

## Long-distance migration of prey synchronizes demographic rates of top predators across broad spatial scales

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**Abstract.** Reproductively and geographically isolated populations of predators may be synchronized by a phenomenon known as the Moran effect—specifically if they exhibit common responses to external processes, such as climate, density dependence (parasites, disease), or prey. Prey has the ability to synchronize predators if geographically isolated predator populations target the same prey species, or if the migration and range of the prey species occurs over a large enough scale to be available to multiple predator populations. The objective of our study was to investigate evidence for correlations of demographic rates between geographically isolated populations of piscivorous killer whales in the Northeast Pacific; using long-term mark-recapture datasets collected over the last 30+ yrs, we constructed a hierarchical occupancy model, linking models of survival and fecundity in a single framework. We found strong support for synchronized demographic rates in Southeast Alaska and Southern Resident killer whales, which are geographically and reproductively isolated. Despite their isolation, they experience extremely correlated dynamics—the correlation in fecundity rates between populations exceeds 0.9. The correlation in demographic rates across these populations of killer whales in different regions of the Northeast Pacific Ocean suggests a common environmental driver. Both killer whale populations are known to prey on Chinook salmon, which have a long-distance coastal migration larger than the habitat range of killer whales. Many of these Chinook salmon are also of the same origin (southern stocks), suggesting that these populations not only consume the same prey species but the same prey populations.

**Key words:** correlated population dynamics; killer whales; long-distance migration; Moran effect; predator-prey; salmon; synchrony.

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### INTRODUCTION

Understanding the mechanisms responsible for metapopulation synchrony is essential for predicting population viability (Hanski and Gil-

pin 1997). Subpopulations may be synchronized not only directly through migration and dispersal but also by external drivers. The synchrony of geographically isolated populations by their response to similar environmental conditions is

known as the Moran effect (Ranta et al. 1997). While the majority of studies showing support for the Moran effect have focused on climate processes, other mechanisms may include parallel responses to parasites (Hudson and Cattadori 1999) or predator-prey dynamics (Vasseur and Fox 2009). A less studied mechanism, also related to prey, is the ability of long-distance migrations of prey populations to synchronize isolated predator communities.

One of the best examples of a prey species synchronizing multiple consumer populations has been research focused on Pacific salmon (*Oncorhynchus* spp.). Three unique characteristics make salmon extremely important in the ecosystems they inhabit: their life histories, metapopulation dynamics, and long-distance migrations. Because they are anadromous, and thus available to be eaten by both terrestrial and aquatic consumers, salmon have the ability to synchronize many types of predators (Schindler et al. 2013). Individual salmon populations from the same species are generally viewed as a metapopulation. Asynchrony between populations has been shown to have a stabilizing effect on the variability of ecosystem services that salmon provide, such as fish available to fisheries (also referred to as the portfolio effect; Schindler et al. 2010). Because of their long-distance migration patterns of over 1000s of kilometers (Trudel et al. 2009), salmon may also synchronize consumers over very large spatial scales. Juvenile salmon from rivers in the United States (Washington, Oregon) and Canada (British Columbia) leave their natal streams and generally migrate northward to higher latitudes in Alaska (Quinn 2005). Several years later as adults, this migration is reversed. During both the juvenile and adult migrations, salmon may be targeted by predators (marine mammals, piscivorous fishes), and during their adult migration they are also targeted by fisheries.

In the Northeast Pacific Ocean, there are six species of salmon, but the king or Chinook salmon (*Oncorhynchus tshawytscha*) is the largest and most commercially valuable. Chinook are targeted by commercial, recreational, and tribal fisheries in the United States and Canada. Recent work on the population dynamics of fish-eating killer whales (*Orcinus orca*, also referred to as “resident” whales) has shown correlations be-

tween killer whale demographic rates and indices of prey (Chinook salmon) across large spatial scales (Ward et al. 2009a, Ford et al. 2010). There are several distinct populations of resident killer whales in the Northeast Pacific, including Southeast Alaska Residents (SEAR), Northern Residents (NR), and Southern Residents (SR). Southern Resident whales’ core habitat is in southern British Columbia and Washington State, Northern Resident whales’ core habitat is in the coastal areas of British Columbia, and SEAR live furthest to the north in Alaskan waters (Fig. 1). Some of these populations have geographically overlapping ranges (SR and NR, NR and SEAR), but each is reproductively isolated (Barrett-Lennard and Ellis 2001).

Over the last 30+ yrs, many of these resident killer whale populations have been the subject of mark-recapture studies. Several significant findings have emerged from these long-term studies. First, resident killer whales are extremely long lived, with some females surviving to age 80 (Bigg et al. 1990). Second, resident killer whales are extremely social and remain in close family groups (matrilines, pods) for their entire lives (Bigg et al. 1990). During their reproductive lifespan between the ages of 10 and early 40s, females may produce offspring every 3–5 yrs. Reproduction ceases by age 45, and like several other long-lived mammals, females exhibit a long postreproductive lifespan (Ward et al. 2009b). The long generation time of this species translates into smaller population growth rates relative to many other marine mammals. Across populations, killer whale growth rates exhibit a latitudinal gradient in the NE Pacific Ocean, with increasing population growth rates at higher latitudes (Ward et al. 2013, Matkin et al. 2014). Differences in the spatiotemporal distribution of prey (including Chinook salmon) likely shape this pattern.

The objective of our analysis is to estimate the degree of synchrony in time-varying demographic rates between two geographically and reproductively isolated populations of killer whales. Our a priori hypothesis is that although the populations have different trends, they experience good and bad years together, in large part because of overlap in diet (including Chinook salmon). This comparison between populations also provides an additional baseline for the SR

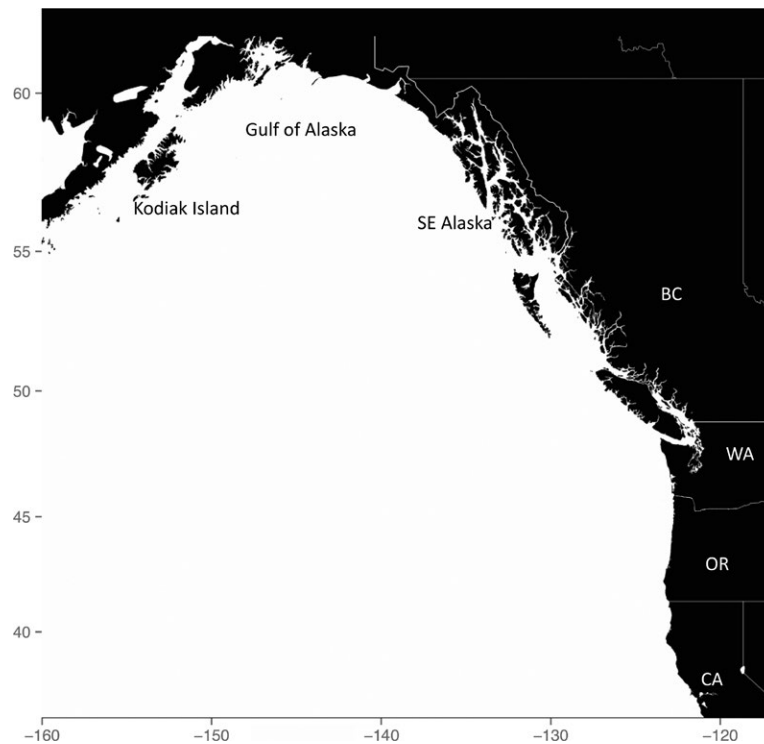


Fig. 1. Map of study region across Canada (British Columbia = BC) and the United States (California = CA, Oregon = OR, Washington = WA, and Alaska).

killer whale population, which is endangered under the U.S. Endangered Species Act. Finally, our modeling framework allows for updated population estimates for the SEAR whales.

## METHODS

### Data

Surveys and censuses of killer whale populations in the NE Pacific Ocean have relied on the fact that individual killer whales are recognizable based on unique pigmentation and fin shape (Bigg et al. 1990). Photographs taken during visual surveys can be compared with existing photo-ID catalogs, allowing the encounter histories of individuals to be reconstructed through time. For all populations, encounter histories have been recorded on an annual basis, typically in summer months.

We used encounter histories from two populations of killer whales: the population known as “Southern Resident” killer whales (SR), which inhabit the waters off southern British Columbia, Washington, and Oregon; and “Southeast Alaska

Resident” killer whales (SEAR), which primarily inhabit the waters of Southeast Alaska, but also make movements west to the central Gulf of Alaska near Kodiak Island. Censuses of the SR population have been done in summer months by the Center for Whale Research in the inland waters of Washington State and British Columbia since 1976. Annual surveys of the SEAR population have been done by the National Mammal Laboratory (NMML) since 1983, and most of these surveys have been done in summer months (e.g., from 1991 to 2014, NMML conducted 9 spring, 18 summer, and 17 fall surveys). Spatially, these surveys covered all major inland waters of Southeast Alaska each year (including Lynn Canal, Icy Strait, Chatham Strait, Stephens Passage, Frederick Sound, Sumner Strait, and Clarence Strait). Whenever possible, smaller bodies of water and areas exposed to the open ocean were also surveyed.

The Southeast Alaska population, estimated at 115 whales in 2014, has been historically separated into two pods, known as AG and AF (Dahlheim et al. 1997, Matkin et al. 1999). As the AF

pod grew in size, it eventually split in the mid-1990s into what is currently known as the AF5s and AF22s (Matkin et al. 2014). Between spring and fall months, AG and AF pods are frequently seen in Southeast Alaska waters (Dahlheim et al. 1997, 2009). AG and AF pod members routinely travel together but have not been seen to intermix with other resident whales that occasionally occur in this area (e.g., whales from the NR population; Dahlheim et al. 1997).

In all, we used data from a total of 346 individual whales (191 SR whales, 155 SEAR whales) to estimate temporal synchrony in fecundity and survival. For the fecundity modeling, we used data from 58 mothers (34 SR whales gave birth to 78 calves, 25 SEAR whales gave birth to 48 calves). Several of the SR females were excluded based on births prior to 1960 because their assigned ages may introduce bias (Ward et al. 2009a).

### Statistical modeling

Previous approaches to analyzing killer whale demographic data have separately modeled survival and fecundity data and ignored uncertainty associated with detection (Olesiuk et al. 1990, Ford et al. 2010). Ignoring detectability in models of SR killer whale demography is not expected to introduce bias, since the entire population is censused in each year (Ward et al. 2009a, 2011). For other populations, however, not including detection may introduce slight biases (Royle et al. 2005). To improve on these existing approaches, we constructed a statistical model of multiple killer whale populations (SR, SEAR) and combined multiple data streams (survival, fecundity) in an integrated modeling framework (Kery and Schaub 2012) to account for imperfect detection of some populations.

When photo-identification surveys of killer whales were initiated in the late 1970s, there was considerable uncertainty in the ages of some of the older animals. As a result, survival of killer whales is generally modeled as stage structured (Ford et al. 2010), while fecundity is typically modeled as age structured (Ward et al. 2009a). We adopted six previously defined stage classes for survival: calves (age 0), juveniles (1–9), reproductive females (10–42), postreproductive females (43+), young males (10–21), and older

males (22+) (Ward et al. 2013). Survival of the  $i$ th animal in year  $t$  can be represented as

$$\text{logit}(\phi_{i,t}) = B_{\text{pop},\text{stage}_{i,t}} + \delta_{t,\text{pop}}$$

where  $B_{\text{pop},\text{stage}_{i,t}}$  represents the fixed-effect intercept unique to a particular stage and population, and  $\delta_{t,\text{pop}}$  represents a time-varying random effect (explained in more detail below). Following the occupancy modeling framework of Royle and Dorazio (2008), we modeled the latent state of each individual (alive/dead), because unobserved animals may be either missing or dead. The state of each animal in each year is a random process,

$$z_{i,t} \sim \text{Bernoulli}(\phi_{i,t-1} \cdot z_{i,t-1}).$$

In other words, an animal alive at time  $t - 1$  is allowed to experience survival, but once an animal has died, they are not allowed to transition from that state. This latent process model is linked to the binary data (detected or not) as

$$Y_{i,t} \sim \text{Bernoulli}(z_{i,t} \cdot p_{\text{pop}})$$

where  $p_{\text{pop}}$  represents the population-specific probability of detection. Because the SR killer whale population is censused annually, we fixed that detection probability at 1. For the SEAR population, which has divided into three larger social aggregations (AF5, AF22, AG pod), we allowed the detection probability to potentially vary by pod.

For the model of killer whale fecundity, we used the model previously found as the best fit to the fecundity-at-age relationship and treated age as a fourth-order polynomial (Ward et al. 2009a) with a population-specific intercept. Mathematically, this means

$$\text{logit}(y_{i,t}) = F_{0,\text{pop}} + F_1 a_{i,t} + F_2 a_{i,t}^2 + F_3 a_{i,t}^3 + F_4 a_{i,t}^4 + \varepsilon_{t,\text{pop}}$$

where  $F_0, F_1$ , etc. represent regression coefficients,  $a_{i,t}$  is the known age of animal  $i$  at time  $t$ , and  $\varepsilon_{t,\text{pop}}$  represents time-varying random effects (shared among all individuals, but allowed to differ between populations). Not all killer whale births are observed because individuals are seen



sporadically throughout the year, and there is some chance that calves are born and die during sighting intervals. Ideally the state of the mother (pregnant or not) could be modeled as a latent state, but the population-specific probability of detecting calves is confounded with  $F_{0,\text{pop}}$ , the population-specific intercept. In other words, a deficit of births in a population may be a result of lower birth rates or lower detection rates.

We included the temporal random effects in survival and fecundity as a correlated random walk, allowing the demographic rates of each population to be correlated (e.g., fecundity is correlated with survival), but also allowing the demographic rates across populations to be correlated (e.g., SR and SEAR survival rates are correlated). The random effects for all demographic rates were modeled as

$$\omega_{t,1:4} \sim \text{MVN}(\rho \cdot \omega_{t-1,1:4}, \Sigma)$$

where  $\rho$  is an autoregressive parameter controlling temporal correlation, and  $\Sigma$  is an unconstrained  $4 \times 4$  covariance matrix modeling the two demographic rates of the two populations. The elements of  $\omega_t$  are simply the combined deviations from the survival model,  $\delta_t = \omega_{t,1:2}$ , and from the fecundity model,  $\varepsilon_t = \omega_{t,3:4}$ . Our inference is partially focused on the off-diagonal elements of  $\Sigma$ , which control the degree of correlation within and between populations. While this approach is flexible, we caution that if it were applied to populations of very different sizes, or with significant data gaps for one population, inferred temporal correlation may be driven by the larger population (or the one with fewer data gaps).

All parameter estimation was conducted in a Bayesian framework. We assigned uniform (0, 1) priors to the detection probabilities, temporal correlation, and survival rate parameters. Coefficients in the fecundity model linking age to births were assigned Normal (0, 1) priors. Because  $\Sigma$  is a covariance matrix, we assigned the Wishart prior to  $\Sigma^{-1}$  (Gelman et al. 2004). Following previous occupancy modeling analyses (Royle et al. 2005), we used the JAGS software via the R2jags package in R (Plummer 2003, R Core Development Team 2015; Su and Yajima 2015). We ran four Markov Chain Monte Carlo chains for a burn-in

of 100 000 iterations, followed by another 20 000 samples (thinning every 10th). Convergence diagnostics were assessed using the Gelman–Rubin diagnostic (Gelman and Rubin 1992).

## RESULTS

We found consistent differences in demographic rates between the SR and SEAR populations, with SR whales having lower estimated survival rates (Fig. 2). Estimates of survival of calves for both populations is near 50% (Fig. 2); the small sample sizes of observed mortalities from each population result in wide credible intervals. The weight of evidence is stronger in our modeling, as stage-specific survival is estimated as fixed effects (allowed to vary by stage), rather than as a constant fixed population effect shared among all age classes (e.g., Ward et al. 2013). The biggest absolute differences in survival rates were between SR and SEAR juveniles, young males, and old males (Fig. 2).

Similar to the differences in survival, we found consistently higher fecundity for SEAR females over SR females (Fig. 3). For example, the probability of giving birth for a SEAR female is 0.258 vs. 0.203 for a SR female (27% higher). These results are comparable to the differences estimated between the overlapping SR and NR populations (Ward et al. 2009a). Within the SEAR population, we also estimated significantly different encounter probabilities for each of the larger social groups (AG, AF groups). The AG pod was estimated to have a higher detection probability ( $\hat{p} = 0.52$ , 95% CIs = 0.48, 0.56) vs. the AF5 pod ( $\hat{p} = 0.44$ , 95% CIs = 0.41, 0.48) and AF22 pod ( $\hat{p} = 0.38$ , 95% CIs = 0.35, 0.42).

By treating the demographic rates from each population as time-varying random effects, and potentially correlated, we were able to estimate the degree of synchrony within and between populations (Figs. 4 and 5). The pairs of demographic rates (survival, fecundity) were correlated within populations ( $\rho = 0.39$  for SR,  $\rho = 0.37$  for SEAR). Though survival and fecundity are correlated with prey abundance (Ford et al. 2010), survival and fecundity may not be perfectly correlated within a year, because of the long gestation period of killer whales (17–18 months). We found higher correlations in demographic

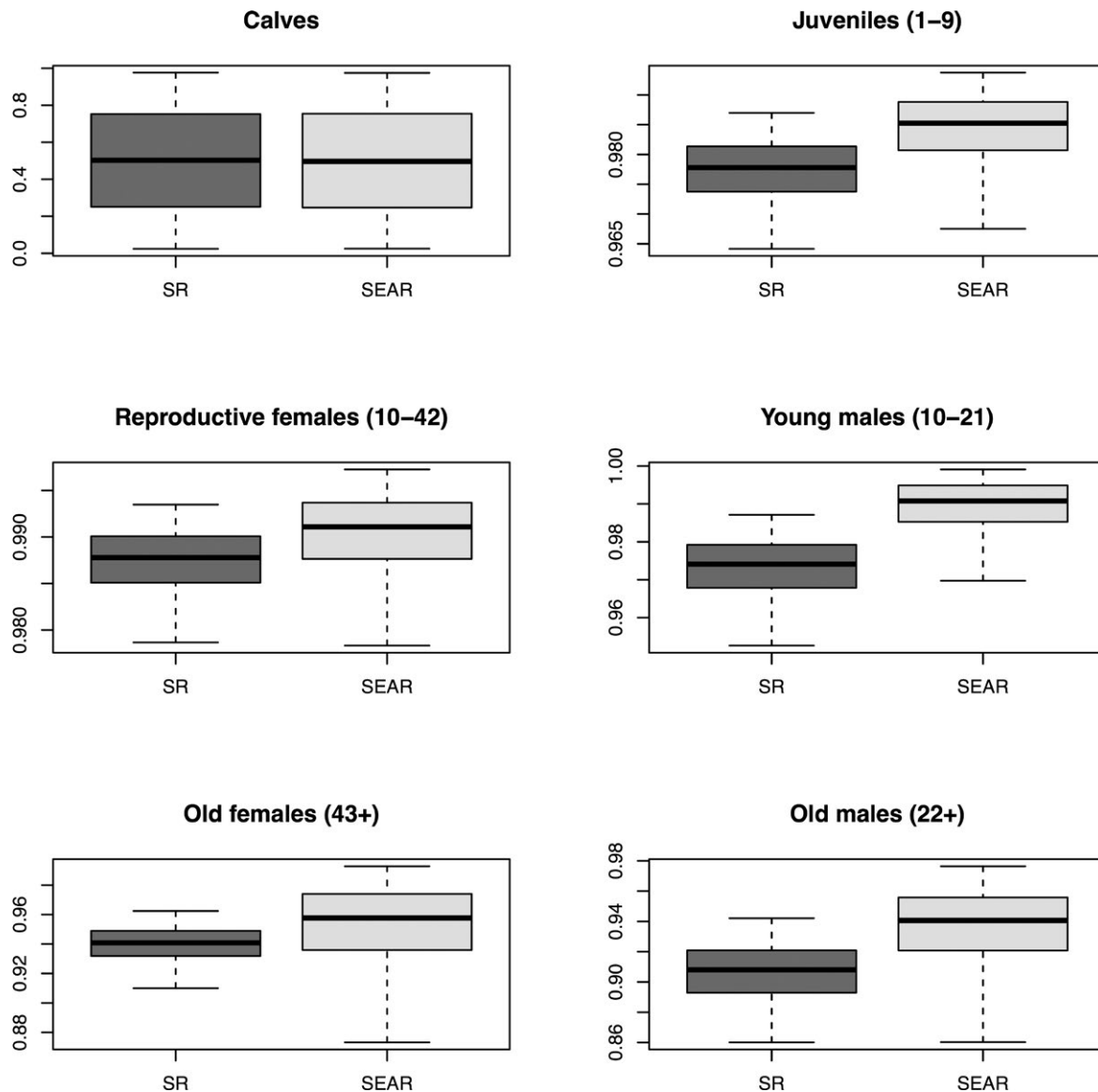


Fig. 2. Estimated survival rates by stage (sex and age) of the two populations of killer whales used in our analysis (Southern Resident = SR, Southeast Alaska Resident = SEAR). We allow survival to be time varying (Figs. 3 and 4), but these rates represent survival in a reference year (1983).

rates across populations, however. Fecundity was most correlated ( $\rho = 0.92$ ), but survival rates were also positively correlated ( $\rho = 0.52$ ).

## DISCUSSION

Increases in the ocean abundance of salmon are thought to be the primary hypothesis for why some fish-eating killer whale populations

have larger growth rates than others (Matkin et al. 2014). The observation that growth rates of killer whale populations increase with latitude is consistent with this hypothesis. The lower survival of the SR population is consistent with other comparative studies (Ford et al. 2010, Ward et al. 2013) and is expected given that the SR population has a lower growth rate than the SEAR population (Matkin et al. 2014).

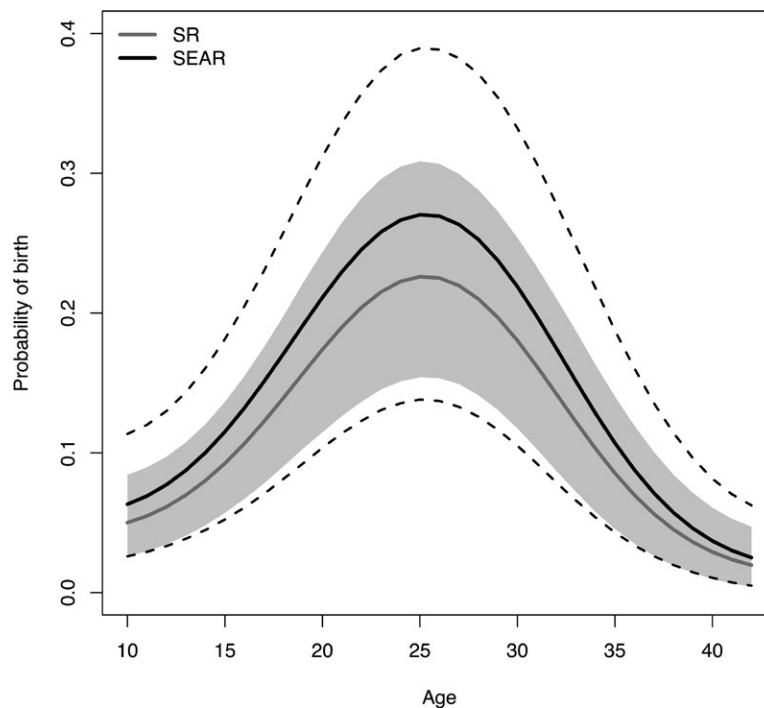


Fig. 3. Estimated probability of live birth by age and population (Southern Resident = SR, Southeast Alaska Resident = SEAR). Rates in our model are time varying, but these represent fecundity in the baseline year (1983). The gray region (SR) and dotted lines (SEAR) represent the 95% CIs.

Chinook salmon is a preferred prey for more southerly distributed killer whale populations (Ford and Ellis 2006, Hanson et al. 2010) and are also thought to be consumed by the more northern Alaska killer whales, such as the SEAR included in our analysis. Chinook salmon overlap in spatial distribution with all populations, because their migration follows a coastal route to and from Alaska waters (Quinn 2005, Weitkamp 2010).

Populations of Chinook salmon are generally correlated with one another coastwide, driven by large-scale environmental drivers, such as the Pacific Decadal Oscillation. Thus, we would expect geographically and reproductively isolated populations of predators, such as SR and SEAR killer whales, to be correlated if Chinook from both regions constituted a significant portion of the diet. If adult Chinook salmon available to fisheries is representative of Chinook available to killer whales, then there is also considerable overlap in the specific salmon populations that dominate coastal waters for SR and SEAR whales. Based on genetic stock identification data collect-

ed by the Alaska Department of Fish and Game 1998–2009, Chinook salmon from Southern United States rivers (in Washington, Oregon, California) represented an average of greater than 60% of Chinook available in Southeast Alaska waters in summer (Crane et al. 2000, Templin et al. 2011, Gilk-Baumer et al. 2013). Including Chinook from southern British Columbia rivers (e.g., Fraser, Thompson) boosts this average to over 80%. Thus, because the majority of adult Chinook available to be captured by fisheries or predators in Southeast Alaska are of southern origin, Chinook-eating predators in Alaska, British Columbia, or Oregon/Washington may be eating the same populations of prey. Further evidence that the SR and SEAR populations may share the same prey stocks are based on contaminant signatures (Ross et al. 2000, Krahn et al. 2009).

The distribution of southern origin Chinook salmon populations in Alaska waters is important for both the management of killer whales and salmon. For the conservation of endangered populations of whales, such as the SR population included in our analysis, predation by more

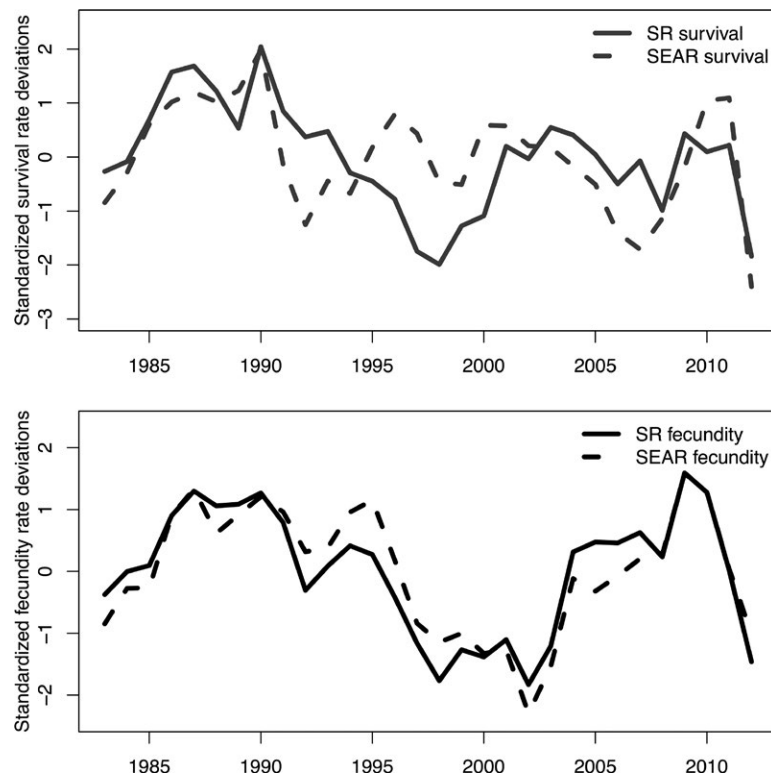


Fig. 4. Standardized trends in survival and fecundity rates for two fish-eating populations of killer whales (Southern Resident = SR, Southeast Alaska Resident = SEAR) over the period 1983–2012. All deviations are shown in logit space.

northern predators may have a negative effect on salmon available to SR killer whales, placing them at a competitive disadvantage. In addition to experiencing a higher encounter rate of Chinook salmon, these more northern populations may also experience a greater size distribution of individual Chinook. For example, after migrating through waters of British Columbia and being intercepted by recreational and commercial fisheries (which target larger fish), the size distribution encountered by SR whales may be smaller than those encountered by SEAR whales.

From a salmon perspective, the availability and ocean distribution of adult Chinook is affected by human harvest, but also by long-term productivity in their natal rivers of origin. Because of habitat loss, the spawning populations of many of these southern Chinook populations have been supplemented by hatchery programs (in the Columbia River and elsewhere). Given increases in these programs in the 20th century,

the majority of Chinook caught in ocean fisheries are of hatchery origin (Barnett-Johnson et al. 2007). As Chinook in Southeast Alaska waters are dominated by fish from southern populations (Fig. S1), an effect of successful hatchery production may be to subsidize some marine mammal predators. Further, the metapopulation variation in these southern Chinook populations (Moore et al. 2010) may buffer top predators from population decline, similar to portfolio effects that have been seen in commercial fisheries (Schindler et al. 2010).

Increases in more northern populations of killer whales (Fig. 6), even during recent downturns of Chinook, may be also indicative of these populations having a broader portfolio of available prey. The western migration of SEAR whales to regions in the central Gulf of Alaska, for example, may enable these whales to consume a more diverse set of prey (other Chinook stocks and other fish species). Compared with SR whales



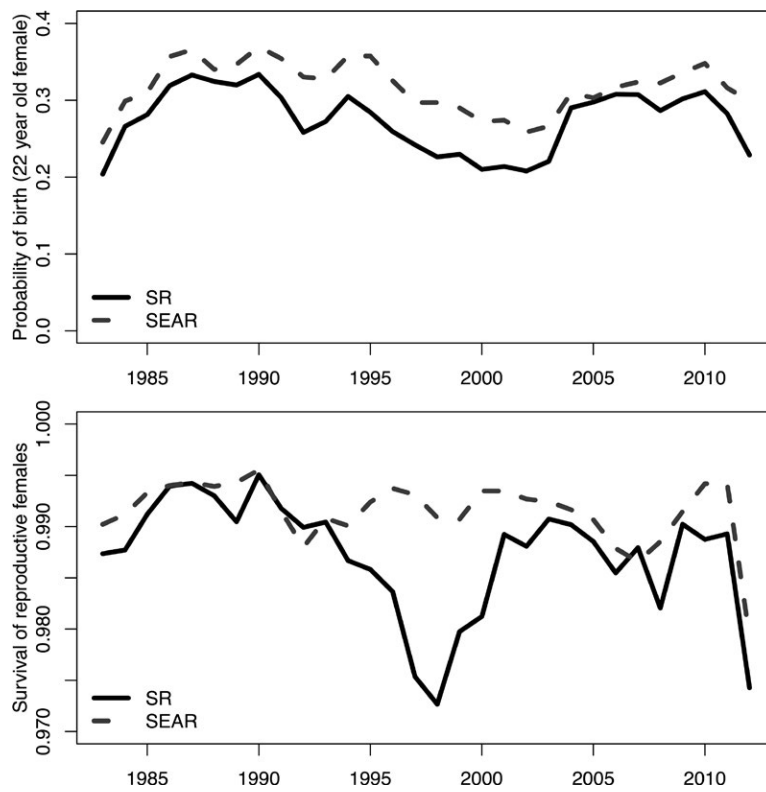


Fig. 5. Trends in fecundity and survival by population. Each line represents the posterior mean, taking into account the age and random year effects. These rates represent the deviations (Fig. 4) in normal space.

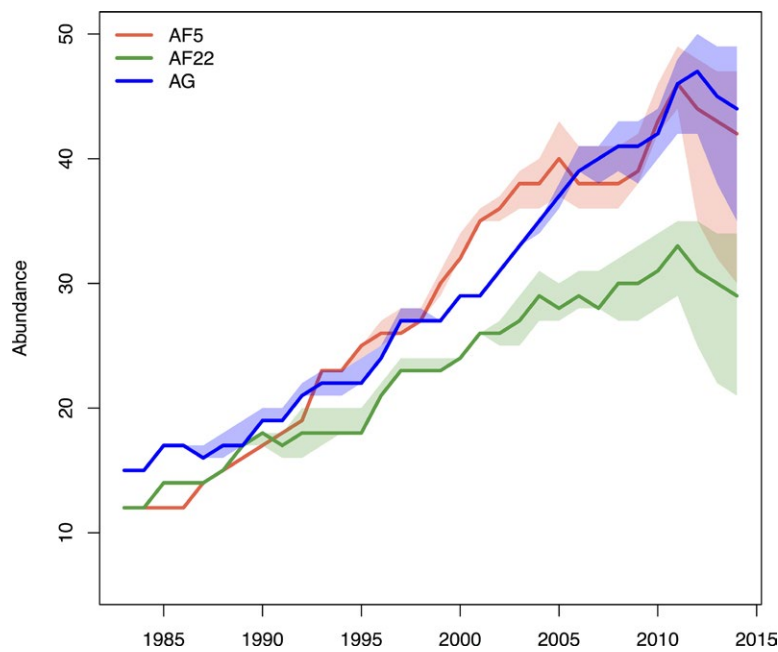


Fig. 6. Trends in abundance for three Southeast Alaska Resident (SEAR) pods included in our analysis. Median estimates for AF5, AF22, and AG pods shown with thick lines, and 95% CIs indicated with shaded regions.

which are thought to eat almost exclusively Chinook salmon in summer (Hanson et al. 2010), the population of SEAR killer whales may have a greater diversity of available prey, including other salmon (e.g., coho) or groundfish (halibut, sablefish). More detailed diet studies of both the SR and SEAR populations are needed to identify seasonal patterns and prey switching in years with low-salmon returns. Recent advances in genetic analyses of fecal samples may represent one approach for tackling this issue (Hanson et al. 2010).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1276/supinfo>