Mesoscale Eddies as a Climate-Linked Mechanism for Driving Inter-Annual Variability in Ocean Survival of Pink Salmon

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The short two-year life history of pink salmon (*Oncorhynchus gorbuscha*), the most abundant of the Pacific salmon, lends itself to better understanding of processes occurring during early marine life history, which might drive the species' considerable ocean survival variation.

Hypotheses that pink salmon ocean survival is determined during their early marine life history date at least as far back as the work of Parker (1968). More recently, Pyper et al. (2001) hypothesized that pink salmon ocean survival is driven during the coastal early marine stage because of spatial co-variation among local (within 10^2 km) stocks. Kline et al. (2008) and Kline (2010) found strong stable isotope correlations with ocean survival rate of those Prince William Sound (PWS), Alaska, pink salmon hatchery stocks that Pyper et al. (2001) found to spatially co-vary. Mesoscale eddies can drive isotopic variation and hence PWS pink salmon ocean survival (Kline 2010). These eddies are a dominant oceanographic and ecological feature in the northeastern Pacific Ocean because they may contain 80% of the primary production during spring months (Crawford et al. 2007).

It is possible to accurately assess pink salmon ocean survival from relatively recent hatchery production. Because hatchery output of pink salmon (number of fry released) is given following the freshwater stage, the relationship between this value and the returning population size potentially provides a more accurate assessment of ocean survival compared to estimates based on natural spawning in streams. For example, ocean survival of natural spawning populations may be assessed by using the ratio of number of returning adults to number of adults in the previous generation or R/S. The R/S necessarily includes mortality taking place during the freshwater stages, such as eggs and alevins that are subject to mortality caused by flooding and de-watering, for example. Hatchery output is also relatively constant from year to year eliminating the number of spawners as a driver of even- and odd-year survival differences that one could have in streams (Table 1). Since the late 1990's all pink salmon hatchery production from PWS has been thermally marked (otoliths) enabling accurate estimation of hatchery production caught in the fishery and in other sampling. Hatchery-specific issues may be reduced by merging production across multiple hatcheries.

Table 1. Prince William Sound pink salmon hatchery production, ocean survival, stable isotope values, and categorization of high, low, and intermediate ocean survival rates based on a combination of $\delta^{13}C$ value and ocean survival are summarized. Red and green colors used to emphasize, respectively, low and high values. Hatchery abbreviations: CCH = Cannery Creek hatchery, WNH = Wally Noerenberg hatchery, and SGH = Solomon Gultch hatchery. The $\delta^{13}C$ values are based on analyses of NLF = northern lampfish juveniles (length < 50 mm) and *Neocalanus cristatus* stage-5 copepodites.

Ocean entry year	CCH fry released	CCH return	WNH fry released	WNH return	SGH fry released	SGH return	Total fry released	Total return	Ocean survival	$\delta^{13}C$		Category
	millions of salmon									NLF	*Neocalanus*	
1998	138	8.1	104	9.5	195	14.9	436	32.5	7.4%	-21.4	-23.4	Intermediate
1999	131	6.5	127	8.4	214	12.4	472	27.2	5.8%	-21.4	**-20.9**	Intermediate
2000	132	2.1	116	7.2	196	16.1	444	25.4	5.7%	-22.2	-23.2	Intermediate
2001	139	1.6	128	5.6	204	5.3	471	12.5	**2.6%**	**-22.9**	**-25.5**	**Low**
2002	139	8.3	106	17.8	203	17.3	447	43.5	**9.7%**	-21.3	**-19.1**	**High**
2003	136	2.8	120	2.7	206	11.1	462	16.6	3.6%	-22.1	**-24.6**	**Low**
2004	136	13.5	110	9.2	222	18.1	468	40.8	**8.7%**	**-20.6**	**-18.3**	**High**
2005	127	2.9	84	4.1	222	9.1	433	16.0	3.7%	-21.6	-22.3	Intermediate
2006	138	7.4	85	7.5	217	23.9	440	38.9	**8.8%**	**-20.8**	**-19.6**	**High**

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Survival rates of three of the four pink salmon hatcheries located in PWS have historically co-varied along with those spawning naturally in streams (Pyper et al. 2001). The one hatchery that has not co-varied is located closer to the open sea than the others (Fig. 1). A goal of this paper is to posit a mechanism that may explain the stable isotope as well as survival observations.

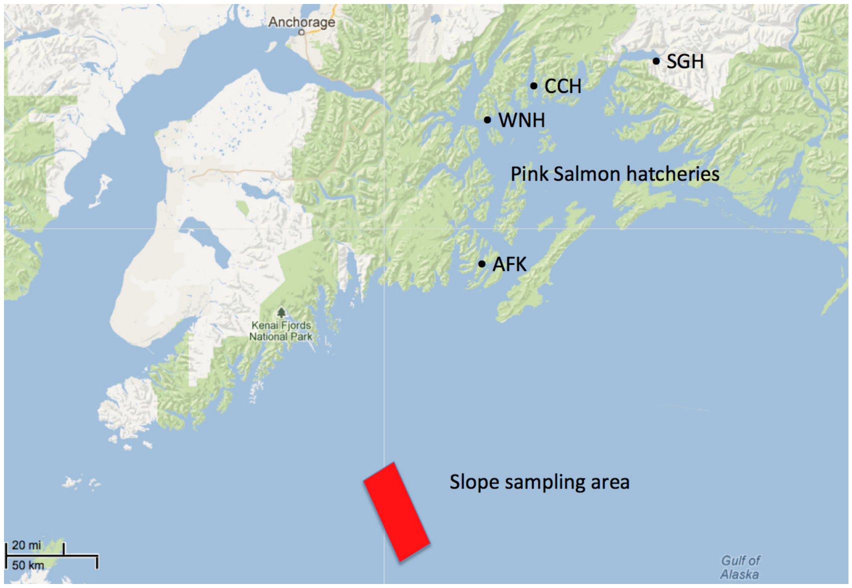

Fig. 1. Sampling location, in red, and locations of Prince William Sound pink salmon hatcheries. Hatchery abbreviations: CCH = Cannery Creek hatchery, WNH = Wally Noerenberg hatchery, SGH = Solomon Gultch hatchery, and AFK = Armin F. Koernig hatchery. Base map from Google.

Sampling took place on long-term observational program oceanographic cruises that began as part of the Northeast Pacific Global Ocean Ecosystem (GLOBEC) research effort (Weingartner et al. 2002). Sampling stations included a transect line known as the Seward Line. Stable isotope data from samples consisting of multiple whole organisms were collected at the set of four stations (GAK 10 to GAK13) that were part of the Seward Line located over the continental slope (Fig. 1). Stage copepodite-5 (*Neocalanus cristatus*) copepods and juvenile (length < 50 mm) northern lampfish (*Stenobrachius leucopsarus*) were sampled systematically (5 copepods per station and 100% of the *Stenobrachius* per station) during May in continental shelf waters during the nine-year time series, 1998 to 2009. Carbon stable isotope values are reported by convention as delta units. The delta unit, which is expressed as $\delta^{13}C$ for $^{13}C/^{12}C$, is the per mil deviation (parts per thousand) from the internationally recognized isotope standard for carbon, Vienna Pee Dee Belemnite (VPDB). Because VPDB is relatively enriched in ^{13}C, organic matter generally has a negative value. Measurement precision is 0.1 per mil. The $\delta^{13}C$ values were corrected for lipid content as described by Kline (2010). Relatively high and low $\delta^{13}C$ values are indicated in Table 1 by, respectively, green and red colors. Positive significant ($p < 0.05$) correlations ($r^2 \sim 0.7$) were found between pink salmon ocean survival and $\delta^{13}C$ values confirming the hypothesis that early marine processes can drive their ocean survival (Kline et al. 2010).

Ocean survival (Table 1) was based on hatchery production data provided by the hatchery operators, the Prince William Sound Aquaculture Corporation and the Valdez Fisheries Development Association (Kline et al. 2008). Relatively high and low ocean survival rates are indicated in Table 1 by, respectively, green and red. Years were categorized as “High”, “Low”, and “Intermediate” using a combination of $\delta^{13}C$ value and ocean survival (Table 1). In 2003, the year with second lowest ocean survival (although not very low) during the observation period is indicated as low in order to have N =2 and also because of the low $\delta^{13}C$. Samples collected in 2001 had both the lowest ocean survival and lowest $\delta^{13}C$ values. Samples collected in 2002, 2004, and 2006 were categorized as high years due to a combination of high ocean survival (≥ 8.7%) and relatively high (> -21) $\delta^{13}C$ values for one or both organisms. Samples collected in 1998, 1999, 2000, and 2005 were designated intermediate years. Intermediate $\delta^{13}C$ values of *Neocalanus* were ~ -23 ±1, other than in 1999.

Mesoscale eddies were identified using sea-surface height anomaly maps generated through the Colorado Center of Atmospheric Research web page (Kline 2009). These maps are shown aggregated by year-category in Fig. 2. Mesoscale eddies have an anticyclonic flow pattern: when they approach the continental shelf near the Seward Line they entrain coastal waters and have an on-shore flow on their leading (western) edge while propagating westward (Okkonen et al. 2003).

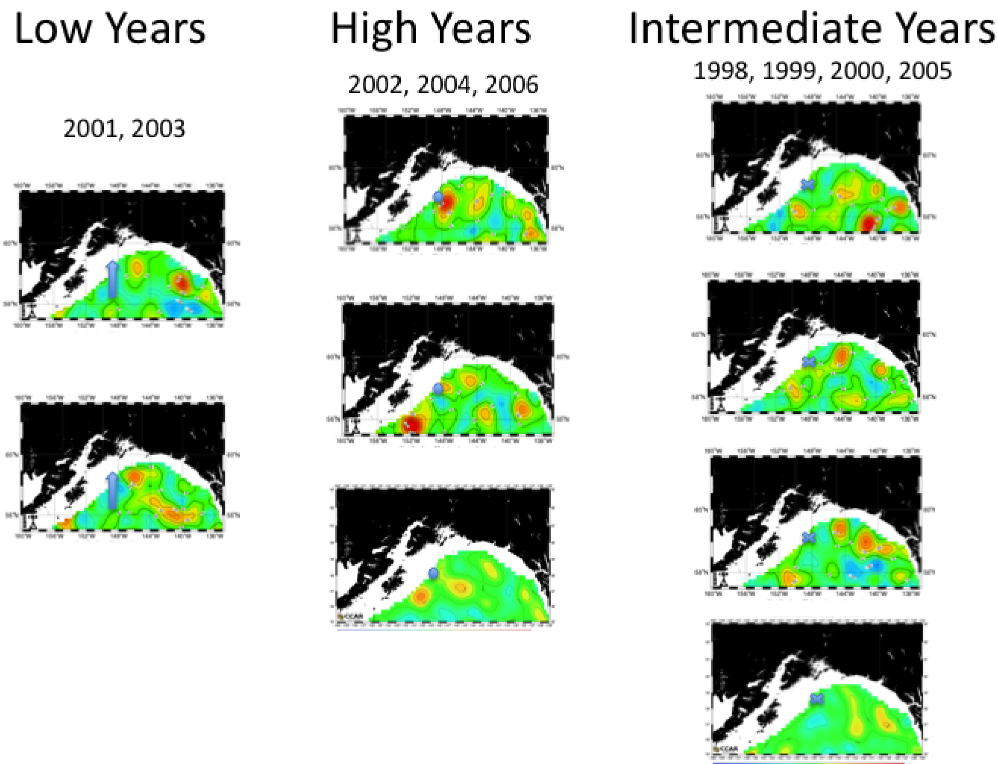

Fig. 2. Sea-surface height anomaly data in May at the time of sampling stable isotopes (Table 1) and interpreted flow pattern by year. Low years, 2001 and 2003, were characterized by eddies immediately east of the sampling area and on-shore flow (blue arrow). High years, 2002, 2004, and 2006, were characterized by eddies present in the sampling area and offshore movement of coastal water (blue circle). Intermediate years, 1998, 1999, 2000, and 2005, were characterized by no eddy in the sampling area or immediately east of the sampling area and thus no cross-shelf flow (blue X).

Anti-cyclonic mesoscale eddies can explain the stable isotope observations (Table 1; Fig. 2). Ocean survival was low for those cohorts when an eddy was located just east of the sampling area in May. The on-shore circulation pattern likely drove the low carbon isotope values observed. Low carbon isotope values were posited to reflect Fe-limited oceanic production (Kline 2010). Conversely, ocean survival was high in years when the May sampling area was located within an eddy and isotope values were high. Eddies entrain and retain coastal waters with their properties and biological constituents (Batten and Crawford 2005). Consequently, oceanic biota in eddies took on high values similar to those more typical of coastal habitats (Kline 2010). No eddy was present in the sampling area in May of years with intermediate ocean survival and intermediate isotope values. These observations suggest that location and presence of mesoscale eddies in May are important factors for driving both ocean survival and isotope value and thus the correlation between isotope value and survival. The multi 100-km spatial scale of eddies is also similar to the spatial scale of co-variation observed of pink salmon populations (Pyper et al. 2001). There is, however, a spatial disconnection between eddies and ocean survival because salmon are not yet in the ocean environment in May. Eddies may thus be important for "setting the stage" for in-coming salmon. Eddies may form a "hot spot" that draw predators away from coastal habitats to the open ocean increasing survival while salmon are still inshore. Eddies thus may "shelter" salmon by providing alternate prey for salmon predators.

Predators heading towards an eddy may exit PWS by passing near the Armin F. Koernig (AFK) hatchery (Fig. 1) providing a potential opportunity for predation. This is a further potential source of variability given that there are multiple pathways between PWS and the open sea; predators may not necessarily pass near AFK and may not be present when pink salmon juvenile are abundant. Stochastic aspects of this hypothetical process may explain the lack of any relationship in the pink salmon ocean survival between AFK and the other hatcheries.

Eddies represent a process that is likely influenced by climate change through the hydrological cycle because they entrain and transport fresher water into the Gulf of Alaska (Crawford 2005). Hydrology (e.g., precipitation) is an important climate variable. Yakutat eddies, in particular, entrain coastal water when they form and retain it as they propagate westward in the northern Gulf of Alaska (Janout et al. 2009). As well, eddies are temporally variable; inter-annual variation has been observed thus far (Henson and Thomas 2008). Eddies should be important components of models that link physical and biological conditions with climatic implications.

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