

Unprecedented biennial pattern of birth and mortality in an endangered apex predator, the southern resident killer whale, in the eastern North Pacific Ocean

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ABSTRACT: We report on an unprecedented, synchronized biennial pattern of birth and mortality in an apex predator inhabiting the eastern North Pacific Ocean—the critically endangered southern resident killer whale *Orcinus orca*. From 1998–2017, mortality of newborn and older whales was 3.6 times higher (61 versus 17 whales) and successful births 50% lower (16 versus 32 whales) in even years than in odd years as the population decreased from 92 to only 76 whales. Percent mortality was 3.1 times higher in even years during the recent 20 yr period of population decline than during an earlier 22 yr period (1976–1997) of population increase and relative high abundance, whereas mortality in recent odd years was 43% lower. Recognized potential mechanisms of decline (low abundance of a key prey species, Chinook salmon *Oncorhynchus tshawytscha*, toxic contaminants, and ship noise) cannot explain this biennial pattern. We present evidence that the causal mechanism is indirectly linked to pink salmon (*O. gorbuscha*), which exhibit a unique and extreme biennial pattern of abundance and interact strongly with other species in marine ecosystems in the North Pacific. Further investigation of this unique biennial pattern in southern resident killer whales is needed to inform recovery efforts for the population.

KEY WORDS: Salish Sea · Orca · Demography · Pink salmon · Chinook salmon · Population recovery · Ecosystem management

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1. INTRODUCTION

Killer whales *Orcinus orca* are apex predators that inhabit all of the Earth's oceans, yet little is known about factors affecting their birth rates, mortality rates, and population trends. In the eastern North Pacific, the southern resident killer whale (SRKW) population declined from 98 whales in 1995 to only 76 whales in late 2017 (CWR 2018) and is currently protected as an endangered species in USA and Canada. In 2018, Washington State and Canada took additional steps to decrease disturbance and increase Chinook

salmon abundance for SRKWs, which continue to show signs of starvation, stress, and decline (DFO 2018, SROTF 2018). Factors thought to be influencing the decline include low abundances of its principal prey, Chinook salmon *Oncorhynchus tshawytscha* (Ward et al. 2009, Ford et al. 2010, 2016), bioaccumulation of toxins (Desforages et al. 2018, Lundin et al. 2018), and vessel traffic and noise that disrupt foraging (Lacy et al. 2017).

The objectives of this investigation were to (1) document the unprecedented, synchronized biennial pattern of birth and mortality in SRKWs, (2) evaluate

the extent to which this pattern has contributed to its population decline, and (3) briefly discuss potential factors driving the biennial birth and mortality pattern. We recognize the need for additional analyses and rationale to explain this pattern, but we wish to facilitate rapid communication of these unique findings because a greater understanding of SRKW demography enhances the likelihood for advancing their recovery.

2. MATERIALS AND METHODS

Annual best estimates of SRKW population abundance and demographic parameters (births and deaths) collected in the Salish Sea (Fig. 1) since 1976 were obtained from the Center for Whale Research, Friday Harbor, Washington (CWR) (CWR 2018), which used photo-identification to accurately enumerate the whale population on July 1 of each year (Bigg et al. 1990, Ward et al. 2009). Prior to this 42 yr period, the aquaria trade removed at least 48 SRKWs during a 15 yr period, and this loss contributed to the low population size (71 whales) at the beginning of our study period (1976) (NMFS 2008). The CWR received federal permits to collect the non-intrusive observational data.

Mortality of individual whales was documented by the CWR after a photo-identified whale was determined to be consistently missing from its pod (the J, K, or L pod that comprise the population) or the overall population for a period of time in the Salish Sea.

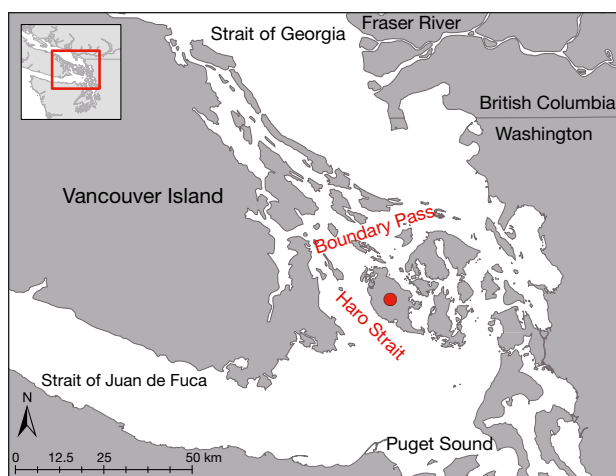


Fig. 1. Central Salish Sea, where southern resident killer whales feed on returning Chinook salmon while interacting with pink salmon from late July through early September. The primary feeding area is Haro Strait and Boundary Pass, immediately west and north of San Juan Island (red dot), Washington (Hauser et al. 2007)

Since SRKWs are highly social, individual whales do not leave the pod for extended periods, nor do whales from other populations join SRKW pods. Some age-0 whales may have died before identification, especially among those born during winter, so mortality of these young whales was likely underestimated (Olesiuk et al. 1990); however, this would not bias the biennial pattern of mortality. Annual whale birth and death statistics were based on a calendar year. Newborn whales that died within the same calendar year were included in the mortality statistics. Total births were examined, but neonate mortalities were not included in the statistics for successful births because lower nutritional status of SRKWs has been linked to higher rates of miscarriages and mortalities of newborns (Wasser et al. 2017). Annual percent mortality calculations included all SRKW births and mortalities. Annual net whale population change was calculated from the difference in births and deaths.

Graphical plots and ANOVA were used to evaluate the presence of a biennial odd/even year signal in SRKW demographics. Visual examination of the pattern of SRKW mortality anomalies since 1976 suggested that the biennial pattern began in 1998 (see Fig. 2B), which corresponded with the period of population decline following peak abundance in 1995. A preliminary 2-factor ANOVA (time period; odd/even year) confirmed strong interaction between the 2 factors across the entire time period. Therefore, separate Model 1 ANOVAs were performed on data corresponding with the period of population growth and high abundance (1976–1997) and the period of population decline (1998–2017) to evaluate the main factor effect (odd/even year), especially during the period of population decline (Zar 1996). ANOVA is robust to assumptions of normality and homogeneity of variance when samples sizes are nearly equal: Shapiro-Wilks and Levene's tests indicated the data did not violate these assumptions. Error terms associated with mean values are standard errors (SE) unless noted otherwise.

3. RESULTS

During the recent period of decline (1998–2017), whale deaths averaged 3.6 times higher in even years (6.1 ± 0.8 whales yr^{-1}) than odd years (1.7 ± 0.5 whales yr^{-1}) ($F_{1,18} = 23.2$; $p < 0.001$) (Fig. 2A). Likewise, the percentage of the whale population dying each year was higher in even years ($7.2 \pm 0.1\%$) than odd years ($2.0 \pm 0.6\%$) ($F_{1,18} = 24.3$; $p < 0.001$) (Fig. 2B). New-

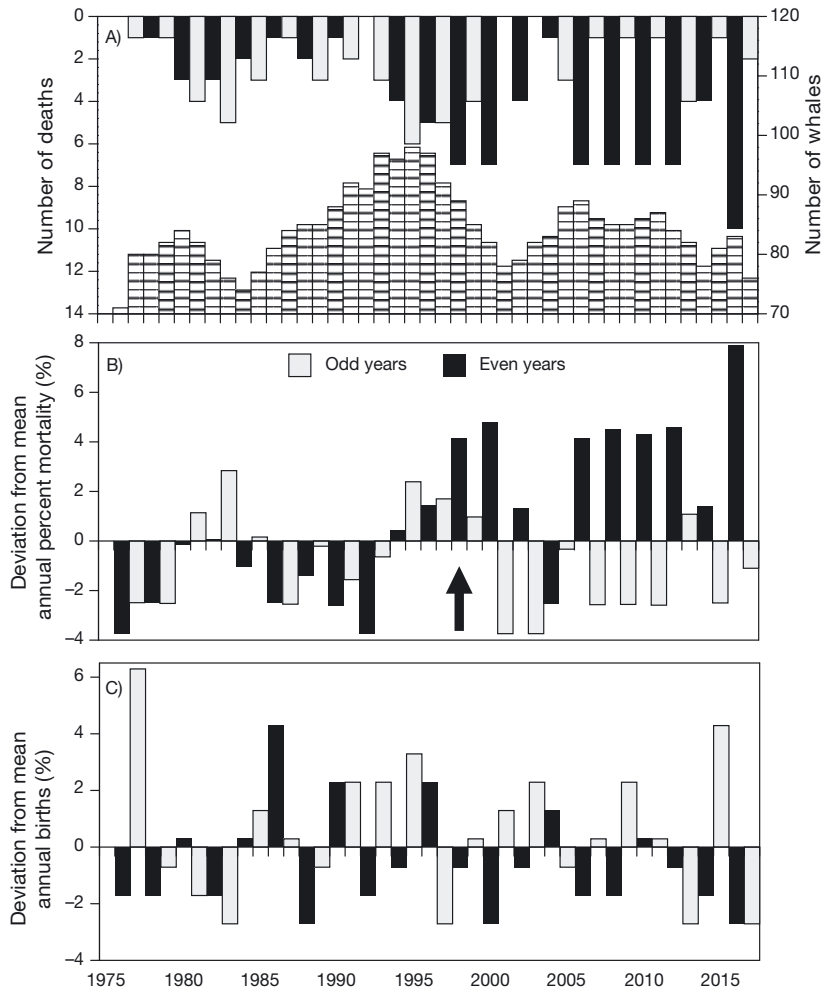


Fig. 2. Southern resident killer whale (A) deaths per year (solid bars) and whale population size (hatched bars) since 1976, (B) annual percent whale mortality in relation to mean mortality during the entire time period (mean \pm SE, $3.7 \pm 0.4\%$), and (C) annual births in relation to mean births during the entire time period (2.7 ± 0.3). Black arrow: beginning of the reduction in fishery harvest of pink salmon in the Salish Sea; also corresponds to the 1997/98 El Niño event, a regime shift in the Pacific Decadal Oscillation, and to changes in the foraging distribution of the whales

born and age-1 whales also tended to die more frequently in even years (13 and 4 whales, respectively) than in odd years (5 and 0 whales). The biennial mortality pattern was consistent between sexes (81% of males and 69% of females died during even years) and among the 3 pods (J— $3.2\times$, K— $2.4\times$, and L— $3.1\times$ greater percent mortality in even years).

During the period of population increase and high abundance (1976–1997), annual whale mortality ($2.9 \pm 0.4\% \text{ yr}^{-1}$) was 37% lower than in the period of decline 1998–2017 ($4.6 \pm 0.8\% \text{ yr}^{-1}$) ($F_{1,40} = 3.76$; $p = 0.060$), and a biennial pattern was not apparent (Fig. 2A,B). Overall higher mortality during the recent period of decline is entirely related to high

mortality during even years, as whale mortality was actually lower in recent odd years, i.e. whale percent mortality averaged 3.1 times higher in recent versus earlier even years, whereas it averaged 43% lower during recent odd years than earlier odd years.

Birth rate of SRKWs was slightly, but not significantly, lower during the recent period of population decline ($2.4 \pm 0.4 \text{ births yr}^{-1}$) than in the earlier period of population growth ($3.0 \pm 0.5 \text{ births yr}^{-1}$) ($F_{1,40} = 0.8$; $p = 0.39$). However, during the recent decline period, successful births were 50% less frequent in even years ($1.6 \pm 0.4 \text{ births yr}^{-1}$) than in odd years ($3.2 \pm 0.7 \text{ births yr}^{-1}$; Fig. 2C) ($F_{1,18} = 3.97$; $p = 0.061$). In comparison, in the growth period, fewer successful births tended to occur (22% fewer) in even years versus odd years. During even years, birth rates tended to be lower in the decline period (39% lower) than in the growth period; in contrast, they were nearly identical in odd years (5% decline between intervals).

As the population decreased during the decline period (1998–2017), net annual change in the SRKW population (births minus deaths) declined by $3.0 \pm 0.9 \text{ whales yr}^{-1}$ in even years and increased by $1.9 \pm 1.0 \text{ whales yr}^{-1}$ in odd years ($F_{1,18} = 13.6$; $p = 0.002$). In contrast, during the earlier growth period (1976–1997), net annual change was positive and similar during both even ($0.9 \pm 0.8 \text{ whales yr}^{-1}$) and odd years ($0.6 \pm 1.2 \text{ whales yr}^{-1}$).

4. DISCUSSION

The odd- versus even-year biennial cycle of elevated mortality and reduced reproduction in SRKWs during the past 20 yr of population decline was previously unrecognized. We suspect that the biennial pattern of mortality and birth is indirectly linked to the extreme biennial pattern in abundance of adult pink salmon *Oncorhynchus gorbuscha* in the Salish Sea—annual returns since 1976 have averaged approximately 17.8 ± 1.8 million fish in odd years but only 0.4 ± 0.1 million fish in even years (Ruggerone & Irvine 2018). This is the only biennial pattern in the

physical or biological environment of the northeastern Pacific Ocean of which we are aware that could potentially drive the demographic pattern observed in SRKWs. Pink salmon have been shown to be very influential in ecosystems elsewhere in the North Pacific, where they initiate pelagic trophic cascades and impact the growth and productivity of various other consumers, including several other species of salmon, other fishes, and seabirds in odd years of high abundance (Ruggerone & Nielsen 2004, Springer & van Vliet 2014, Ruggerone & Connors 2015, Shaul & Geiger 2016, Batten et al. 2018, Springer et al. 2018). In the Salish Sea, pink salmon have had a significant biennial effect on the survival of juvenile Chinook salmon, but age diversity among returning Chinook salmon inhibits a biennial pattern in adult Chinook salmon abundance (Ruggerone & Goetz 2004). We believe the linkage to pink salmon is necessarily indirect since the SRKWs rarely consume pink salmon (Ford et al. 2016) despite encountering high densities of these fish from late July through early September in odd years while foraging on summer and fall Chinook salmon in the Salish Sea.

One hypothesis that would explain the observed biennial pattern in the SRKW population is that highly abundant odd-year pink salmon interfere with the ability of whales to feed on co-migrating summer and early fall Chinook salmon in the Salish Sea during a 2 mo period when the SRKWs are highly dependent on the already depleted Chinook salmon (Chasco et al. 2017). Pink salmon are currently ~50 times more abundant than the co-migrating Chinook salmon in this area. Reduced foraging efficiency of the whales would lower their nutritional status, which would be expressed in the following even year because these large mammals have a strong physiological buffering capacity (Ford et al. 2010). Furthermore, the finding that lower nutritional status of SRKWs is linked to higher rates of miscarriages and mortalities of newborns (Wasser et al. 2017) supports our observation of higher newborn mortality in even years.

An alternative hypothesis is that pink salmon enhance the ability of whales to feed, resulting in lower mortality in odd years of high pink salmon abundance. According to this hypothesis, higher mortality of SRKWs in even years, when few pink salmon are present, is the current norm, generally tracking the abundance of Chinook salmon throughout the SRKW's range. High even-year mortality is the driver of declining numbers of SRKWs, which might be even greater were it not for the hypothesized positive effect of odd-year pink salmon since

1998. As noted earlier, mortality of SRKWs in odd years since 1998 has been 43% lower than in odd years during 1976–1997. However, at present we do not have a mechanistic explanation for how pink salmon would enhance SRKW foraging on Chinook salmon.

The emergence of the biennial demographic pattern coincided with a large decline in commercial harvests of pink salmon in the Salish Sea after 1998 (PSC 2016), which allowed the fish to migrate free from the commercial fishery disturbance that likely disrupted their natural schooling behavior. Approximately 135% more odd-year pink salmon have escaped the fishery since 1998 and potentially interact with the SRKWs that forage along the west side of San Juan Island and into Boundary Pass, where both pink and Chinook salmon migrate (Fig. 1).

The biennial pattern also coincided with shifts in the foraging distribution of SRKWs. Since 2001, whales have spent fewer days per month in the core foraging area in the Salish Sea between April and September, apparently in response to lower availability of Chinook salmon (Shields et al. 2018, CWR 2018). This lower daily presence has occurred even though overall salmon harvests and fishing effort, which overlap core foraging areas in the Salish Sea, declined significantly in the mid-1990s and thereafter (PSC 2017). Since 1998, SRKWs have been observed more frequently in the Salish Sea during fall and winter (NMFS 2008, Ford et al. 2017), potentially reflecting the 46% increase in the abundance of chum salmon *Oncorhynchus keta* in Puget Sound (Ruggerone & Irvine 2018) as well as increased observation effort. A biennial pattern of presence of the L pod in the Salish Sea in December of recent years (Ford et al. 2017) may have developed in response to the generally lower odd-year abundances of late-returning Puget Sound chum salmon, which were also inversely correlated with pink salmon (Ruggerone & Nielsen 2004) and which might further lower the nutritional status of the SRKWs in odd years.

The beginning of the biennial pattern also coincided with the strong 1997/98 El Niño and a regime shift in the Pacific Decadal Oscillation (PDO; Overland et al. 2008), which has had a large effect on Pacific salmon and other marine species (Peterson & Schwing 2003). However, despite compelling evidence that climate variability, at various scales, is correlated with variability in salmon production and abundance dynamics (Mueter et al. 2002, Mantua & Hare 2002, Mantua 2015), we cannot envision how climate would initiate and maintain such an extreme, synchronized biennial signal in SRKWs.

Likewise, we cannot envision how vessel noise and disturbance or toxic contaminants could drive the SRKW biennial pattern. Biennial fluctuations in abundance of their primary prey, Chinook salmon, might drive the SRKW biennial pattern, but as noted above, such a pattern among juvenile Chinook salmon would be masked by the age diversity of returning adult salmon.

Unlike the majority of mysticete cetaceans, which are capital breeders that can produce calves every year, most odontocete cetaceans, including killer whales, are income breeders that skip at least 1 to 2 yr between calves (Würsig et al. 2017). SRKWs skip approximately 5.7 yr, on average, between calves and there is considerable variation within and among individual whales, indicating the biennial birthing pattern is not a stochastic process. Furthermore, birthing schedules of female odontocetes are individual-based, not synchronized. The demographic pattern we report for SRKWs differs from other odontocetes in respect to the biennial synchronicity within the population. Strictly biennial breeding patterns are rare in all mammals (Patil et al. 2015). We are unaware of any biennial patterns of mortality in other mammals.

5. CONCLUSIONS

We have identified a previously unknown odd/even-year factor linked significantly to survival ($p < 0.001$) and low birth rate ($p = 0.061$) of SRKWs. None of the purported factors of SRKW decline (Chinook salmon abundance, toxic contaminants, ship noise) can directly explain the biennial demographic pattern. In contrast, the extreme biennial pattern in abundance of pink salmon, coupled with the known or suspected effects they have on other species and ecosystem processes elsewhere in the North Pacific, is consistent with the demographic pattern observed in SRKWs. Increased understanding of SRKW demographics in relation to this biennial pattern will provide greater opportunities for advancing their recovery. For example, a field study that quantifies foraging efficiency of SRKWs during even versus odd years could be designed to test the 2 pink salmon hypotheses identified here. Modeling of SRKW demographics in relation to Chinook salmon and pink salmon abundance would also be informative. We recommend further investigations such as these to evaluate mechanistic elements of SRKW biennial mortality and birth rates in their own right and in the context of ecosystem management and conservation, and to inform recovery efforts of the critically endangered SRKW population.

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LITERATURE CITED

- ✦ Batten SD, Ruggerone GT, Ortiz I (2018) Pink salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands. *Fish Oceanogr* 27:548–559
- Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep Int Whaling Comm* 12:383–405
- ✦ Chasco B, Kaplan IC, Thomas A, Acevedo-Gutiérrez A and others (2017) Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. *Can J Fish Aquat Sci* 74:1173–1194
- ✦ CWR (Center for Whale Research) (2018) Annual SRKW demographic data. Center for Whale Research, Friday Harbor, San Juan Island, WA. <https://www.whaleresearch.com/orcasurvey>
- ✦ Desforges JP, Hall A, McConnell B, Rosing-Asvid A and others (2018) Predicting global killer whale population collapse from PCB pollution. *Science* 361:1373–1376
- ✦ DFO (Department of Fisheries and Oceans) (2018) Southern resident killer whale: a science based review of recovery actions for three at-risk whale populations. Fisheries and Oceans Canada, Ottawa. <http://waves-vagues.dfo-mpo.gc.ca/Library/40680022.pdf>
- ✦ Ford JKB, Ellis GM, Olesiuk PF, Balcomb KC (2010) Linking killer whale survival and prey abundance: Food limitation in the oceans' apex predator? *Biol Lett* 6:139–142
- Ford JKB, Pilkington JF, Reira A, Otsuki M and others (2017) Habitats of special importance to resident killer whales (*Orcinus orca*) off the west coast of Canada. Canadian Science Advisory Secretariat Research Document 2017/035. Fisheries and Oceans Canada, Ottawa
- ✦ Ford MJ, Hempelmann J, Hanson MB, Ayres KL and others (2016) Estimation of a killer whale (*Orcinus orca*) population's diet using sequencing analysis of DNA from feces. *PLOS ONE* 11:e0144956
- ✦ Hauser DW, Logsdon MG, Holmes EE, VanBlaricom GR, Osborne RW (2007) Summer distribution patterns of southern resident killer whales *Orcinus orca*: core areas and spatial segregation of social groups. *Mar Ecol Prog Ser* 351:301–310
- ✦ Lacy RC, Williams R, Ashe E, Balcomb KC III and others (2017) Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. *Sci Rep* 7:14119
- ✦ Lundin JI, Ylitalo GM, Giles DA, Seely EA and others (2018) Pre-oil spill baseline profiling for contaminants in southern resident killer whale fecal samples indicates possible exposure to vessel exhaust. *Mar Pollut Bull* 136:448–453
- ✦ Mantua NJ (2015) Shifting patterns in Pacific climate, West Coast salmon survival rates, and increased volatility in ecosystem services. *Proc Natl Acad Sci USA* 112:10823–10824

- ✦ Mantua NJ, Hare SR (2002) The Pacific Decadal Oscillation. *J Oceanogr* 58:35–44
- ✦ Mueter FJ, Ware DM, Peterman RM (2002) Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the northeast Pacific Ocean. *Fish Oceanogr* 11:205–218
- ✦ NMFS (2008) Recovery plan for southern resident killer whales (*Orcinus orca*). National Marine Fisheries Service, Seattle, WA. <https://repository.library.noaa.gov/view/noaa/15975>
- Olesiuk, PF, Bigg, MA, Ellis, GM (1990) Life history and population dynamics of resident killer whales (*Orcinus orca*) in coastal waters of British Columbia and Washington State. *Rep Int Whal Comm Spec Issue* 12:209–243
- ✦ Overland J, Rodionov S, Minobe S, Bond N (2008) North Pacific regime shifts: definitions, issues and recent transitions. *Prog Oceanogr* 77:92–102
- ✦ Patil VP, Karels TJ, Hik DS (2015) Ecological, evolutionary, and social constraints on reproductive effort: Are hoary marmots really biennial breeders? *PLOS ONE* 10: e0119081
- ✦ Peterson WT, Schwing FB (2003) A new climate regime in northeast Pacific ecosystems. *Geophys Res Lett* 30:1896
- ✦ PSC (Pacific Salmon Commission) (2016) Report of the Fraser River panel to the Pacific Salmon Commission on the 2015 Fraser River sockeye and pink salmon fishing season. Pacific Salmon Commission, Vancouver. <https://www.psc.org/publications/annual-reports/fraser-river-panel/>
- ✦ PSC (2017) Annual report of catch and escapement. Pacific Salmon Commission Joint Chinook Technical Committee Report TCChinook (17)-2. Pacific Salmon Commission, Vancouver. <https://www.psc.org/publications/technical-reports/technical-committee-reports/chinook/>
- ✦ Ruggerone GT, Connors BM (2015) Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean. *Can J Fish Aquat Sci* 72:818–833
- ✦ Ruggerone GT, Goetz F (2004) Survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*O. gorbuscha*). *Can J Fish Aquat Sci* 61:1756–1770
- ✦ Ruggerone GT, Irvine JR (2018) Numbers and biomass of natural- and hatchery-origin pink, chum, and sockeye salmon in the North Pacific Ocean, 1925–2015. *Mar Coast Fish* 10:152–168
- ✦ Ruggerone GT, Nielsen JL (2004) Evidence for competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. *Rev Fish Biol Fish* 14:371–390
- Shaul LD, Geiger HJ (2016) Effects of climate and competition for offshore prey on growth, survival, and reproductive potential of coho salmon in Southeast Alaska. *N Pac Anadr Fish Comm Bull* 6:329–347
- ✦ Shields MW, Lindell J, Woodruff J (2018) Declining spring usage of core habitat by endangered fish-eating killer whales reflects decreased availability of their primary prey. *Pac Conserv Biol* 24:189–193
- ✦ Springer AM, van Vliet GB (2014) Climate change, pink salmon, and the nexus between bottom-up and top-down forcing in the subarctic Pacific Ocean and Bering Sea. *Proc Natl Acad Sci USA* 111:E1880–E1888
- ✦ Springer AM, van Vliet GB, Bool N, Crowley M and others (2018) Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem. *Proc Natl Acad Sci USA* 115:E5038–E5045
- ✦ SROTf (Southern Resident Orca Task Force) (2018) Report and recommendations. www.governor.wa.gov/sites/default/files/OrcaTaskForce_reportandrecommendations_11.16.18.pdf (accessed Nov 2018)
- ✦ Ward EJ, Holmes EE, Balcomb KC (2009) Quantifying the effects of prey abundance on killer whale reproduction. *J Appl Ecol* 46:632–640
- ✦ Wasser SK, Lundin JI, Ayres K, Seely E and others (2017) Population growth is limited by nutritional impacts on pregnancy success in endangered southern resident killer whales (*Orcinus orca*). *PLOS ONE* 12:e0179824
- Würsig B, Thewissen JG, Kovacs KM (eds) (2017) *Encyclopedia of marine mammals*, 3rd edn. Academic Press, Cambridge, MA
- Zar JH (1996) *Biostatistical analysis*, 3rd edn. Prentice Hall, Upper Saddle River, NJ

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