Pink salmon (*Oncorhynchus gorbuscha*) marine survival rates reflect early marine carbon source dependency

Thomas C. Kline Jr. [a,*], Jennifer L. Boldt [b], Edward V. Farley Jr. [c], Lewis J. Haldorson [d], John H. Helle [c]

[a] *Prince William Sound Science Center, Cordova AK 99574, USA*
[b] *School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA*
[c] *Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, Alaska 99821, USA*
[d] *Fisheries Division, University of Alaska, Fairbanks, 11120 Glacier Highway, Juneau, AK 99801, USA*

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ABSTRACT

Marine survival rate (the number of adult salmon returning divided by the number of salmon fry released) of pink salmon runs propagated by Prince William Sound, Alaska (PWS) salmon hatcheries is highly variable resulting in large year-to-year run size variation, which ranged from ~20 to ~50 million during 1998–2004. Marine survival rate was hypothesized to be determined during their early marine life stage, a time period corresponding to the first growing season after entering the marine environment while they are still in coastal waters. Based on the predictable relationships of $^{13}C/^{12}C$ ratios in food webs and the existence of regional $^{13}C/^{12}C$ gradients in organic carbon, $^{13}C/^{12}C$ ratios of early marine pink salmon were measured to test whether marine survival rate was related to food web processes. Year-to-year variation in marine survival rate was inversely correlated to $^{13}C/^{12}C$ ratios of early marine pink salmon, but with differences among hatcheries. The weakest relationship was for pink salmon from the hatchery without historic co-variation of marine survival rate with other PWS hatcheries or wild stocks. Year-to-year variation in $^{13}C/^{12}C$ ratio of early marine stage pink salmon in combination with regional spatial gradients of $^{13}C/^{12}C$ ratio measured in zooplankton suggested that marine survival was driven by carbon subsidies of oceanic origin (i.e., oceanic zooplankton). The 2001 pink salmon cohort had $^{13}C/^{12}C$ ratios that were very similar to those found for PWS carbon, i.e., when oceanic subsidies were inferred to be nil, and had the lowest marine survival rate (2.6%). Conversely, the 2002 cohort had the highest marine survival (9.7%) and the lowest mean $^{13}C/^{12}C$ ratio. These isotope patterns are consistent with hypotheses that oceanic zooplankton subsidies benefit salmon as food subsidies, or as alternate prey for salmon predators. Oceanic subsidies are manifestations of significant exchange of material between PWS and the Gulf of Alaska. Given that previously observed inter-decadal cycles of oceanic zooplankton abundance were climatically driven, exchange between PWS and the Gulf of Alaska may be an important process for effecting synoptic changes in marine populations of higher trophic levels, and thus an important consideration for climate-change models and scenarios.

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1. Introduction

Pink salmon (*Oncorhynchus gorbuscha*) is the most numerous Pacific salmon species and contributes to major fisheries. In Alaska, as of 2006, about 100 million pink salmon are caught annually, comprising ~80% of the state's salmon fishery (http://www.cf.adfg.state.ak.us/geninfo/finfish/salmon/salmon_harvest.php#forecasts).

Consequently, fluctuations in the size of pink salmon runs drive variability in the size of the total annual salmon harvest in Alaska.

The size of pink salmon populations returning to Prince William Sound (PWS) hatcheries in recent years has fluctuated by tens of millions (Table 1). Pink salmon populations in PWS are comprised of those that are artificially propagated and those that occur naturally at a ratio of approximately three to one (Wertheimer et al., 2004). Upwards of one half billion pink salmon are released into PWS each year by four hatcheries (Table 1). All pink salmon from hatcheries are identifiable from otolith thermal marks purposefully induced during their hatchery incubation (Hagen et al., 1995; Smoker and Linley 1997).

* Corresponding author.
E-mail address: tkline@pwssc.gen.ak.us (T.C. Kline).

Table 1
Production statistics of Prince William Sound hatchery pink salmon production during the 1998–2004 observation period

Cohort Early marine year	AFK hatchery			Cannery creek hatchery			WN hatchery			Solomon Gulch hatchery			AFK+CCH+SGH+WNH			CCH+SGH+WNH		
	Fry released (millions)	Return (millions)	Marine survival (%)	Fry released (millions)	Return (millions)	Marine survival (%)	Fry released (millions)	Return (millions)	Marine survival (%)	Fry released (millions)	Return (millions)	Marine survival (%)	Fry released (millions)	Return (millions)	Marine survival (%)	Fry released (millions)	Return (millions)	Marine survival (%)
1998	106.0	8.7	8.25	137.6	8.1	5.87	103.7	9.5	9.13	195.2	14.9	7.65	542.4	41.2	7.60	436.4	32.5	7.44
1999	133.2	6.9	5.19	131.2	6.5	4.96	127.4	8.4	6.57	213.9	12.4	5.77	605.6	34.1	5.63	472.5	27.2	5.76
2000	142.5	4.8	3.37	132.2	2.1	1.60	116.1	7.2	6.19	195.8	16.1	8.24	586.6	30.2	5.15	444.1	25.4	5.73
2001	150.3	7.8	5.16	139.2	1.6	1.14	127.7	5.6	4.40	203.9	5.3	2.58	621.1	20.2	3.26	470.8	12.5	2.65
2002	156.0	7.1	4.53	138.6	8.3	5.98	106.2	17.8	16.80	202.6	17.3	8.56	603.4	50.5	8.38	447.4	43.5	9.72
2003	146.4	5.2	3.57	135.6	2.8	2.04	119.5	2.7	2.26	206.4	11.1	5.40	607.9	21.8	3.59	461.5	16.6	3.60
2004	174.4	10.1	5.80	136.3	13.5	9.90	109.6	9.2	8.36	222.5	17.8	8.02	642.8	50.6	7.87	468.4	40.5	8.64
Mean:	144.1	7.2	5.12	135.8	6.1	4.50	115.7	8.6	7.67	205.7	13.6	6.60	601.4	35.5	5.93	457.3	28.3	6.22

AFK = Armin F. Koernig htachery, WNH = Wally Noerenberg hatchery, CCH = Cannery Creek hatchery, SGH = Solomon Gulch hatchery.

Pink salmon have the shortest life cycle among the *Oncorhynchus*, reproducing at age two. Their life cycle can thus be described as consisting of three years: (1) the brood year, (2) the early marine year, and (3) the return year. The returning year creates the brood year of the next generation. This study focused on early marine year pink salmon because mortality occurring during the early marine year was hypothesized to determine survival from juvenile to adult stages (Parker 1968; Hartt 1980). Because of their short life history, pink salmon were expected to be particularly sensitive to year-to-year variability in oceanic forcing.

Survival rates of pink salmon from three of the four PWS hatcheries and PWS wild stocks have co-varied since their inception (1975–1985) to 1996 (Pyper et al., 2001). Furthermore, survival rates of wild PWS pink salmon and wild stocks over the northern Gulf of Alaska region spanning Kamishak Bay (Lower Cook Inlet) to Yakutat (northern Southeast Alaska) have co-varied over the previous ~ four decades (Pyper et al., 2001). These patterns of spatial co-variation in pink salmon survival rate were hypothesized by Pyper et al. (2001) to be driven by processes occurring during the coastal (i.e., early) phase of the marine life history of pink salmon. One such process that may affect salmon survival is diet and food availability.

One may infer the source of pink salmon prey in terms of space and time, rather than by taxon, using stable isotope analysis (SIA). Based on the predictable relationship between the stable isotopic composition of a consumer and its diet (reviewed by Michener and Schell, 1994), the stable isotope composition measured in a particle-feeding copepod such as *Neocalanus cristatus* reflects that of its low trophic level diet, which consists of phytoplankton and protozoa (Liu et al., 2005). Similarly, the stable isotope composition measured in pink salmon would reflect that of their zooplankton diet (Boldt and Haldorson 2002), which, in turn, reflects that of the diet of zooplankton, which consists of phytoplankton and protozoa.

A relatively high carbon stable isotope ratio cross-shelf gradient, but a relatively low nitrogen stable isotope ratio cross-shelf gradient exists in the study area (Kline, 1999). The carbon stable isotope ratio gradients were such that lower carbon stable isotope ratio values were diagnostic of carbon from outside PWS and used to infer oceanic subsidies, which were temporally variable and may contribute >50% of the carbon of PWS fish food webs (Kline, 1999; Kline and Willette, 2002). These isotopic gradients were based upon systematic observations of late feeding stage individuals of *N. cristatus* (a regionally ubiquitous copepod that comprises a significant part of the meso-zooplankton biomass during the spring bloom; Coyle and Pinchuk, 2003, 2005) and bulk net zooplankton samples (Kline, 1999). The *N. cristatus* data were more definitive than bulk samples because they provided a better statistical sample and avoided complications arising from the uncertain nature of bulk samples. Cross-shelf gradients were thus verified for this study period by comparing carbon stable isotope ratio values of individual *N. cristatus* from PWS with those from the adjacent Gulf of Alaska during the same years that pink salmon were sampled.

Pink salmon from three PWS hatcheries with a co-variation history (Pyper et al., 2001) were hypothesized to respond to a common forcing. Oceanic zooplankton subsidies were hypothesized to provide this common forcing. Oceanic subsidies were observed to vary between two local PWS hatchery pink salmon populations sampled in 1994 (Kline and Willette, 2002). Oceanic subsidies in PWS were observed to shift concordantly from one year to the next in juvenile herring (*Clupea pallasii*), juvenile pollock (*Theragra chalcogramma*), and diapausing (over-wintering resting phase) *Neocalanus* copepods (Kline, 1999). The goal of this study was to assess whether there was a relationship between such inter-annual shifts in oceanic subsidies, measured using carbon stable isotope ratios,

and pink salmon marine survival rate in the pattern of Pyper et al. (2001).

2. Materials and methods

2.1. Study area

The study area consisted of southwestern PWS and the shelf waters offshore and southwest of PWS, as far as Resurrection Bay, near Seward, Alaska. Sampling sites were described in detail by Boldt and Haldorson (2002). Pink salmon are released from PWS hatcheries during the zooplankton bloom throughout May. Hatchery operators determine the time of fry release using careful monitoring of local zooplankton populations, particularly late-stage, large bodied *Neocalanus* copepod spp. (Boldt and Haldorson, 2002; Cooney et al., 2001). The Armin F. Koernig Hatchery (AFK) was the only PWS salmon hatchery located within the study area. This was also the hatchery from which the survival rate of pink salmon did not co-vary with either PWS wild salmon or those from other PWS hatcheries (Pyper et al., 2001). The three other PWS hatcheries producing pink salmon, the Wally Noerenberg hatchery (WNH), the Cannery Creek hatchery (CCH), and the Solomon Gulch hatchery (SGH), are located in the northwestern and northeastern portions of PWS. Salmon migration pathways from these three hatcheries into the Gulf of Alaska (GOA) take them through the region sampled.

2.2. Pink salmon production and survival

Salmon release and return data for the PWS hatcheries were provided by the non-profit corporations that own them (Table 1). AFK, WNH, CCH data were provided by the Prince William Sound Aquaculture Corporation; data for the SGH were provided by the Valdez Fisheries Development Association.

The number of fry released from hatchery H in a given early marine year i is defined as P_{Hi}. The number of salmon returning from the production of hatchery H in year $i + 1$ is defined as R_{Hi}. The marine survival rate for each hatchery cohort (early marine year i), $S_{Hi} = R_{Hi} \times (P_{Hi})^{-1}$. Marine survival rate was calculated by cohort (year i) for hatchery aggregates: for each cohort (year i), the number of fry released for each hatchery was summed, and then divided into the total number salmon returning in year $i + 1$. This was done for all four PWS hatcheries and for the three hatcheries with a history of co-variation (CCH, SGH, and WNH).

2.3. Carbon isotope nomenclature

The delta notation used to express carbon stable isotope ratios is reported as the ‰ deviation relative to the Vienna Peedee belemnite (VPDB) international standard. The conventional delta notation used to express carbon stable isotope ratios relative to the international standard is defined by the following expression:

$$\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000‰ \tag{1}$$

where $R = {}^{13}C/{}^{12}C$. By definition, the isotope standards have delta values of zero, i.e. $\delta^{13}C = 0$ for VPDB.

The method of McConnaughey and McRoy (1979) was used to calculate lipid-normalized carbon stable isotope ratios. The method is based on using the C/N atom ratio derived from the %C and %N data generated for each sample during mass spectrometry, assumes that a C/N atom ratio of 4.0 is normal, and adjusts $\delta^{13}C$ accordingly. The parameter L based on C/N was calculated first:

$$L = 93/[1 + 1/(0.246 \times C/N - 0.775)] \tag{2}$$

L and uncorrected $\delta^{13}C$ values were then used to calculate a lipid-normalized value ($\delta^{13}C'$):

$$\delta^{13}C' = {}^{13}C + 6[3.9/(1 + 287.1/L) - 0.2068] \tag{3}$$

In general, normalization reduces a source of ${}^{13}C/{}^{12}C$ variability, enabling comparing organisms of disparate lipid storage ability without the confounding effects of varying lipid content. Normalization is less important for comparing salmon data with salmon data than for comparing salmon data with *N. cristatus* data, which had mean C/N atom ratios of 3.98 (SD = 0.15) and 5.07 (SD = 1.92), respectively. Nevertheless, pink salmon C/N atom ratio explained 5% of the variability of their $\delta^{13}C$ values ($P < 0.0001$), whereas C/N atom ratio did not with respect to their $\delta^{13}C'$ values ($P = 0.4$). Using $\delta^{13}C'$ values when comparing juvenile pink salmon thus minimizes lipid storage as a factor during data interpretation.

2.4. Verification of cross-shelf $\delta^{13}C'$ gradients

1570 terminal feeding stage *N. cristatus* sampled on 21 Long-Term Observation Program (LTOP; Weingartner et al., 2002) cruises that took place from May 1998 to October 2004 were analyzed individually for $\delta^{13}C'$ abundance using protocols described by Kline (1999). Stable isotope data of *N. cristatus* are available from samples collected on LTOP cruises conducted during May of each of these seven years, two Marches (2003 and 2004), two Aprils (2001 and 2003), four Julys (2001, 2002, 2003, and 2004), three Augusts (2001, 2002, and 2003) and three Octobers (2002, 2003, and 2004). Zooplankton were systematically sampled using a MOC-NESS at designated stations on each LTOP cruise (Coyle and Pinchuk, 2003, 2005). Sampled sites include 13 stations, GAK1 to GAK13, crossing the continental shelf and slope near Resurrection Bay, Alaska (called the Seward Line), and five stations within PWS. The first net (drogue net) of the MOCNESS sampled >~500 m³ of water from deployment at the surface to 100m depth, where it was closed. Live zooplankton samples thus collected were sieved, picked for late-stage *N. cristatus*, and frozen individually in vials as described by Kline (1999). Samples were freeze-dried and SIA performed as described below.

N. cristatus SIA data were aggregated across the period of the project into four cross-shelf zones, each zone comprised of four or five stations, to evaluate the nature of isotope gradients to assist interpreting pink salmon isotope data. These four zones were the Sound, which consisted of the five stations within PWS, the inner-shelf, which consisted of stations GAK1 to GAK5, outer-shelf, which consisted of stations GAK6 to GAK9, and slope, which consisted of stations GAK10 to GAK13. These zones are similar to those of other studies, e.g., Liu et al. (2005). SIA was performed on 399, 386, 456, and 329 *N. cristatus* from Sound, slope, and outer-shelf, and inner-shelf zones, respectively. One question remaining from Kline (1999) that would be addressed by zonal comparisons was whether gradients existed as a step in $\delta^{13}C'$ value between PWS and the adjacent GOA or whether gradients extend across the shelf proper. The mean zonal *N. cristatus* $\delta^{13}C'$ values are assumed to be a proxy for carbon in plankton food webs of each zone. However, because of trophic isotope effects, e.g., ${}^{13}C$ is enriched with each feeding step, the $\delta^{13}C'$ values expected of a zooplanktivore such as a pink salmon fry consuming carbon derived exclusively from one of these zones would not necessarily be identical to the zonal mean *N. cristatus* $\delta^{13}C'$ value. This uncertainty is similar in magnitude as that of the ${}^{13}C$ enrichment leading to salmon. For example, pink salmon food chain length is variable during the early marine year (Kline and Willette, 2002). Fractionation of carbon isotopes by lower trophic levels may vary according to feeding mode within the plankton food web (e.g., herbivory vs. carnivory; Vander Zanden and Rasmussen, 2001). An arbitrary a priori constant net trophic fractionation effect of 1‰ was added to *N. cristatus* $\delta^{13}C'$ values

to *estimate* a hypothetical zooplanktivore's $\delta^{13}C'$ values for exclusive consumption of carbon from each zone. The extreme zonal mean values would comprise end-member values using geochemical terminology. Uncertainty is assumed to be about the same as the trophic fractionation effect, i.e., ~1‰. This uncertainty is less than the cross-shelf $\delta^{13}C'$ gradient observed by Kline (1999).

2.5. Fish sampling and analysis

Pink salmon fry were sampled using a surface trawl and gillnets as described by Boldt and Haldorson (2002). The samples obtained were used by a number of projects such that some individual fish received multiple analyses. Otoliths were removed for assessment of hatchery origin, stomachs were removed for stomach content analysis, and whole fish minus their otoliths and stomach contents were dried and ground to a fine powder for energy content analysis (Boldt and Haldorson, 2002). These results were compiled into a database from which samples were selected for SIA.

Pink salmon without otolith thermal marks were assumed to be non-hatchery or 'wild' but of unknown geographical origin because any one fish, although caught in PWS, may not have been propagated in PWS. Because of this potential ambiguity, only hatchery pink salmon were analyzed in this study.

Up to five pink salmon juveniles from a given hatchery from a given station per sampling cruise were selected for SIA. The number of fish sampled varied by what was feasible due to weather constraints and what was caught during research cruises, which were conducted from July to October from 1998 to 2004. Individual fish were analyzed, however data were aggregated into hatcheries and years (Table 2).

SIA was performed at the University of Alaska Fairbanks Stable Isotope Facility using Finnegan Delta Plus mass spectrometers, equipped with continuous flow elemental analyzers. A single SIA generated the following data: $^{13}C/^{12}C$ ratio expressed in standard delta units, $\delta^{13}C$, and %C and %N. Mass spectrometric analysis quality assurance protocols consisted of running of laboratory standards before and after groups of ten "unknowns" and by duplicate analyses.

3. Results

The large range in number of pink salmon returning to PWS during the course of the project (Table 1) provided a good opportunity for hypothesis testing. The lowest return of ~20.2 million fish in 2002 (from the 2001 cohort) was followed by a return of ~50.5 million the following year (2002 cohort). The contribution from each hatchery varied considerably by year during 1998–2004. Two hatcheries (WNH and SGH) each contributed more than 17 million fish to the enormous 2003 run, each contributing more than double that of either AFK or CCH.

Differences in run size were driven by marine survival rates (Table 1), which ranged from a low of ~1.1% for the CCH 2001 cohort to a high of ~16.8% for the WNH 2002 cohort. Mean (1998–2004) marine survival rate, which was ~6%, varied among hatcheries. The WNH had the highest mean survival rate of ~7.7% whereas CCH had the lowest at 4.5%. Like Pyper et al. (2001), two out of six pair-wise correlations of marine survival rate among hatcheries were significant during 1998–2004 (Table 3). Of special interest is that, like Pyper et al. (2001), none of the pairs involving AFK were significant. Hatchery survival rates for the three hatcheries with a correlative history (Pyper et al., 2001) were significantly (Spearman's $\rho \geqslant 0.786$, $P \leqslant 0.05$) correlated to the aggregate survival rate during 1998–2004 (Table 3; same statistical result whether a three or four hatchery aggregate was considered). Marine survival rate of AFK pink salmon was not correlated to the

aggregate marine survival rate (Spearman's $\rho = 0.393$, $P \gg 0.05$). The correlations of marine survival rate between the individual hatcheries and the aggregate survival rate followed a pattern similar to that found by Pyper et al. (2001) for the hatcheries compared to wild stocks (Table 3).

Inter-annual variability of monthly mean $\delta^{13}C'$ values was qualitatively greater than within year variability (Fig. 1). For example,

Table 2
Stable isotope data with descriptive statistics of early marine pink salmon sampled in Prince William Sound and the Gulf of Alaska by hatchery of origin (abbreviations as for Table 1) listed by early marine year

Hatchery sampling area	Year	$\delta^{13}C'$	SD	SE	N	N by month
Gulf of Alaska						
AFK	1998	−20.7	0.28	0.07	17	0,9,8,0
	1999	−20.5	0.50	0.16	10	0,7,0,3
	2000	−20.9	0.34	0.08	17	0,17,0,0
	2001	−19.3	0.67	0.17	15	8,5,1,1
	2002	−20.5	0.94	0.22	19	10,9,0,0
	2003	−20.0	0.45	0.10	19	19,0,0,0
	2004	−19.7	0.38	0.07	33	18,15,0,0
CCH	1998	−20.7	0.74	0.22	12	1,9,0,2
	1999	−20.3	0.36	0.07	25	0,18,1,6
	2000	−20.5	0.44	0.16	8	0,8,0,0
	2001	−19.9	0.36	0.15	6	0,5,0,1
	2002	−21.8	0.78	0.16	25	4,21,0,0
	2003	−20.1	0.44	0.12	14	10,4,0,0
	2004	−20.3	0.22	0.05	17	13,4,0,0
SGH	1998	−21.2	0.61	0.22	8	0,8,0,0
	1999	−20.5	.	.	1	0,1,0,0
	2000	−20.8	0.54	0.08	51	0,51,0,0
	2001	−19.2	0.46	0.21	5	4,0,1,0
	2002	−20.6	0.42	0.13	11	11,0,0,0
	2003	−20.3	0.46	0.12	15	14,1,0,0
	2004	−20.4	0.49	0.11	19	19,0,0,0
WNH	1998	−21.0	0.57	0.16	13	4,9,0,0
	1999	−20.3	0.21	0.09	6	0,3,1,2
	2000	−20.8	0.38	0.06	46	0,46,0,0
	2001	−19.5	0.58	0.29	4	4,0,0,0
	2002	−20.6	0.43	0.11	16	15,1,0,0
	2003	−20.1	0.28	0.14	4	2,2,0,0
	2004	−20.4	0.34	0.10	13	10,3,0,0
AFK + CCH + SGH + WNH	1998	−20.9	0.57	0.08	50	
	1999	−20.4	0.38	0.06	42	
	2000	−20.8	0.46	0.04	122	
	2001	−19.4	0.61	0.11	30	
	2002	−21.0	0.92	0.11	71	
	2003	−20.1	0.45	0.06	52	
	2004	−20.1	0.48	0.05	82	
Prince William Sound						
AFK	2001	−18.4	0.14	0.08	3	1,0,2,0
	2002	−20.8	0.88	0.33	7	5,2,0,0
	2003	−19.7	0.45	0.17	7	7,0,0,0
	2004	−19.6	0.28	0.11	7	7,0,0,0
CCH	2001	−18.5	0.66	0.21	10	2,5,3,0
	2002	−21.0	0.63	0.18	12	10,2,0,0
	2003	−20.0	0.33	0.11	9	9,0,0,0
	2004	−20.3	0.37	0.11	11	11,0,0,0
SSG	2001	−18.5	0.64	0.16	16	11,5,0,0
	2002	−20.5	0.42	0.13	10	10,0,0,0
	2003	−19.9	0.44	0.14	10	10,0,0,0
	2004	−20.7	0.38	0.15	6	6,0,0,0
WNH	2001	−19.0	.	.	1	1,0,0,0
	2002	−20.6	0.52	0.20	7	4,3,0,0
	2004	−20.3	0.43	0.14	10	10,0,0,0
AFK + CCH + SGH + WNH	2001	−18.5	0.60	0.11	30	
	2002	−20.8	0.63	0.11	36	
	2003	−19.9	0.40	0.08	26	
	2004	−20.2	0.51	0.09	34	

Sample size by month (July, August, September, October) is given in rightmost column.

Table 3
Spearman correlation statistics for data plotted in Fig. 3 and similar regressions not plotted

Variable 1	Variable 2	GOA ρ	PWS ρ	ρ	Pyper	Variable 2
Marine survival compared with marine survival						
AFK	CCH			0.563	0.30	
AFK	SGH			−0.143	0.13	
AFK	WNH			0.500	0.34	
CCH	SGH			0.571	**0.61**	
CCH	WNH			**0.786**	0.59	
SGH	WNH			**0.714**	0.50	
AFK	Aggregate			0.393	0.34	Wild
CCH	Aggregate			**0.929**	**0.76**	**Wild**
SGH	Aggregate			**0.786**	**0.70**	**Wild**
WNH	Aggregate			**0.929**	**0.80**	**Wild**
Isotope values compared with isotope values						
AFK	CCH	**0.821**	0.800			
AFK	SGH	**0.929**	0.400			
AFK	WNH	**0.857**	1.000			
CCH	SGH	**0.893**	0.800			
CCH	WNH	**0.857**	1.000			
SGH	WNH	**0.964**	0.500			
Isotope values (variable 1) compared with marine survival (variable 2)						
AFK	AFK	0.214	0.600			
CCH	CCH	−0.500	−0.800			
SGH	SGH	−0.679	−0.800			
WNH	WNH	−0.679	−1.000			
AFK	Aggregate	−0.321	−0.800			
CCH	Aggregate	**−0.750**	−1.000			
SGH	Aggregate	−0.536	−0.800			
WNH	Aggregate	−0.607	−1.000			
Aggregate[a]	Aggregate	−0.607	**−1.000**			
August[a]	Aggregate	**−0.714**				
July[a]	Aggregate		**−1.000**			
AFK	AFK			0.326		
CCH	CCH			**−0.578**		
SGH	SGH			**−0.748**		
WNH	WNH			**−0.710**		
AFK	Aggregate			−0.509		
CCH	Aggregate			**−0.844**		
SGH	Aggregate			**−0.665**		
WNH	Aggregate			**−0.636**		
Aggregate	Aggregate			**−0.700**		

Columns showing Spearman's ρ organized by sampling area where appropriate, otherwise ρ is given in a third column. The lower block of this third column shows the Spearman correlations for the 11 area-years as described in the text. Spearman's ρ values $\geqslant$ Zar (1984) critical value for $P = 0.05$ are shown as bold. Pyper et al. (2001) correlations are shown in the rightmost block. Wild stocks were variable 2 as indicated. Significance for Pyper et al. (2001) correlations indicated by: bold ($P \leqslant 0.05$), italics ($P > 0.05$ and $\leqslant 0.10$), plain text ($P > 0.10$).
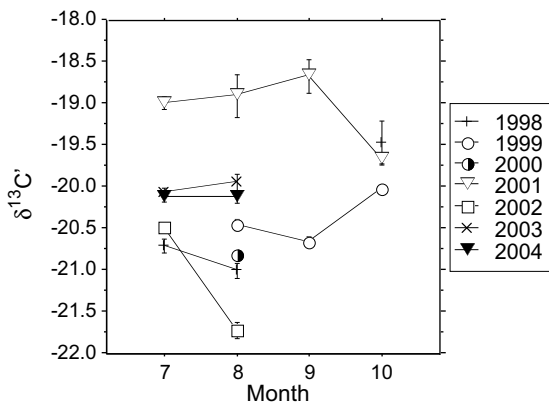
[a] Plotted in Fig. 3.

Fig. 1. Inter-annual versus monthly variation in early marine pink salmon δ^{13}C′ value. Data points are for the combined sampling areas and combined hatcheries sampled within given month in a given early marine year. Standard errors of monthly means are shown by error bars.

in 2001 monthly δ^{13}C′ values were much higher than other years. Within-year monthly mean δ^{13}C′ values varied by as much as

~1‰, which was a relatively small amount, with no consistent seasonal pattern. The greatest within-year δ^{13}C′ shift took place in 2002, when values trended to the lowest observed monthly mean values.

The standard errors of mean stable isotope values stratified by hatchery, year, and sampling area were generally less than analytical precision of 0.2‰ (Table 2). The exceptions all had samples sizes of 7 or less. The standard errors of aggregated hatchery (three and hour hatcheries) mean stable isotope values stratified by year and sampling area were all less 0.2‰. There were thus significant differences in mean stable isotope values among years. In 2001, the early marine year leading to the lowest survival rate, the δ^{13}C′ values were the highest observed in each data block in Table 2 (see Fig. 2). The lowest values δ^{13}C′ observed were not as consistent, e.g., the lowest mean δ^{13}C′ value of each hatchery was observed in different years. When data were aggregated among hatcheries and only stratified by year and sampling area, the lowest mean values were observed in 2002, the early marine year leading to the highest marine survival rate. Correlation of annual mean δ^{13}C′ values among hatcheries was positive (Spearman's $\rho \geqslant .821$) and significant ($P \leqslant 0.05$) for GOA data but not for the PWS data, probably reflecting that there were only four years of observation (three for WNH). Spearman's rank correlation analysis was also
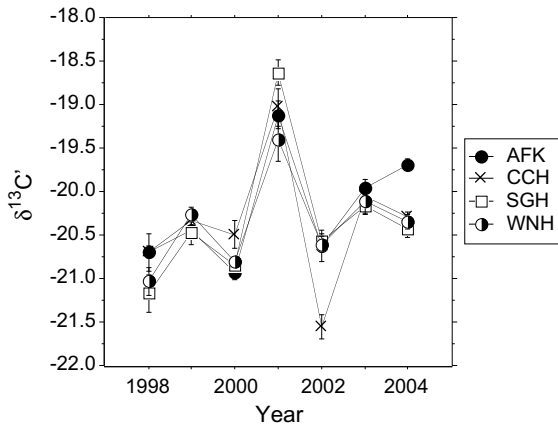
Fig. 2. $\delta^{13}C'$ data of early marine pink salmon by hatchery of origin of and early marine year. Standard errors of annual means are shown by error bars.

used to assess the relationship between $\delta^{13}C'$ values and marine survival rate.

Marine survival rate and $\delta^{13}C'$ values were negatively correlated (Fig. 3 and Table 3). However, Spearman's ρ were often not significant ($P > 0.05$). This was the case whether hatchery $\delta^{13}C'$ values were compared to individual hatchery marine survival rate, to marine survival rates of three or four hatchery aggregates, or aggregated $\delta^{13}C'$ values (mean among hatcheries) were compared to aggregate marine survival rates. The exception was CCH and PWS aggregated data. The correlations of three-hatchery aggregate marine survival rate with July $\delta^{13}C'$ values for PWS and August $\delta^{13}C'$ values for GOA (the area-months that had the largest sample sizes; Table 2, Fig. 1) are marginally significant (Spearman's ρ = critical value for the sample sizes). The plots of this relationship and that for all data are similar (Fig. 3) suggesting that as few as one point may have driven significance, suggesting a limitation of the seven-year duration of the project. A longer project would have increased the number of points being correlated. To test whether an increase in number of points (and thus years of study) could potentially yield a greater number of significant correlations, year-areas were treated as independent observations.

The two sampling areas, PWS and GOA are separated by distance, ~50 km, and separated by islands forming the southwest boundary of PWS. Sampling was destructive so no individual fish

could be sampled twice. The isotope data from the two sampling areas thus have a degree of independence. The collective 11 year-areas are thus assumed to be 'independent' for the purposes of the sample size exercise. Both areas in given years had the same survival rates making them 'ties' for Spearman ranking, which was accounted for (the adjusted ρ values, which are shown in Table 3, were slightly lower). Nevertheless, with $N = 11$ and the ties considered, non-AFK correlations of mean hatchery $\delta^{13}C'$ values and marine survival rate, whether by individual hatchery or by hatchery aggregate (either three or four hatcheries), are negative ($\rho \leqslant -.578$) and significant ($P \leqslant 0.05$).

The 1998–2004 mean $\delta^{13}C'$ values of N. cristatus were −23.0‰, −22.7‰, −21.8‰, and −19.9‰, respectively, for slope, outer-shelf, inner-shelf and PWS zones (SE was 0.1‰ or less). The corresponding estimated zooplanktivore $\delta^{13}C'$ values for exclusive consumption of slope, outer-shelf, inner-shelf and PWS carbon were thus respectively, −22.0‰, −21.7‰, −20.8‰, and −18.9‰ (Fig. 4). Zonal effects were statistically significant (one-way ANOVA, $P < 0.0001$). Fisher's post hoc tests suggest that all zone pair-wise comparisons were statistically different ($P < 0.0001$) except for the outer-shelf – slope pair ($P = 0.0686$). The $\delta^{13}C'$ difference between the slope and Sound was 3.1‰ whereas the difference between the outer-shelf and slope was 0.2‰. Box and whisker plots of a hypothetical zooplanktivore feeding exclusively in each zone graphically confirm that low $\delta^{13}C'$ values are only found in the GOA, and that there is a fairly large step of 1.9‰ between the Sound and GOA measured at the inner-shelf.

4. Discussion

There was considerable year-to-year variation in mean $\delta^{13}C'$ values of early marine pink salmon produced by PWS hatcheries during 1998–2004 that was inversely correlated with marine survival rate, which also had considerable year-to-year variation. Because survival rate among hatcheries was correlated to a lesser degree than $\delta^{13}C'$ during this period, sources of inter-hatchery survival rate variation limited achieving a good correlation between pink salmon $\delta^{13}C'$ values and marine survival within this project's duration. Nevertheless, survival tended to be higher when $\delta^{13}C'$ was lower. Combining $\delta^{13}C'$ data of all four hatcheries during analysis was justified because pink salmon $\delta^{13}C'$ values of all hatchery pairs were correlated, not just those with a history of correlative survival. Lower $\delta^{13}C'$ values are inferred to reflect greater oceanic subsides for early marine pink salmon production. Discussion is
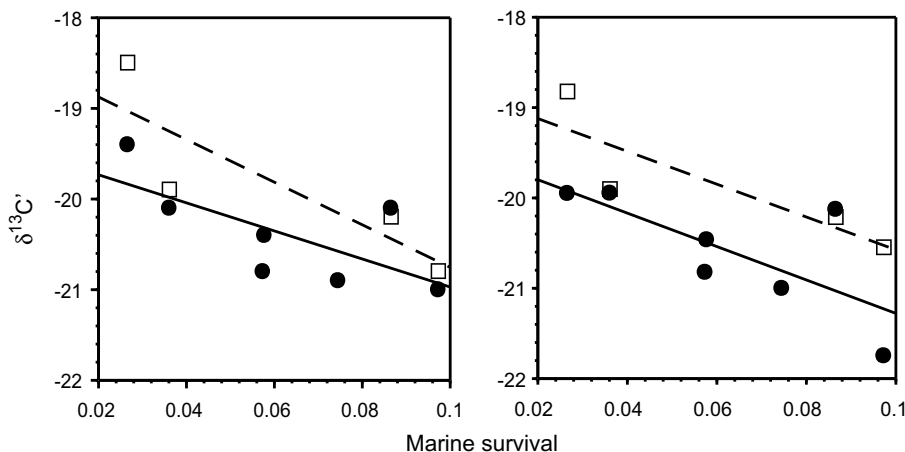

Fig. 3. Inverse relationships between mean $\delta^{13}C'$ values and three-hatchery aggregate marine survival rates. The left panel shows annual mean values for each area (GOA = filled circles, PWS = open squares). The right panel shows the mean August values for GOA samples (filled circles) and the mean July values for PWS samples (open squares). Regressions for GOA data are shown as solid lines whereas those for PWS are shown as dashed lines. Spearman correlation values are given in Table 3.
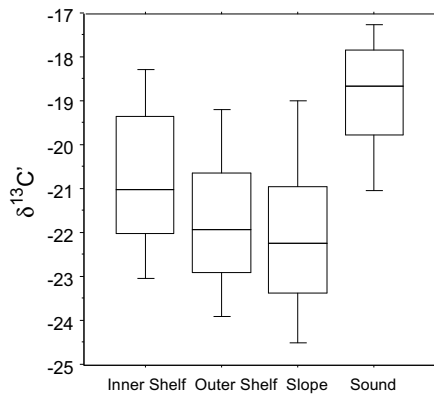
Fig. 4. Pelagic production spatial $\delta^{13}C'$ gradients in the study area. The $\delta^{13}C'$ values expected of a zooplanktivore consuming carbon exclusively from each cross-shelf zone in the study area shown as box and whisker plots based on terminal feeding stage *Neocalanus cristatus* data. Box and whisker plots show 10, 25, 50, 75, and 90 percentiles in the data.

thus focused on sources and causes of survival and isotopic variation in pink salmon, in particular the significance of regional isotopic gradients for the inferred role of oceanic subsidies.

4.1. Survival rate variation

Survival rate was highly variable among years and among PWS hatcheries over the course of the project. The survival difference between the 2001 and 2002 cohorts is comparable to the size of pink salmon runs of 20–40 million returning to all of Alaska during the early 1960s providing a qualitative indication of this magnitude. Overall there was good survival, e.g., there were no individual hatchery survival rates of <1%, such as have occurred historically, and the collective survival rate of the 'low' survival rate year was ~3%. Given that years of poor survival more strongly reflect those processes driving marine mortality, it would have been better for understanding processes controlling survival if there had been more and lower survival years. The seven-year data series of $\delta^{13}C'$ values may not be long enough to conclude that there is a statistically significant relationship between the survival of hatchery fish and oceanic carbon subsidies. Nevertheless, because Pyper et al. (2001) showed coherence in inter-annual pink salmon survival of the SGH, WHN, and CCH, they were pooled for the three-hatchery aggregate analysis. Analyses based on the marine survival rate of the three-hatchery aggregate tended to be more significant because local, hatchery effects on survival rate were masked. By coincidence, the rank order of the mean survival rate of all four hatcheries was the same as for the three-hatchery aggregate, thus it made no difference whether a three- or four hatchery aggregate marine survival rate was used for a given Spearman rank correlation analysis. This would likely not have been the case in a longer study.

That hatchery pink salmon $\delta^{13}C'$ values were well- and better correlated than marine survival confirms that stable isotope variation reflects meso-scale variation in regional oceanographic processes as postulated by Kline (1999) and that pink salmon marine survival rate may also depend on finer scale processes or other factors than those measured with stable isotopes. The postulated meso-spatial-scale was ~100 km and postulated meso-temporal-scale was inter-annual (Kline, 1999). Finer-scale, hatchery effects reflected differences that occurred at distances less than those between the hatcheries, i.e., ≪100 km, and may reflect differences in condition at time of release as well as possible local differences in food availability and predation. These are finer scale processes than what may be driven by oceanographic forcing,

which was of interest to the project (Batchelder et al., 2005). Stable isotopes may thus be a better indicator of the effects of these processes than marine survival rate of individual hatcheries. However, the collective marine survival rates (three-hatchery aggregate) may be more reflective of meso-scale processes. The aggregate correlations (e.g., August GOA data) suggest that as much as half of the aggregate marine survival rate variation may be explained by processes reflected by $\delta^{13}C'$ variation. Subsidies of oceanic origin carbon were likely the cause of low $\delta^{13}C'$ values measured in early marine pink salmon and increased marine survival rates of PWS hatchery pink salmon with a co-variation history.

4.2. Diagnostic value of stable carbon isotope values

The $\delta^{13}C'$ value of PWS carbon occurred in a well-defined range in agreement with Kline (1999). A PWS zooplanktivore would be expected to have a $\delta^{13}C'$ 'signature' characteristic of Prince William Sound. Low $\delta^{13}C'$ values are diagnostic of carbon from outside the Sound. Shelf $\delta^{13}C'$ values were intermediate of those from PWS and those from the slope and may reflect mixing of plankton from PWS and slope and possibly farther offshore. This is substantiated because *Neocalanus* spp. reproduce at depths ⩾300 m, so their occurrence on the shelf is a result of horizontal onshore transport.

Pink salmon hatchery cohort $\delta^{13}C'$ low and high extreme values of −21.8‰ and −18.4‰ correspond well with oceanic and coastal carbon end-member values of, respectively, −22.0 ± 2.2‰ and −18.9 ± 1.6‰, that were based on mean $\delta^{13}C'$ values of *N. cristatus* from the continental slope of −23.0‰ (SD = 2.2) and PWS of −19.9‰ (SD = 1.6). This correspondence affirms the assumed 1‰ fractionation effect between *N. cristatus* and pink salmon. The results confirmed the postulate that low $\delta^{13}C'$ values (e.g., −22.0 ± 2.2‰) are diagnostic of oceanic carbon (Kline, 1999).

4.3. Forms of oceanic subsidies

Oceanic subsidies inferred from $\delta^{13}C'$ values of juvenile pink salmon most likely came in the form of zooplankton. Because the major isotopic fractionation step occurs at the primary producer level, oceanic subsidies reflected by low $\delta^{13}C'$ values reflect particulate organic subsidies, rather than dissolved states. Dissolved subsidies are not precluded and are assumed to occur during deep-water renewal (Niebauer et al., 1994). Primary producers may double in number on the order of days suggesting rapid turnover. For the subsidies to consist of phytoplankton, the exchange between PWS and GOA would have to be extremely rapid. If this did happen, the *Neocalanus* $\delta^{13}C'$ values would reflect that of the phytoplankton subsidies so that those in PWS would be like those in the GOA during years when oceanic subsidies were high. This was not the case, *Neocalanus* $\delta^{13}C'$ values in PWS were very consistent over time. Zooplankton grow at a much slower rate than phytoplankton and thus have a slower turnover rate. A large feeding stage zooplankter could have a turnover time of days to weeks. This is probably slow enough that a GOA zooplankter would retain its $\delta^{13}C'$ value while transported into PWS. Kline (1999) postulated that deep-water renewal could be a mechanism facilitating oceanic subsides. This would more likely transport zooplankton than phytoplankton since they occur deeper in the water column. The occurrence of *Neocalanus* with GOA $^{13}C'$ values diapausing in the deep-waters of PWS provided additional evidence that oceanic subsidies are in zooplankton form (Kline, 1999).

Fish migration is an alternate way for GOA subsidies to enter PWS. This is not as likely as zooplankton forming the subsidies for juvenile pink salmon since nearly all of them would have to leave PWS to pick up the GOA $\delta^{13}C'$ signature, then re-enter PWS to be sampled there when subsidies were high. This does not seem likely. Furthermore, multiple species have been shown to respond

simultaneously to oceanic subsidies in PWS (Kline 1999, 2006). During the summer of 1995, six 'forage fish' taxa including those found near shore (Pacific sand lance; *Ammodytes hexapterus*) shifted to lower $\delta^{13}C'$ suggesting that oceanic subsidies were systemic in PWS (Kline, 2006).

Exchange of waters from PWS with those of the GOA was postulated to vary so that in some years PWS is very lake-like (little exchange) while in others years it is river-like (strong exchange; Cooney et al., 2001). When exchange is river-like, zooplankton arising in PWS during the spring would be washed out and salmon survival would be diminished. The strongest evidence of PWS carbon in coastal GOA waters was in 2001 when the $\delta^{13}C'$ value of early marine pink remained like PWS when they were sampled on the inner-shelf until at least September, if one assumes the continued high $\delta^{13}C$ values were due to export of PWS carbon. More observations like this need to be made during low survival years to be more certain.

Data are not available to assess whether increased offshore to onshore subsidies in some years were due to year-to-year differences in exchange of water between PWS and the GOA or to relative differences in zooplankton production between PWS and the GOA. Zooplankton abundance in PWS has a very strong seasonal dependence (Cooney et al., 2001). The seasonal amplitude in zooplankton population size is much greater than year-to-year differences making them difficult to assess. SIA is thus sensitive to an ecological phenomenon that is otherwise difficult if not impossible to measure.

Subsidies of zooplankton originating from the open ocean led to low $\delta^{13}C'$ values measured in early marine pink salmon and increased marine survival from three PWS hatcheries with a co-variation history. That is, depending on the year, juvenile pink salmon consumed carbon of a range that was nearly exclusively of oceanic origin to nearly exclusively of PWS origin. The relative importance of oceanic subsidies was highly variable from year to year. High $\delta^{13}C'$ values ($>-20‰$) were consistently observed in pink salmon during 2001 (the cohort with the lowest survival rate) suggesting that oceanic carbon subsidies were systematically low that year. Individual fish in 2001 were also within the bounds of PWS carbon defined by the SD of *N. cristatus* $\delta^{13}C'$ values. Conversely, low $\delta^{13}C'$ values ($\leqslant -20.5‰$) were consistently observed in pink salmon during 2002 (the cohort with the highest survival rate) suggesting large oceanic carbon subsidies. Furthermore, individual 2002 fish were within the SD-defined bounds of inferred oceanic carbon consumers. Pink salmon survival rate was thus suggested to be influenced by oceanic subsidies during the early marine feeding stage.

Pink salmon from AFK responded similarly to the other three hatcheries in terms of shifts in mean $\delta^{13}C'$ values, and thus subjected to oceanic subsidies. However, unlike pink salmon from the other three hatcheries, there was no consistent relationship between $\delta^{13}C'$ values and marine survival of AFK salmon. The concordant response by pink salmon by three of four PWS hatcheries was also consistent with historical survival patterns (Pyper et al., 2001). Pyper et al. (2001) found co-variation in pink salmon recruitment measured as returns per spawner (R/S) among the WNH, CCH, and SGH hatchery stocks and PWS wild stocks. Furthermore, Pyper et al. (2001) found co-variation between PWS and other wild stocks over a similarly large (100's of km) spatial scale as other northeast Pacific stocks investigated in their study. Pyper et al. (2001) found no significant R/S co-variation between AFK and other PWS hatchery or wild stocks. AFK pink salmon thus stand out as an anomaly, both locally and regionally. Pyper et al. (2001) hypothesized that spatial co-variation among pink salmon was due to coastal processes taking place during marine and not their freshwater life history. This study provides a line of empirical evidence substantiating their hypothesis.

Although early marine pink salmon from the AFK hatchery varied in $\delta^{13}C'$, not unlike those from the other hatcheries, this was not correlated with their survival. The AFK hatchery is located in southwest PWS, nearest the Gulf, enabling the salmon from there to be better poised to receive oceanic subsidies (Kline and Willette, 2002). Nevertheless, the AFK marine survival rate tended to vary less than the other three hatcheries during this study; in particular it was not as high as the other hatcheries in 2002 and 2004. AFK fish thus did not benefit from oceanic subsidies in terms of marine survival. This could imply that oceanic zooplankton subsidies do not directly benefit pink salmon by providing additional prey; instead it supports the other hypothesis that they provide alternate prey for pink salmon predators located within PWS (Willette et al., 1999). AFK pink salmon had to migrate away from the GOA to have been sampled in PWS. Year-to-year differences in AFK survival rate may thus reflect variation in migration behavior patterns not related to oceanic subsidy.

Oceanic carbon subsidies in PWS have broader significance than pink salmon marine survival rate. Multiple species in PWS have been shown to shift concordantly in their $\delta^{13}C'$ values suggesting that subsidies are a system-wide phenomenon (Kline, 1999, 2006). The effects of oceanic subsidies may be evident in pink salmon survival because of their short life history and because hatchery propagation provides large numbers for which good survival data exists. Nevertheless, other species found in PWS such as the juvenile stages of Pacific herring and walleye pollock may also be subject to the effects of predation and the benefits of zooplankton subsidies (Cooney et al., 2001).

Included within the plankton are species with planktonic dispersal stages. The particularly long planktonic larval stages of some rockfishes (e.g., >1 year) and oceanic subsidies could explain their occasional occurrence in PWS (e.g., PWS rockfish species list in Kline, 2006). The exchange of GOA waters with PWS that probably facilitated oceanic subsidies may also facilitate recruitment into PWS of spawning stocks from outside PWS. This exchange process may facilitate region-wide shifts in populations (Anderson and Piatt, 1999). Otherwise, how could given species increase or decrease in abundance more or less simultaneously throughout the northern Gulf of Alaska, from PWS to the Alaska Peninsula?

Oceanic subsidies may link climate-driven inter-decadal subarctic northeast Pacific oceanic zooplankton population cycles with salmon population cycles (e.g., Brodeur and Ware, 1992; Hare et al., 1999). Subsidy potential should be greater during oceanic zooplankton population peaks and be diminished or even reversed during decades when oceanic zooplankton stocks are much weaker (Brodeur and Ware, 1992). This observational program took place during a period of relative high salmon survival compared to the 1980s (Wertheimer et al., 2004). For example, only the 2001 cohort had a marine survival rate typical of a low survival decade. Further observations are needed to incorporate additional low and high survival years but also periods of time when oceanic zooplankton populations are low.

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