988	7.55	6.63	5.39	0.28	4.91
1989	7.78	6.15	5.70	-1.03	3.70
1990	8.20	6.79	6.22	-0.50	3.99
1991	7.80	6.56	5.56	-0.83	4.34
1992	6.98	7.23	5.97	0.09	4.88
1993	7.73	7.19	6.35	-0.14	4.29
1994	7.50	6.96	5.79	0.83	4.94
1995	7.88	6.40	6.00	-0.90	4.47
1996	8.43	6.97	6.45	0.39	4.42
1997	8.35	7.83	6.18	0.34	4.54
1998	8.03	6.73	5.92	0.56	5.42
1999	7.15	5.92	4.78	-2.14	4.29
2000	8.05	6.69	5.75	-0.97	4.19
2001	7.15	7.13	5.99	1.46	5.11
2002	8.03	6.89	5.78	-0.88	4.17
2003	8.25	6.97	6.27	1.83	5.80
2004	8.10	6.99	6.27	-0.31	4.86
2005	7.91	NA ⁴	7.11	1.33	5.14
2006	7.24	NA	5.65	-0.98	4.40
2007	7.30	NA	5.09	-2.77	3.77
2008	7.44	NA	4.68	-0.87	4.21

¹Provided from T. Nagasawa

²NOAA NCD C Smith-Reynolds Optimum Interpolation SST

³Alaska Climate Research Center average of monthly values

⁴Data not available

Table 2. Effort, catch and CPUE for the June south Alaska Peninsula fishery and total western Alaska sockeye salmon abundance.

Year	Days fished	Units of gear	Gear days	Sockeye catch (x 1000)	Sockeye CPUE	Chum catch (x 1000)	Chum CPUE	Western Alaska sockeye run (millions)*
1975	10	109	1,090	240	220	101	93	26.7
1976	19	149	2,831	305	108	410	145	14.3
1977	17	131	2,227	242	109	116	52	12.8
1978	23	159	3,657	487	133	122	33	23.2
1979	33	198	6,534	851	130	104	16	42.9
1980	30	226	6,780	3,206	473	509	75	67.3
1981	24	243	5,832	1,821	312	564	97	38.6
1982	30	251	7,530	2,119	281	1,095	145	27.9
1983	11	281	3,091	1,964	635	786	254	51.6
1984	5	280	1,400	1,388	991	337	241	47.7
1985	9	305	2,745	1,791	652	434	158	43.3
1986	8	298	2,384	471	198	352	148	27.3
1987	12	290	3,480	794	228	443	127	32.8
1988	8	301	2,408	757	314	527	219	27.2
1989	5	305	1,525	1,745	1,144	455	298	47.1
1990	13	321	4,173	1,345	322	519	124	51.0
1991	8	334	2,672	1,549	580	773	289	46.8
1992	8	321	2,568	2,458	957	426	166	50.9
1993	10	328	3,280	2,974	907	532	162	57.1
1994	14	324	4,536	1,461	322	582	128	55.5
1995	18	331	5,958	2,105	353	537	90	66.1
1996	16	313	5,008	1,029	205	360	72	41.1
1997	18	292	5,256	1,628	310	322	61	23.1
1998	18	283	5,094	1,289	253	246	48	21.0
1999	10	277	2,770	1,375	496	245	88	44.4
2000	18	278	5,004	1,251	250	239	48	34.0
2001	5	128	640	151	236	48	75	25.7
2002	9	181	1,629	591	363	379	233	20.2
2003	9	177	1,593	453	288	282	179	28.8
2004	19	190	3,610	1,348	373	482	134	46.8
2005	19	190	3,610	1,004	278	428	119	42.8
2006	19	188	3,572	932	261	300	84	48.2
2007	19	185	3,515	1,590	452	298	85	50.4
2008	19	196	3,724	1,714	460	411	110	44.8

* Catch plus escapement for Chignik, north Alaska Peninsula and Bristol Bay.

casts of abundance of Bristol Bay sockeye salmon. Effort, measured as the product of the total number of days the fishery was open and the total number of vessels fishing during the month, varied over a wide range as the result of management measures and variable participation by fishermen. Adding effort as an independent variable in step-wise multiple regression only results in a small change in the amount of variance explained in the relation between June fishery catches and total western Alaska sockeye salmon abundance ($P = 2.15 \times 10^{-7}$, $R^2 = 0.63$ vs. $P = 5.8 \times 10^{-7}$, $R^2 = 0.55$). Because management measures had a relatively small effect on catches, CPUE should be a measure of the availability

of salmon to the June fishery. The time series of CPUE for sockeye salmon and the CPUE for chum salmon have a significant linear positive relation ($P = 4.4 \times 10^{-5}$, $R^2 = 0.42$). However, total abundance data are only available for sockeye salmon, so the balance of the analysis was restricted to sockeye salmon.

Regressions

Regressions and step-wise multiple regressions were performed between time series of annual June south Peninsula fishery CPUE, the abundance of the western Alaska

sockeye salmon run, and five SST time series for the areas in Fig. 2 for the same year and for lags in temperature preceding the catch by 1, 2, and 3 years. Adult returns in a single year incorporate several ages since out-migration. Rogers (1987) and Isakov et al. (2000) have shown that age since out-migration is most important with respect to the influence of temperature on growth and subsequent survival. This analysis, similar to that of Francis and Hare (1994) but different from Rogers (1987) and Isakov et al. (2000) was conducted from the perspective of year of adult return which results in a dilution of the power of the analysis.

The analysis was performed for all years combined and separately for the periods 1975–1993 and 1994–2008 in order to detect changes that might be associated with the apparent shift in CPUE in the fishery. An important consequence of partitioning the 34-year time series is the reduction in sample size by a factor of two with a consequent reduction in analytical power.

Ryding and Skalski (1999) found a non-linear relation between SST and survival for hatchery released coho salmon

(*O. kisutch*) in Washington State which they evaluated with quadratic regressions and interpreted as reflective of an optimum for survival of salmon in the marine environment. In this study, all linear regressions were evaluated for evidence of such an optimal relation and a quadratic model was fit for the case where it occurred in the Bering Sea.

RESULTS

Time-Pooled Analysis

June CPUE and SST

There were no areas with statistically significant relations between June fishery CPUE and SST over the period 1975–2008.

June CPUE and Western Alaska Run Size

There is a significant positive relation between CPUE in the June fishery and total western Alaska sockeye salmon abundance ($P = 0.001$, $R^2 = 0.284$, $b = 9.9$) over the period

Table 3. Results of regression analysis of sea surface temperature with June south Peninsula sockeye salmon CPUE (A) and with the run size of the western Alaska sockeye salmon (B). Asterisks * and ** indicate $P < 0.05$ and $P < 0.01$, respectively. Bold italic categories reflect a decrease in importance across time-stratified analysis.

A. June south Peninsula sockeye salmon CPUE										
Area	Time-pooled analysis				Time-stratified analysis					
	Lag (years)	P	R ²	b (°C)	1975–1993			1994–2008		
May Kodiak-Shumagin	0	0.760	0.003	25.7	0.137	0.125	244.8	0.002	0.521	-100.8
Kodiak Winter Air	0	0.800	0.002	-8.5	0.964	0.000	-2.6	0.005	0.473	-46.0
May Kodiak-Shumagin + Kodiak Winter Air								<i>P</i>	<i>R²</i>	<i>b</i>
								0.006	0.578	-65.73 -23.18
Western Alaska Sockeye run size	0	<i>0.001**</i>	<i>0.284</i>	<i>9.9</i>	<i>0.002**</i>	<i>0.450</i>	<i>15.2</i>	<i>0.193</i>	<i>0.126</i>	<i>2.3</i>
June south Peninsula CPUE			400			458			327	

B. Western Alaska sockeye salmon run size										
Area	Time-pooled analysis				Time-stratified analysis					
	Lag (years)	P	R ²	b (10 ⁶ /°C)	1975–1993			1994–2008		
July Bering Sea	1	<i>0.009**</i>	<i>0.263</i>	parabolic	0.138	0.129	b (10 ⁶ /°C) parabolic	0.034*	0.430	parabolic
June Eastern Aleutian	1	0.124	0.080	6.6	0.037*	0.231	10.3	<i>0.698</i>	<i>0.016</i>	<i>-4.0</i>
	2	0.017*	0.175	9.3	0.073	0.177	8.7	0.054	0.297	17.3
May Kodiak-Shumagin	1	0.155	0.062	6.7	0.061	0.191	14.2	<i>0.860</i>	<i>0.002</i>	<i>1.2</i>
	2	0.024*	0.150	10.4	0.0498*	0.208	14.6	<i>0.180</i>	<i>0.134</i>	<i>10.0</i>

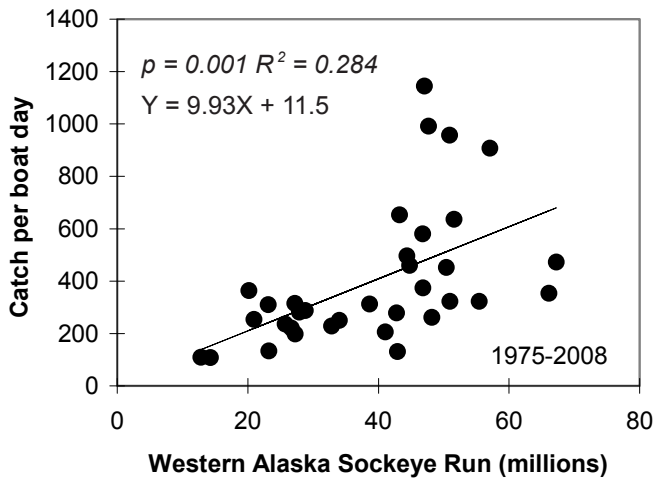


Fig. 3. Relation between June south Peninsula sockeye CPUE and the size of the western Alaska sockeye run, 1975–2008.

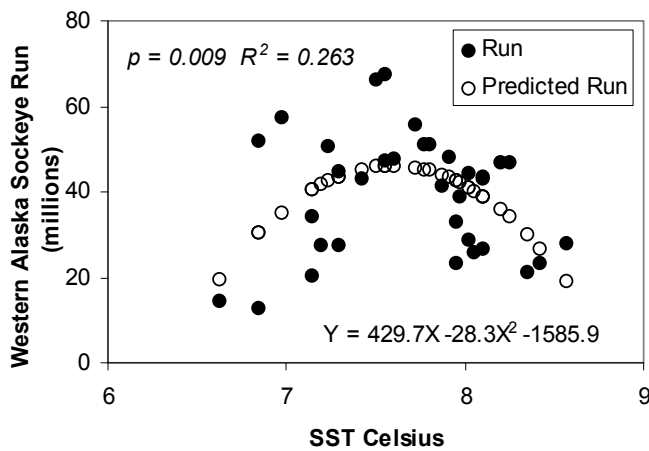


Fig. 4. Relation between western Alaska adult sockeye salmon abundance and previous year July Bering Sea dateline sea surface temperature, 1975–2008.

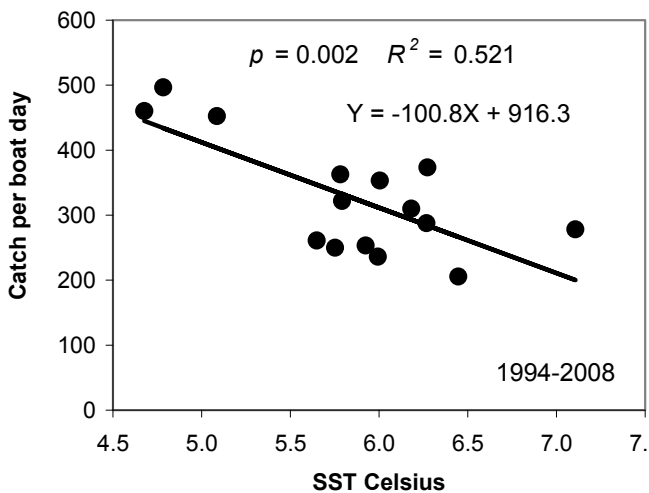


Fig. 5. Relation between June south Peninsula sockeye salmon CPUE and May Kodiak-Shumagin SST 1994–2008.

(Table 3A, Fig. 3). Addition of each of the temperature time series to the abundance of the western Alaska sockeye salmon run size in step-wise multiple regression did not result in significant improvement in the explanatory power with respect to the June fishery CPUE. This was true at lags in temperature with respect to the year of adult returns of one, two and three years.

Western Alaska Run Size and SST

There are significant positive relations between total western Alaska sockeye salmon abundance and July Bering Sea, June eastern Aleutian and May Kodiak-Shumagin SST (Table 3B). A narrow range of July Bering Sea temperatures produced uniformly large returns of sockeye salmon to western Alaska the next year. The temperature range 7.40–7.93°C corresponds to average returns one year later of 52 million, with a minimum return of 41 million fish. Cooler years averaged 29 million and warmer years averaged 34 million adult sockeye salmon returning to western Alaska. While there was no significant relation between the abundance of western Alaska sockeye salmon and a linear model for the previous year July Bering Sea SST, the relation with the parabolic model was significant ($P = 0.009$, $R^2 = 0.263$) for temperatures the summer previous to the adult return (Fig. 4).

Temperatures two years prior to the adult return were positively related to the adult return for both June eastern Aleutian SST ($P = 0.017$, $R^2 = 0.175$, $b = 9.3$ M/°C) and May Kodiak-Shumagin SST ($P = 0.024$, $R^2 = 0.150$, $b = 10.4$ M/°C). One-year lags in temperature ahead of year of adult return did not produce significant results for these same areas over the 1975–2008 time period.

For time-pooled analysis the null hypothesis that there are no significant relations between June fishery CPUE and SST is not rejected ($P < 0.05$) but the null hypothesis of no significant relation between June CPUE and the size of the western Alaska sockeye salmon run is rejected ($P < 0.01$).

Time-Stratified Analysis

June CPUE and SST

The only significant relations between June south Peninsula sockeye salmon CPUE and SST occur for the period 1994–2008 for May Kodiak-Shumagin ($P = 0.002$, $R^2 = 0.521$, $b = -100.8$) and Kodiak winter air temperature ($P = 0.005$, $R^2 = 0.473$, $b = -46.0$) (Table 3A, Fig. 5). Cooler winter and spring temperatures to the east of the fishery are related to higher CPUE in June.

June CPUE and Western Alaska Run Size

The significant positive relation from 1975–2008 between June fishery CPUE and the size of the western Alaska run is split before and after 1994/1993 with a significant relation for the early period ($P = 0.002$, $R^2 = 0.450$, $b = 15.2$) but not for the late ($P = 0.193$, $R^2 = 0.126$, $b = 2.3$). In step-wise multiple regressions for the period 1994–2008 the size

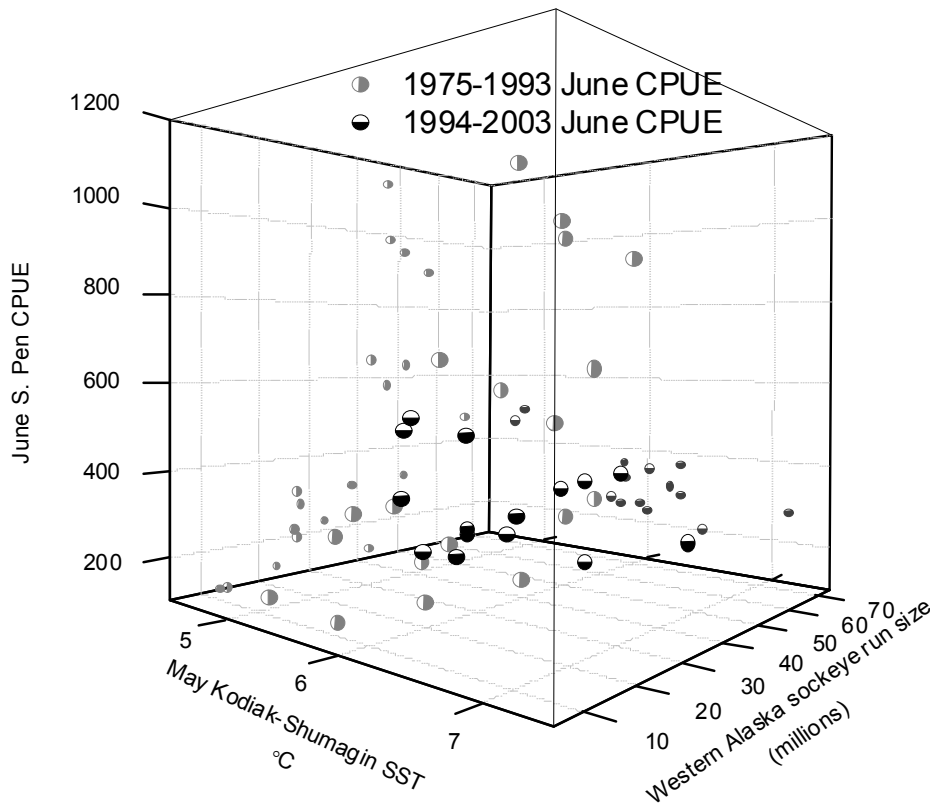


Fig. 6. The combined effect of May Kodiak-Shumagin SST and the size of the western Alaska sockeye salmon run on June south Peninsula sockeye CPUE for time-stratified analysis. Small grey symbols on the CPUE/western Alaska run size plane and small black symbols on the CPUE/May Kodiak-Shumagin SST plane show the shift of dominant influence on June CPUE from the size of the western Alaska sockeye salmon run for 1975–1993 ($P = 0.002$, $R^2 = 0.450$) to the May Kodiak-Shumagin SST from 1994–2008 ($P = 0.002$, $R^2 = 0.521$). See Figs. 3 and 5.

of the western Alaska sockeye salmon run adds only a little explanatory power with respect to the June fishery CPUE compared to those of each of May Kodiak-Shumagin and Kodiak winter air temperature time series alone.

The combined effects of temperature and the size of the western Alaska sockeye salmon run on the June south Peninsula sockeye salmon CPUE over the period 1975–2008 appear to have been dominated by the positive relation with size of the western Alaska sockeye salmon run, but since 1994 temperatures immediately to the east of the fishery have had a significant effect. The combined effects of different dominant influences on June CPUE before and after 1994/1993 are shown in a composite 3D view of June CPUE against western Alaska run size and May Kodiak-Shumagin SST with the respective 2D linear relations shown in the background (Fig. 6).

Western Alaska Run Size and SST

For immature sockeye salmon (one-year lag) the area of greatest influence on the size of the adult return in the early period was the June eastern Aleutian Islands ($P = 0.037$, $R^2 = 0.231$, $b = 10.3$), while in the later period the region of greatest importance had shifted to the central Bering Sea ($P = 0.034$, $R^2 = 0.430$) with very little influence of temperature in the June eastern Aleutian and May Kodiak-Shumagin ar-

ea ($P = 0.698$, $R^2 = 0.016$, $b = -4.0$; $P = 0.860$, $R^2 = 0.002$, $b = 1.2$, respectively). The influence of a narrow range of temperatures in the central Bering Sea on the size of the western Alaska sockeye salmon run increased from the early period (Table 3B, Fig. 7). For juvenile sockeye salmon (two-year

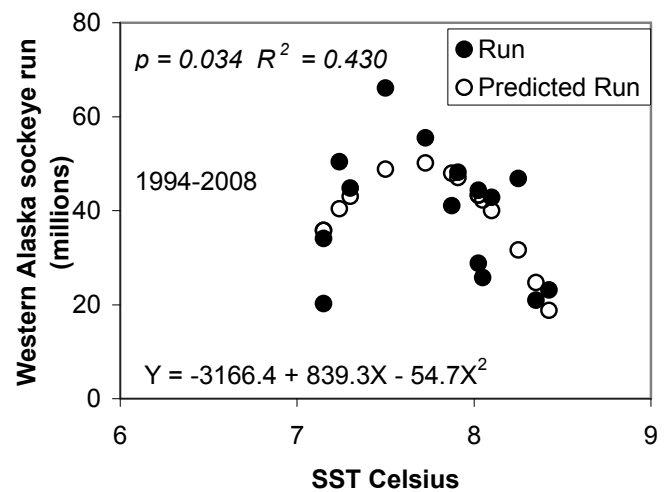


Fig. 7. Relation between western Alaska adult sockeye salmon abundance and previous July Bering Sea dateline sea surface temperature, 1994–2008.

lag) the greatest decline in area of importance was for the May Kodiak-Shumagin which had been more important than the June eastern Aleutians in the early period but became less important in the later period. For juvenile sockeye salmon the June eastern Aleutians area has become somewhat more important in the recent period ($P = 0.054$, $R^2 = 0.297$, $b = 17.3$).

For time-stratified analysis, the null hypothesis that there are no changes in significance of relations across the time strata for the influence of SST on June CPUE is rejected for two of the five areas examined ($P < 0.01$). Kodiak-Shumagin May SST and Kodiak winter air temperatures both have had a significant negative relation with June CPUE since 1994 but not before. The null hypothesis of no change in significance for the influence of the size of the western Alaska sockeye salmon run on June CPUE is also rejected ($P < 0.01$). The positive relation of western Alaska sockeye salmon on June CPUE from 1975–1993 is not significant for the later period.

The null hypothesis that there are no changes in the significance of relations across the time strata for the influence of SST on the size of the western Alaska sockeye salmon run is also rejected ($P < 0.05$). For one year of lag between SST and abundance, the Bering Sea became more important and the eastern Aleutians area became less important after 1993. For two years of lag of SST to adult run size, the Kodiak-Shumagin area became less important after 1993.

DISCUSSION

There is a clear pattern of decreasing influence of temperature on western Alaska sockeye salmon run size for most maturity stages of sockeye salmon in areas to the east of the Bering Sea, and an increase in the influence of temperature in the central Bering Sea with time. For maturing sockeye salmon, June south Peninsula CPUE was positively correlated with the abundance of the western Alaska sockeye salmon run before 1994 ($P = 0.002$, $R^2 = 0.450$, $b = 15.2/M$ run) but not after.

If the abundance of maturing adults is primarily driven by marine mortality then juvenile sockeye salmon appear to be about 50% more sensitive to temperature than immature sockeye salmon for the time-pooled analysis (b_2/b_1 ; $(9.3 + 10.4)/(6.6 + 6.7) = 1.48$). For the 1975–1993 period in time-stratified analysis the influence of temperature by age is not apparent, but for the combined maturity stages temperatures in May to the east of the Shumagin Islands were about 50% more important than temperatures in June to the west of the Shumagins for survival to adult maturity. Apparently at sea younger western Alaska sockeye salmon initially utilized waters offshore of the eastern Aleutian Islands, Alaska Peninsula, Kodiak, and the Shumagin Islands and only as immatures relied significantly on waters of the Bering Sea (Table 3B).

Time-stratified analysis by maturity stage in the eastern Aleutians and Kodiak-Shumagin areas shows that the in-

fluence of temperature on the survival of immature fish to adult maturity virtually vanished for the 1994–2008 period which suggests that there was a reduction in use of these areas during the later period. In contrast, the effect of temperature on immature sockeye salmon survival to adult maturity increased in the central Bering Sea between the early and late periods in time-stratified analysis. These apparent shifts in use are probably a combination of changes in both the seasonality of use and annual use. The selection of the May–June time period was intended primarily to address the adult maturity stage with respect to the June south Peninsula fishery, and analysis of other seasons might produce different results for younger maturity stages.

Earlier work by Francis and Hare (1994), Rogers (1987), and Isakov et al. (2000) found evidence for the importance of Gulf of Alaska temperatures for growth and survival of juvenile sockeye salmon. Both studies relate the influence of temperature to possible ocean distribution early in marine life. The later period in the time-stratified analysis of this study continues well after the years of the earlier studies, and it appears that shifts in areas of influence and implied shifts in migration patterns have occurred. Temporal-spatial shifts in oceanic habitat utilization over time are probably normal.

Unlike the studies mentioned above, this analysis included temperatures from the central Bering Sea. It is interesting that a narrow range of SST in the middle of the Bering Sea is correlated with strong production of western Alaska sockeye salmon, probably reflecting an environmental optimum to which these populations are adapted. This effect has been stronger since 1994 than from 1975–1993.

Spatial Considerations

The apparent shifts in area of use for juvenile and immature sockeye salmon are likely to have occurred for maturing fish as well. If the June south Alaska Peninsula fishery location were in a position central to the shoreward distribution of sockeye salmon returning to the Bering Sea then variations in run size should be reflected in a positive relation with the June fishery CPUE. The data show that this was the case before 1994 but not since, which suggests that the fishery takes place at the eastern and shoreward margins of the migration of sockeye salmon toward the Bering Sea.

Warmer temperatures in the Bering Sea likely lead to expansion of the margins of optimal habitat for immature sockeye salmon up to about 7.6°C. Above that temperature the location of the optimal habitat is likely further north, although the areal extent of optimal habitat may start to diminish. Warmer July temperatures also imply a longer duration of suitable habitat in the Bering Sea. The combination of more northerly distributions and longer durations in the Bering Sea must result in shorter durations and less geographic extent for immature sockeye salmon in the North Pacific through the next winter. Apparently the eastward extent of immature sockeye salmon has been reduced enough by ex-

tended use of the Bering Sea to lead to reduced CPUE of maturing salmon in the south Peninsula fishery the following June.

One model which is consistent with the aggregate of these results focuses on the role of the Alaskan Stream in the homeward migration of maturing salmon. The Alaskan Stream may act as a collector and conveyor to the west for salmon across a wide area of the eastern North Pacific Ocean. If photoperiod were the dominant factor over SST on the timing of northward departure from the Alaskan Stream toward the Alaska Peninsula and Aleutian passes into the Bering Sea this would be consistent with the observed stable timing of catches in the June south Peninsula fishery. If SST were the dominant factor in the timing of the initiation of migration northward into the Alaskan Stream then warmer conditions would result in a more westerly distribution within the Alaskan Stream prior to departure toward the Alaska Peninsula and Aleutian passes. This is consistent with the observed lower CPUE in the June fishery in spite of high abundance during the warm period from 1994–2005. Homeward migration may also be more protracted in time and space for warmer years where the onset of migration occurs earlier. The corollary is that the distribution of returning adults in cooler years would be relatively more concentrated in time and space and further to the east which is consistent with the observed higher CPUE in cooler springs. If ocean distributions are far enough to the east of the June fishery, the abundance of western Alaska sockeye salmon could become the dominant factor in the June fishery CPUE instead of nearby spring SST. The interplay of these factors, and doubtless many others, must be variable and subtle.

French and Bakkala (1974) found “Evidence of varying catch rates of Bristol Bay sockeye salmon by the Japanese mothership fishery west of longitude 175°W (rates have varied between years from 2.2 to 35.2% of the total run) suggests that the distribution of maturing sockeye salmon shifts to the east in fall and winter and that the magnitude and extent of this movement governs the availability of sockeye salmon to the Japanese fishing fleet.” This variability is remarkably similar to the results for the June fishery CPUE, with the difference that the June fishery harvest rate on Bristol Bay stocks is much smaller (ave. ~3%, range 2–8%). It seems likely that variations in east-west distribution would have reciprocal influence on catch rates in each fishery and that SST is a major factor contributing to variations in the east-west distributions.

Changes in Temperature Trends

The influence of temperatures from the years 2006–2008 on trends in the time series is significant. All three of the time series west of Kodiak had significant warming trends from 1975–2005 but the addition of the last three years of data has diminished the significance those trends. Data are not available for the June eastern Aleutian SST time series

since 2004, but cooling for the July Bering Sea dateline and May Kodiak-Shumagin time series since 2005 has decreased the slope of the those temperature relations since 1975 by a factor of two in just three years (decreased R^2 by a factor of three and increased $P > 0.05$). If warming SSTs account for the reductions in the June fishery CPUE since 1994 it will be interesting to see if cooling will reverse that effect. June fishery CPUE increased in 2007 and 2008, which were the coldest and seventh coldest temperatures for the May Kodiak-Shumagin area in the 34-year analysis period. Temperatures from the years 2006–2008 for July Bering Sea on the dateline were in the cooler half of the 34-year temperature range but not at the coldest end of that range.

CONCLUSIONS

A variety of management measures were implemented for the June south Peninsula fishery throughout the period of this study and while those measures are certain to have produced variations in CPUE it is notable that environmental factors are still apparent in the relation between CPUE and SST. One interpretation of these results is that there may be a geographic cline from east to west for the importance of environmental factors on all stages of marine life for western Alaska sockeye salmon and that there may have been a shift to the west for this cline around 1994. The evidence of an optimum temperature in the Bering Sea with respect to adult abundance suggests that the extended period of high western Alaska sockeye salmon production is a consequence of a historically unprecedented period of near-optimal utilization of the Bering Sea.

Implementation of a similar analysis but with the incorporation of ocean age-specific returns as those data become available should further clarify the potential for shifts in regions of importance for the marine survival of sockeye salmon. Sea surface temperature databases performed well relative to the Kodiak winter air time series with respect to effects on juvenile (two-year lag) and immature sockeye salmon.

To the extent that the Alaskan Stream may be an important factor in the migration of maturing salmon south of the Alaska Peninsula and Aleutian Islands, some means to measure and understand its movement is needed. Finer spatial resolution for measurement of SST from satellite observations might be enough to provide some insight into variations in the position of the Stream and the consequences for CPUE of nearshore fisheries. Salinity is also important for salmon migration (Fujii 1975) and it should not be neglected in spite of the difficulty in measuring it remotely.

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